

Increasingly complex bimanual multi-frequency coordination patterns are equally easy to perform with on-line relative velocity feedback

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Abstract An experiment was conducted to determine whether multi-frequency continuous bimanual circling movements of varying difficulty (1:2, 2:3, 3:4, and 4:5) could be effectively performed following relatively little practice when on-line continuous relative velocity feedback is provided. The between-subjects results indicate extremely effective bimanual multi-frequency performance for all coordination patterns with relatively stable and continuous movements of both limbs. The findings suggest that the previous performance effects using Lissajous feedback with reciprocal movement can be extended to circling movements using on-line relative velocity feedback. Contrary to the long-held position that these coordination patterns result in increasing difficulty, we failed to find systematic relative velocity error, variability, or bias differences between the participants performing the various multi-frequency coordination patterns. Indeed, coordination error, variability, and biases were remarkably low for each of the tasks. The results clearly indicate the ease with which participants are able to produce bimanual coordination patterns typically considered difficult if not impossible when salient visual information is provided that allows the participants to detect and correct their coordination errors.

Keywords Bimanual coordination · Perception–action dynamics · Polyrhythm · Relative velocity

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Introduction

A large number of bimanual coordination experiments over the last 40 years “... have revealed quite remarkable temporal constraints between the two hands when they are functioning together” (Kelso and deGuzman 1988) such that only a few bimanual movement patterns other than in-phase ($\phi = 0^\circ$) and anti-phase ($\phi = 180^\circ$) can be effectively performed without extensive practice. Thus, many 1:1 rhythmic movements of the limbs (e.g., fingers, arms) with relative phase patterns other than in-phase and anti-phase are not inherently stable (Tuller and Kelso 1989; Yamani-shi et al. 1980), and the motor system shows a bias toward what has been labeled the intrinsic dynamics of in-phase and anti-phase coordination (Schöner and Kelso 1988). This tendency toward preferred coordination patterns has also been observed in bimanual multi-frequency rhythmic tasks. For example, 2:1 and 3:1 tapping ratios have been produced effectively by novice participants after 1 or 2 sessions of practice, and with little or no additional practice by trained musicians (e.g., Deutsch 1983; Peper et al. 1995a, b; Summers et al. 1993). However, continuous bimanual (reciprocal or circling) limb motion of other multi-frequency ratios appears to pose quite difficult challenges for the nervous system (e.g., Byblow and Goodman 1994; Sternad et al. 1999a; Treffner and Turvey 1993; Swinnen et al. 1997a), 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 et al. 2002, p. 702).

More than 60 years ago, Fraise (1946) described limitations in participants’ ability to produce simple and complex

ratios (e.g., 1:1, 1:2, 2:3) with difficulty functionally increasing as one moves down the branches of the Farey tree (see Fig. 1a). This difficulty was thought to arise, at least theoretically, from decreasing widths of the resonance regions or 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 and Turvey 1993 for discussions). This coupled with the fact that some coordination patterns required for the ratios lower in the Farey tree are increasingly closer to a 1:1 in-phase coordination pattern as is the case for 4/5 polyrhythm, for example, or results in an increasing number of times that the patterns move through 1:1 in-phase coordination pattern as is the case for the 1/5 simple rhythm, both of which theoretically should exert strong phase attraction. 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 polyrhythms (e.g., 2:3, 4:3, and 5:3) were not only thought to be difficult, but were also thought to be virtually impossible to perform effectively in continuous movement tasks. Although difficult to perform, higher-order frequency ratios have been investigated in continuous motion tasks using hand-held pendulums in one or both hands (e.g., Treffner and Turvey 1993) and with augmented feedback (e.g., Kovacs et al. 2010a, b; Mechsner et al. 2001).

The reason for the difficulty in producing simple and complex ratios is thought to arise from a coalition of constraints (see Swinnen and Wenderoth 2004) including strong phase attraction toward 1:1 coordination, specifically in-phase and anti-phase that are intrinsic in the human and animal nervous system. However, perceptual/cognitive explanations have also been explored. Mechsner et al. (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. 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 et al. 1992; Riek and 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.” Mechsner et al. also demonstrated that a complex 4:3 polyrhythm could be performed relatively well when perceptual symmetry was established. To do this, 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

