

Visual–spatial and anatomical constraints interact in a bimanual coordination task with transformed visual feedback

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Abstract There is a debate in the literature about the influence of spatial and anatomical constraints on bimanual coordination dynamics. In the present experiment, participants swung hand-held pendulums about the wrist while attending to visual feedback about relative phase (superimposed phase plots of each pendulum) that was displayed on a screen. Participants were instructed to maintain in-phase or anti-phase coordination in the visual display. Visual–spatial and anatomical constraints were dissociated by introducing a phase shift in the visual display so that visual feedback differed from the movements being performed by the participants in 15° increments from –180° to +180°. Analysis of mean relative phase and its variability suggested that visual–spatial and anatomical constraints interact in bimanual coordination dynamics.

Keywords Coordination dynamics · Relative phase · Spatial constraints · Anatomical constraints

Introduction

The intrinsic coordination dynamics of bimanual movements are such that we easily perform two bimanual phase relations, in-phase [relative phase (ϕ) = 0°] and anti-phase (ϕ = 180°), with ϕ = 0° being consistently more stable than ϕ = 180° (Kelso 1984, 1995; Kelso et al. 1986, 1987). There is a debate, however, about whether ϕ is best defined spatially or anatomically. The present study examined the influence of visual–spatial and anatomical constraints by

having participants coordinate the movements of hand-held pendulums while presenting them with transformed visual feedback so that they would perform ϕ from –180° to +180° in order to maintain visual in-phase or visual anti-phase (ϕ_{vis} = 0° or 180°). The impact of visual–spatial and anatomical constraints was evaluated by comparing the effects of visual relative phase and performed relative phase.

Bimanual coordination dynamics

Using bimanual coordinated finger oscillations, Kelso (1984) demonstrated that ϕ = 0° and 180° are the two intrinsically stable modes of coordination, with both the variability of ϕ and phase transitions indicating that ϕ = 0° is more stable than ϕ = 180° (see also, Kelso 1995). The intrinsic dynamics have been formalized in the following dynamical model (Haken et al. 1985; Kelso et al. 1990; Schöner et al. 1986):

$$\dot{\phi} = \Delta\omega - a \sin \phi - 2b \sin 2\phi + \sqrt{Q}\zeta_t \quad (1)$$

According to the deterministic portion of Eq. 1, the rate of change of relative phase, $\dot{\phi}$, is a function of the difference between the uncoupled frequencies of two limbs, $\Delta\omega = \omega_{\text{left}} - \omega_{\text{right}}$; and the coupling coefficients a and b . In addition to the deterministic terms, $\dot{\phi}$ is also influenced by the stochastic noise term $\sqrt{Q}\zeta_t$. The locations of the attractors of ϕ for the given values of $\Delta\omega$, a , and b are found by locating the negative zero-crossings in the deterministic portion of Eq. 1; the locations of the repellers are found by locating the positive zero-crossings of this same equation. For $\Delta\omega = 0$, this approach yields one attractor at $\phi = 0^\circ$ and a weaker attractor at $\phi = \pm 180^\circ$ along with repellers at $\phi = \pm 90^\circ$. The strength of each attractor and repeller is determined by the slope of the function through zero,

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referred to as the Lyapunov, λ ; a steeper slope indicates a greater attraction towards, or repulsion from, the value of ϕ at the zero-crossing. The observed variability of relative phase, $SD\phi$, around a given attractor is determined by the values of both λ at that attractor and $\sqrt{Q}\zeta_t$ (Gilmore 1981; Schöner et al. 1986):

$$SD\phi = \sqrt{\frac{Q}{2|\lambda|}}. \quad (2)$$

Although $\phi = 0^\circ$ and 180° are the two intrinsically stable modes of coordination, participants can perform a range of relative phases with instruction. Yamanishi et al. (1980) had participants tap two fingers together at a constant frequency, but at different relative phases from memory. Participants were most stable when performing $\phi = 0^\circ$ and $\phi = 180^\circ$. Furthermore, values of ϕ near 0° shifted towards 0° , while those near 180° shifted towards 180° . This attraction towards $\phi = 0^\circ$ and $\phi = 180^\circ$ has also been shown for normal, skilled (musicians), and split-brain participants when visual metronome pacing—specifying an alternate intermediate relative phase—was provided throughout the trials (Tuller and Kelso 1989).

Tuller and Kelso (1989) analyzed the mean phase shift [$\phi_{\text{dev}} = \text{mean relative phase } (\phi_{\text{ave}}) - \text{intended relative phase } (\phi_{\text{int}})$]. At $\phi_{\text{int}} = 0^\circ$ and 180° , $\phi_{\text{dev}} = 0$, indicating that participants correctly performed those instructed patterns. The fact that the slopes of $\phi_{\text{dev}} = f(\phi_{\text{int}})$ through $\phi_{\text{int}} = 0^\circ$ and 180° (zero-crossings) were negative identified the fact that $\phi = 0^\circ$ and $\phi = 180^\circ$ attracted neighboring relative phases by causing the phases below to advance and the phases above to retreat. $\phi_{\text{dev}} = 0$ was also observed around $\phi = 90^\circ$ and $\phi = -90^\circ$, but the slopes around these points were positive, indicating that they repelled neighboring phases. The standard deviations of relative phase across a trial ($SD\phi$) also identified the preference for performing in-phase and anti-phase over the intermediate relative phases (Tuller and Kelso 1989). Standard deviations were minimized at $\phi_{\text{int}} = 0^\circ$ and 180° with inverted U-shaped curves from 0° to $\pm 180^\circ$. The results of Yamanishi et al. (1980) and Tuller and Kelso (1989) have been accommodated by extending the model in Eq. 1 with an additional 2π periodic term (Schöner and Kelso 1988a, b).

Spatial and anatomical constraints

There is currently some debate over whether the phase relations described above should be defined spatially or anatomically. Defined spatially, in-phase (anti-phase) movements are those in which the movements are in the same direction at the same time (opposite directions at the same time). Defined anatomically, in-phase (anti-phase)

movements are those in which there is a synchronized (asynchronous) co-activation of homologous muscles. In many cases, such as the tapping and pendulum tasks described above, spatial and anatomical definitions of relative phase are identical.

Despite the fact that spatial and anatomical definitions of ϕ are often identical, it is easy to create situations where they differ (Baldissera et al. 1982, 1991; Carson et al. 1995, 2000; Jeka and Kelso 1995; Kelso et al. 1991; Kelso and Jeka 1992; Li et al. 2004; Mechsner et al. 2001; Mitra et al. 1997; Park et al. 2001; Riek et al. 1992; Swinnen et al. 1996, 1997, 1998). For example, when the palm of the right hand is facing down and the palm of the left hand is facing up, the co-activation of homologous muscles for index finger oscillations produces spatial anti-phase movements. The question raised by these studies is whether the most stable phase relation is spatial or anatomical in-phase. Further, these studies ask whether movements are controlled on the basis of spatial constraints, anatomical constraints, or some combination of the two.

Using bimanual finger oscillation and bimanual four-finger tapping, Mechsner et al. (2001) showed that the most stable modes of coordination were those in which the fingers were moving in the same direction at the same time, irrespective of the activation pattern of homologous muscles. Participants tended to remain in, or transition to, spatial in-phase, particularly at higher frequencies. On the basis of those results, the authors concluded that there was no tendency towards the co-activation of homologous muscles and that motor control was driven by spatial constraints. Other studies have found similar results (Baldissera et al. 1982, 1991; Carson et al. 1995; Jeka and