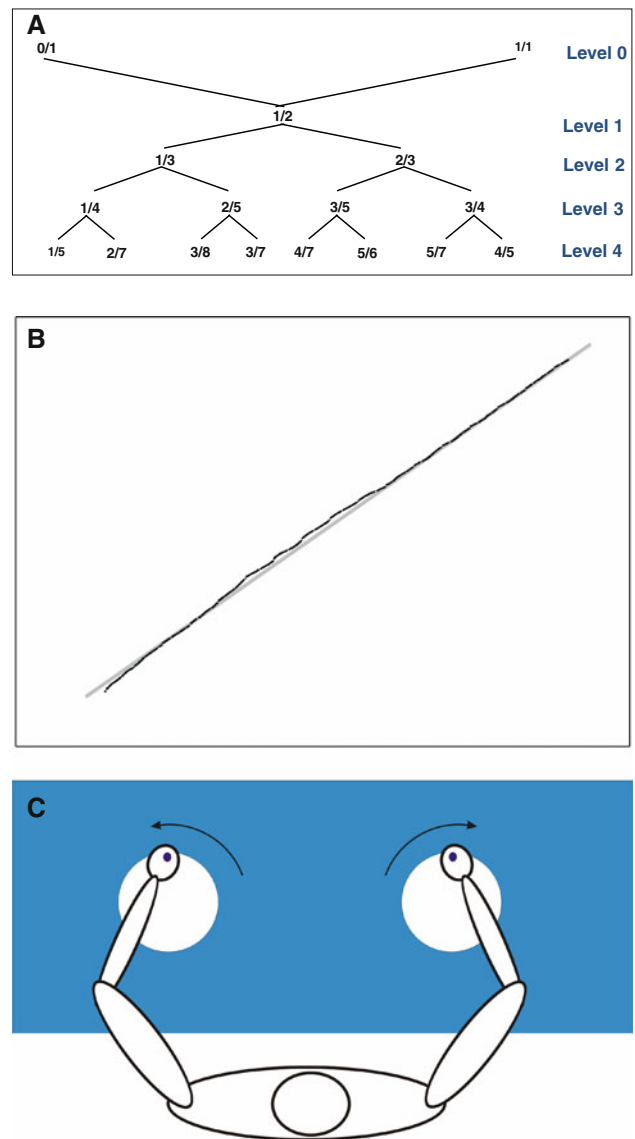


Fig. 1 Farey tree illustrating a sequence of rational numbers forming successive levels of difficulty when applied to bimanual multi-frequency coordination (a). An illustration of the feedback display for a goal ratio of 1:2 and participant performing circle movements are also provided (b, c). In the feedback display, the lighter line represents the goal movement and the darker trace illustrates the participant's performance

for the other flag were set at 4:3 requiring a $\frac{3}{4}$ 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 min 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. 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 and Lee 2006; Lee et al. 1995; Swinnen et al. 1995, 1997b, 1998) and to perform 2:1 coordination patterns (e.g., Summers et al. 2002; Swinnen et al. 1997a). These experiments demonstrated the utility of Lissajous feedback, but substantial practice was still required to achieve moderate levels of performance. However, recent experiments by Kovacs et al. (2010a, b) have demonstrated that when Lissajous feedback and a goal template were used and attentional distractions were reduced that participants could produce a variety of multi-frequency coordination patterns (e.g., 2:1, 3:2, 4:3) with remarkably low relative phase errors and variability ($\approx 10^\circ$) after only a few minutes of practice. Attentional distractions were reduced by eliminating vision of the moving limb and eliminating the use of visual or auditory metronomes to pace the movements. 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. It should be noted that a Lissajous plot as a source of perceptual information may also 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 toward 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. It is also important to note that participants using this and other forms of salient feedback to tune-in various bimanual coordination patterns are utilizing different neural pathways and control processes than when the feedback is not provided. Debaere and colleagues (Debaere et al. 2001, 2003, 2004) have provided fMRI evidence that suggested the cortico-cortical and subcortico-cortical neural pathways used during bimanual coordination with augmented feedback are distinct from that observed when the feedback was not available.

While Lissajous plots and template have been used with great success in experiments using reciprocal movements of the limbs, this type of feedback may not provide the most salient information when circling movements are used. When Lissajous plots are used with circling movements only one dimension of the circle movement can be plotted for each limb. For example, the y -axis movement of the left limb and x -axis movement of the right limb could be plotted in the Lissajous plot—movements in the x -axis for the left limb and y -axis for the right limb are disregarded. This appears to pose problems for the performer

because the way in which they attempt to correct an error would be different depending on where they are in the cycle (see Shea and Boyle 2011). The solution to this problem is relatively simple when the radius of movement is fixed. That is, in circle movements with a fixed radius, it is relatively easy to determine relative angle and/or relative velocity on-line and use this information as direct feedback to the participant in much the same way as Lissajous feedback has been used. On-line relative phase or relative phase velocity would be difficult to determine on-line in reciprocal (flexion/extension) tasks because the movement reversal has to be determined before phase values can be determined (See Wilson et al. 2010 for a discussion of feedback issues).

A bimanual multi-frequency coordination experiment using circle movements was conducted in an attempt to demonstrate that multi-frequency coordination between the limbs is more stable than typically demonstrated when participants are provided on-line relative velocity information and a relative velocity goal. In the experiment, participants were assigned to one of four goal multi-frequency ratios (1:2, 2:3, 3:4, 4:5, and 5:6), which differed in terms of the level in the Farey tree and difficulty. A between-subject design was used to reduce any carry-over effects that may be present and to demonstrate that very little practice is required to produce the various coordination patterns when on-line relative velocity information is provided. Participants were asked to produce the required multi-frequency ratio by continuously turning one manipulandum (counterclockwise circular motion) with their left limb and the other (clockwise circular motion) with their right limb. The only difference between the ratio conditions was the goal relative velocity provided in the visual display. The goal was depicted as a straight line with a slope representing the specific relative velocity ratio to which the participant was assigned with difference in the left-hand velocity (slower moving) and right-hand velocity (faster moving) determining the slope. Based on our recent work (Shea and Boyle 2011) investigating the relative utility of various forms of on-line feedback in circle movements, we hypothesize that participants provided this form of feedback would be able to effectively produce the various multi-frequency coordination patterns with little practice. The movements were not paced by a metronome(s) as is typical in many of these types of experiments, but participants were encouraged 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 previous research indicated that the use of metronomes introduced attentional demands and control strategies that can negatively influence bimanual coordination (e.g., Kovacs et al. 2009a). Only 4 min of practice was provided because we propose that given the appropriate perceptual information

that participants can quickly and effectively tune-in the required motor responses to achieve the goal coordination pattern.

Method

Participants

Right-handed undergraduate students ($N = 24$, 6 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 (10 cm radius) that could be moved in a circular motion 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 360° in the horizontal plane over the table surface. Near the distal end of each lever, a vertical handle was attached (Fig. 1c). The circular movement of the levers was monitored (200 Hz) by potentiometers that were attached to the lower ends of the axles. The on-line data were used to present a cursor (as a small circle) on a screen directly to the front of the participant. The motion (counter clock-wise) of the left lever resulted in moving the cursor from the starting position to the right and the motion (clock-wise) of the right lever moved the cursor upward from the starting position. Projected onto the screen was a line that represented the goal movement ratio (1:1, 1:2, 2:3, 3:4, and 4:5). For participants in the 1:2 goal ratio condition, for example, the reference line represented a 1:2 movement ratio (Fig. 1b). The cursor and reference lines were generated with customized software and displayed on the wall in front of the participant with the projector mounted above and behind the participant. The movement of the cursor occurred in real time. The delay was only limited by the screen refresh rate (60 Hz).

Procedure

Upon entering the laboratory, the participants were randomly assigned to one of the four (1:2, 2:3, 3:4, or 4:5) bimanual coordination ratios. Participants sat on a height adjustable chair at a table with their fingers holding the handle attached to the distal end of the levers. All participants

were initially provided the instruction (Trials 1 and 2) to make continuous circular movements of the left (counter clock-wise) and right (clock-wise) limbs such that the right and left limbs completed each cycle at the same time (goal ratio 1:1). Participants were told that if the limbs moved together, as instructed, then the cursor would follow a horizontal blue line displayed in front of them. Performance on Trial 2 was used as a baseline from which to evaluate performance on the more complex ratios. On Trials 3–14, the participant was told to attempt to move the right limb at a faster rate than the left limb. Participants were told that if the limbs moved at the correct velocity then the cursor would follow the red line displayed in front of them (goal ratio 1:2, 2:3, 3:4, or 4:5). The red line represented the relative velocities of the limb required to produce the ratio assigned to their group. Following each trial, participants were reminded that they should attempt to move both limbs in a continuous/smooth manner and that increasing the rate of the right limb relative to the left limb would cause the cursor to climb faster.

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 a total of 14 trials (20 s each). They were informed that Trials 1–2 were reference trials and that they should be able to perform this task relatively easily. Further, participants were told that the task on trials 3–14 would be quite difficult with Trials 3–12 used as practice and Trials 13–14 used as test trials. After completing Trial 12, participants were provided a short break followed by the test trials (Trials 13–14). The test trials were conducted under the same conditions as experienced during Practice trials 3–12.

Measures and data reduction

The acquisition program provided the left and right limb movements as wrapped angle values such that 360° was added for each complete cycle of the lever. The phase values representing the limbs' displacements were low-pass filtered with a second-order dual pass Butterworth with a cutoff frequency of 10 Hz. Velocity signals were computed with each signal filtered (Butterworth, 10 Hz) before performing the next differentiation. The analyses will focus on both bimanual coordination performance of the required frequency ratio and unimanual cycle durations and variability of the right and left limbs.

Unimanual measures

Cycle durations and cycle duration variability were computed on a cycle basis. Cycle duration variability was defined as the standard deviation of the cycle-to-cycle durations.

Bimanual measures

Three ratio measures of multi-frequency limb performance were determined. The individual limb mean cycle frequencies were used to compute a cycle duration 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 and was determined from the cycle duration values. To examine the spatial–temporal coordination of the limbs' motion, a ratio of continuous angle velocity for the two limbs was computed by dividing the instantaneous angle velocity of the right limb (faster moving) by the instantaneous angle velocity of the left limb (slower moving). Lastly, a regression analysis was used to determine the fit and slope of the regression line for instantaneous relative angle values of the left and right limb. It should be noted that the goal ratio values (right faster moving limb/left slower moving limb) for the 1:2, 2:3, 3:4, and 4:5 ratios are 2, 1.5, 1.33, and 1.25, respectively.

Next, the individual relative velocity values were subtracted from the goal relative velocity ratio. The absolute values of the relative velocity errors were used to determine absolute error (AE). The signed values of relative velocity errors were used to determine constant (CE) and variable (VE) errors.

Results

Examples of relative velocity relationship for one participant in each of the goal ratio conditions are provided in Fig. 2a. Continuous relative angle velocity errors for the same participants are provided in Fig. 2b–e. Figure 3 illustrates the mean relative velocity ratio (A), relative cycle duration ratio (B), and slope of the regression analysis of relative angle (right–left limbs) (C), as well as VE (D) CE (E) and AE (F) relative velocity errors. These measures were analyzed in 4 goal ratio (1:2, 2:3, 3:4, and 4:5) ANOVAs, and the results are presented in the bimanual performance section. It should be noted that performance on the 1:1 baseline task is provided for reference in Fig. 3a–f. Mean cycle duration (G) and standard deviation of cycle duration (H) data are also presented in Fig. 3 by goal ratio and limb. These measures were analyzed in 4 goal ratio \times 2 limb (left, right) ANOVAs with repeated measures on limb and 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 velocity ratio (Fig. 3a) indicated a main effect goal ratio, $F(3,20) = 637.00$, $P < .01$, $\eta_p^2 = 0.99$.

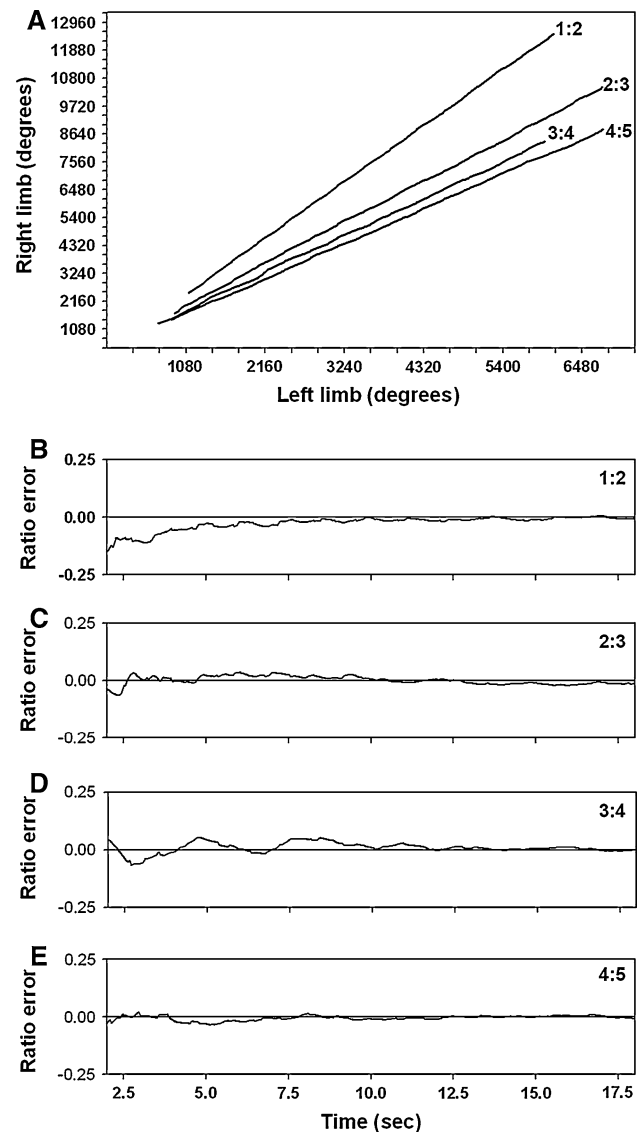
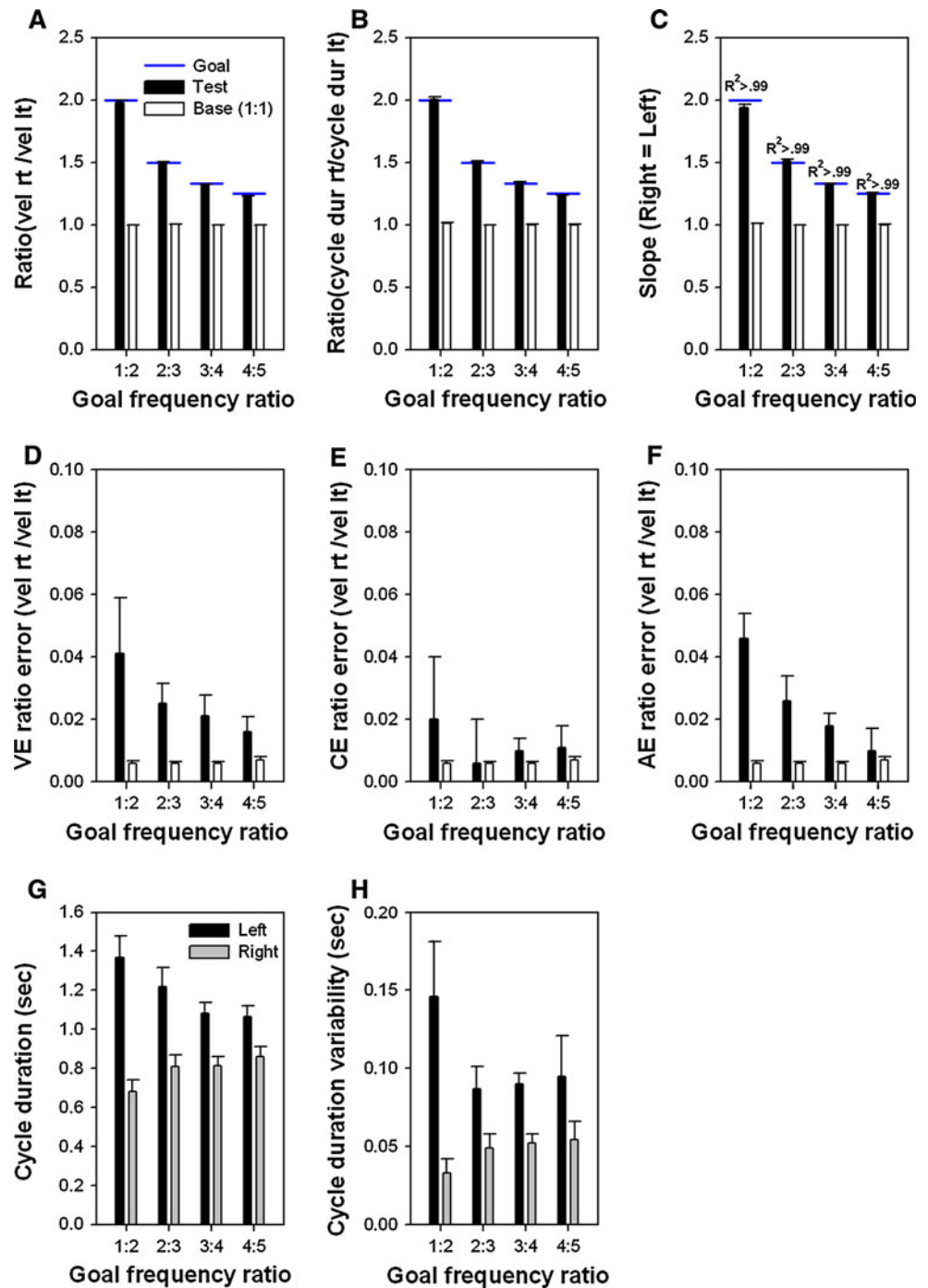


Fig. 2 Examples of the time series for one participant in each of the multi-frequency conditions (a). Lower panels (c–f) illustrate examples of the coordination error time series for the respective conditions

Duncan's new multiple range tests indicated that the velocity ratio significantly decreased with each decrease in the goal ratio. The analysis of VE, CE, and AE of velocity ratio error (Fig. 3d–f) indicated main effects of goal ratio, $F(3,20) = 3.72$, $P < .05$, $\eta_p^2 = 0.35$ and $F(3,20) = 4.13$, $P < .05$, $\eta_p^2 = 0.38$ for VE and AE, respectively. Duncan's new multiple range tests detected higher AE and VE values for participants that performed the 1:2 ratio than those that performed the other ratios. No differences in AE and VE were detected between the 2:3, 3:4, and 4:5 goal ratio conditions. The analysis of CE failed to detect any main effects or interaction.

The analysis of the cycle duration ratio (Fig. 3b) revealed a main effect of goal ratio, $F(3,20) = 745.60$,

Fig. 3 Mean ratios based on relative velocity (a) relative cycle durations (b), slope of the regression line (c). In addition, AE, CE, and VE of relative velocity error (d–f, respectively) and cycle duration (g) and variability of cycle duration (h) of the limbs are provided. Note that performance on the 1:1 baseline task is provided for reference in Fig. 2a–f. Error bars represent standard errors



$P < .01$, $\eta_p^2 = 0.99$. The Duncan's new multiple range tests indicated that cycle duration ratio significantly decreased for each decrease in the goal cycle duration ratio. The analysis of relative phase slope (Fig. 3c) taken from the regression analysis for individual participants also indicated a main effect of goal ratio, $F(3,20) = 383.88$, $P < .01$, $\eta_p^2 = 0.98$. Duncan's new multiple range tests indicated relative phase slope significantly decreased as the goal relative phase ratio moved down the Farey tree.

Unimanual performance

As expected, the analysis of the mean cycle duration (Fig. 3e) indicated a main effect of limb, $F(1,21) = 531.90$, $P < .01$, $\eta_p^2 = 0.96$, with the right limb having shorter cycle durations than the left limb in all goal ratio conditions. The main effect of goal ratio, $F(3,21) < 1$, $P > .05$, was not significant. However, the Goal ratio \times Limb interaction, $F(3,21) = 39.67$, $P < .01$, $\eta_p^2 = 0.85$, was significant. Sim-

ple main effects analysis of the Goal ratio \times Limb interaction indicated lower cycle duration for the right limb than the left limb for each goal ration condition. However, the differences decreased as the goal ration changed from 1:2 to 2:3 to 3:4 to 4:5. In terms of the standard deviation of cycle duration (Fig. 3f), the main effect of limb, $F(1,21) = 34.38$, $P < .01$, $\eta_p^2 = 0.62$, was significant with the left limb durations more variable than the right limb cycle durations.¹ The main effect of goal ratio, $F(3,21) < 1$, $P < .01$, and the Goal ratio \times Limb interaction, $F(3,21) = 3.07$, $P < .05$, were not significant.

Discussion

The purpose of the experiment was to determine extent to which participants provided on-line relative velocity information, and goal template can effectively perform multi-frequency bimanual coordination patterns of various difficulties with relatively little practice. Theoretically, the coordination patterns become increasingly more difficult if not impossible as the ratio moves down the Farey tree. However, Kovacs and colleagues (e.g., Kovacs et al. 2009a, b, 2010a, b, Kovacs and Shea 2010) using flexion/extension movements of the arm at the elbow have demonstrated that participants provided Lissajous plots and templates can very effectively produce a wide variety of phase-shifted bimanual coordination patterns and select multi-frequency bimanual coordination patterns with only a few minutes of practice. However, circling movements, which are thought to be more difficult because of the increased degrees of freedom and the more complex interaction of various muscle groups used to transition through the circular pattern, have not been systematically studied using salient feedback. In the case of circular movements, Lissajous feedback has been shown to be only moderately effective because only one dimension (x or y) of each limb can be utilized in the Lissajous plot (see Shea and Boyle 2011). The Lissajous information in circling tasks does provide relatively good error information but this information is difficult for the participant to use in generating corrective movements. However, in circling tasks where the movement radius is fixed, relative angle and/or relative velocity can be easily determined and provided as on-line feedback. Indeed, Shea and Boyle have determined the effectiveness of this form of feedback in allowing participant to produce

1:1 bimanual circle movements with 90° phase shift. Interestingly, we are not aware of any experiments systematically comparing performances on a range of increasingly difficult multi-frequency ratios using reciprocal or circle movements. Presumably, the lack of experiments on this topic is related to the difficulty in producing these coordination patterns with either reciprocal or circle movements. Contrary to current theory, we predict that participants will be able to effectively produce each of the ratios when provided on-line relative velocity feedback and template because this form of feedback provides the basis from which participants can easily determine and correct coordination errors.

The analysis of the bimanual measures confirmed our preliminary predictions. Participants, following less than 4 min of practice, very effectively performed each of the multi-frequency ratios with all three measures of overall performance (relative velocity, relative cycle frequency, and slope of the right–left limb relative angle relationship), indicating very effective performance. The analysis of relative velocity error (AE) and variability (VE) indicated that the performance of the 1:2 ratio did result in significantly higher relative velocity error and variability than the other ratios, although errors and variability were remarkably low for all of the multi-frequency ratios. No differences in relative velocity error or variability were detected between ratios at Level 2–4 in the Farey tree (2:3, 3:4, and 4:5). The finding of slightly poorer performance on the 1:2 ratio relative to performance on the 2:3, 3:4, and 4:5 ratios is particularly interesting because the ratios (2:3, 3:4, and 4:5) which were performed with smaller error and variability have been considered to be more complex and presumably more difficult ratios to perform. In terms of unimanual measures, the results indicated that cycle durations for the right (faster moving) limb were shorter than for the left (slower moving) limb across all multi-frequency coordination tasks with the difference in cycle durations between the limbs decreasing as the goal ratio moved down the Farey tree. In all cases, the cycle duration of the faster moving limb was maintained at or below the 1 Hz target frequency. Recall that a metronome was not used but rather participants were simply encouraged to increase their movement frequency if cycle frequency fell below 1 Hz.

Recall also that continuous multi-frequency bimanual coordination patterns have been deemed almost impossible to produce effectively by Summers et al. (2002). However, given recent research on reciprocal movements of the limbs using Lissajous plots (e.g., Kovacs et al. 2009a, b, 2010a; Kovacs and Shea 2010) and the present research on circle movements using on-line relative velocity information, participants have been able to very effectively perform a wide range of bimanual coordination patterns following remarkably little practice. These findings bring into question the

¹ Comparisons across limbs of the variability of the cycle duration means should be viewed with caution because in all subjects and all conditions the left limb 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.

interpretation of earlier research on bimanual coordination, which focused on the coalition of constraints imposed on these tasks. 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., deGuzman and Kelso 1991; Haken et al. 1996; Kelso and deGuzman 1988; Peper et al. 1995a, c; Treffner and Turvey 1993). It should be noted also that as the ratios selected for study move down the Farey tree, the movement pattern required moves closer and closer to the in-phase coordination pattern, which should at least theoretically increase the opportunity for phase attraction. However, the literature has demonstrated that through extensive practice, the coupling strength for a given pattern increases and attractor landscapes are altered, resulting in increasingly stable performance for initially unstable relative phase relationships (Zanone and Kelso 1992) or higher-order frequency ratios. Swinnen et al. (1997a), 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°). Presumably in the present experiment, the visual information from the relative velocity display very quickly alters the coupling strength and attractor landscape affording stable performance for the specified goal ratio.

In the present experiment, participants' performance of the 1:2, 2:3, 3:4, and 4:5 ratio patterns of bimanual coordination were remarkably stable after less than 4 min of practice. We argue that this was possible because perceptual/informational changes in the performance environment—namely the presentation of visual information provided in the form of the cursor representing the current velocity ratio and a goal template (line). This visual display together with the reduced attentional demands (e.g., elimination of metronomes and covered limbs) 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 and 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 profoundly changed. Indeed,

it is plausible to argue that changes in the resonance regions occurred at a perceptual level.

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 increase coupling strength between limbs and/or reduced phase attraction linked to the system's intrinsic dynamics. In the present experiments, the information provided through the relative velocity display permitted participants to quickly and effectively (low relative velocity error and variability) tune-in the required frequency ratios. We feel this was accomplished, in part, because the relative velocity template and cursor allowed participants to easily determine when they deviated from the desired coordination pattern and provided information that could be used to accurately re-tune their actions. This finding is important because it clearly demonstrates that the perceptual-motor system is fully capable of producing an amazing range of bimanual coordination patterns when provided salient visual information that are difficult if not impossible to effectively produce with this augmented information. When provided information necessary to detect and correct errors, our movement repertoire is greatly enhanced.

Role of perception in perception–action dynamics

Abstract models based on non-linear coupled oscillators perturbed by stochastic forces have been at the forefront of the coordination dynamics approach to identifying the laws that govern the production of stable coordination patterns between limbs and joints (Haken et al. 1985, 1996; Kelso 1995; Schönner et al. 1986). These modeling approaches have described the coupling among the component oscillators in abstract mathematical terms with the functional aspects of the coupling not linked to any specific perceptual and/or motor process. However, the notion of neural cross-talk has been proposed to play a role in determining stability differences, phase transitions, and difficulty in producing simple and complex ratio bimanual patterns based on interactions in forward command streams (for review, see Swinnen 2002). Emphasis has also been 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 cortico-motoroneuronal projections, segmental networks) that can occur across the many levels through which these command signals travel (for review, see Carson and Kelso 2004). This contribution to the coupling and stability characteristics of bimanual coordination clearly resides in forward motor commands and the interactions that arise from the shared neural pathways (Ridderikhoff et al. 2005). However, the patterns of activation changes when augmented visual feedback provide the

information necessary for error detection and correction relative to more automatic performance based on forward control (e.g., Debaere et al. 2003, 2004).

So what role does augmented visual information play in the production and stabilization of bimanual coordination patterns? Bingham and colleagues (e.g., Bingham et al. 1999; Bingham 2004a, b; Wilson et al. 2005a, b) have argued that bimanual coordination can be limited by the performer's ability to visually detect a given relative phase pattern. They proposed 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. This proposal is based on the basic assumption that the reason for poor performance in some bimanual tasks is that participants are unable to detect their errors and therefore are not able to initiate effective corrections. The tacit assumption of this argument is that when augmented visual information is provided that allows effective error detection, participants will be able to initiate effective corrections allowing stable performance to be effectively tuned-in. Mechsner et al. (2001) demonstrated that a highly complex 4:3 polyrhythm could be performed relatively well with little practice when available visual information simplified error detection and correction. The task required participants to turned cranks with each arm so that two flags driven by the cranks moved either in an in-phase or anti-phase relationship. It should be noted that the cranks were geared differently so that in order to produce the in-phase coordination pattern with the flags they would actually produce a 4:3 coordination pattern. What the Mechsner et al. finding suggest was that because participants could, within some tolerance, determine whether the flags were moving in the assigned pattern (in-phase and anti-phase), they could detect and correct errors in order to tune-in the difficult 4:3 coordination pattern without extensive training.

In recent experiments using reciprocal movements of the left and right limbs, augmented visual information provided in Lissajous plots (cursor and goal template) facilitated the participant's ability to detect coordination errors and essentially provided a prescription for correction. This combination allowed for a very rapid tuning in of difficult multi-frequency bimanual coordination patterns (Kovacs et al. 2010a, b). When vision of the limbs was provided, performance deteriorated suggesting that attention was directed away from the extrinsic information contained within the Lissajous plot 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 augmented visual information that facilitates error detection and correction, when atten-

tion splitting features of a task are removed, can free the perceptual-motor system from constraints that typically limit it to 1:1 in-phase and anti-phase coordination patterns without extensive practice. The ease and rapidity with which the perceptually defined patterns were mapped onto the system indicates that the motor system's capabilities are truly extensive when integrated visual information is provided that allows effective error detection and correction. Future research needs to identify how these integrated visual displays afford the perceptual-motor system an opportunity to override intrinsic constraints that tend to pull the system toward in-phase and anti-phase coordination. In other words, the visual display does not eliminate neural crosstalk or proprioception nor does the visual display eliminate perceptual attraction to in-phase or anti-phase coordination, but the displays clearly decreased the influence of these factors and probably others (e.g., asymmetric coupling, phase attraction). In short, the integrated visual display appears to allow the perceptual-motor system to initiate effective forward-based motor commands that are minimally constrained by motoric, and/or proprioceptive factors. The Kovacs et al. findings suggest that a key component in revealing the cooperative process that couple motor output with augmented visual information is removal of attentional demands on the moving limbs. These results emphasize that a true understanding of the "design of the brain" will only be forthcoming when the roles of both the motor side (e.g., Kelso and deGuzman 1988) and the perceptual side (e.g., Mechsner et al. 2001) are integrated in a true perception–action dynamics perspective (see Atchy-Dalama et al. 2005; Bingham 2004a; Bingham et al. 1999; Carson and Kelso 2004; Swinnen and Wenderoth 2004; Zaal et al. 2000).

Emerging picture

The present findings using relative velocity feedback in circling movements add to the growing number of recent bimanual coordination (Kovacs et al. 2009a, b, 2010a, b; Kovacs and Shea 2010; Mechsner et al. 2001; Tomatsu and Ohtsuki 2005), visuo-motor tracking (Wilson et al. 2005a, b; Ryu and Buchanan 2009), and rapid aiming (Kovacs et al. 2008; Boyle and Shea 2011; Fernandez and Bootsma 2008) experiments which report that salient perceptual information can override some aspects of the system's intrinsic dynamics, which have typically linked to motor output control. The strong tendencies toward phase attraction found in numerous previous bimanual coordination studies as well as the difficulties in producing simple and complex ratios in reciprocal and circling movements may actually represent detrimental effects attributable to the perceptual information available in the environment. Given integrated visual information and a clear goal participants

can with little practice essentially tune-in complex multi-frequency bimanual coordination patterns. 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 higher ratio coordination patterns are substantially more difficult to produce in continuous tasks (e.g., Summers et al. 2002). The bottom line is that we should expect poor and variable performance when participants are directed to use attention splitting information (e.g., visual or auditory metronomes) because participants do not seem able to extract from this feedback or other intrinsic sources information quickly or effectively enough to be used to detect and ultimately correct coordination errors. Thus, participants are ineffective in taking corrective action (Bingham 2004a, b; Wilson et al. 2005a, b, 2010). The feedback and learning literature in the motor domain are replete with demonstrations of the simple principal that learning requires a clear goal and access to clear information that can be used to assess performance relative to that goal. Bimanual coordination does not appear to result in an exception to this principle.

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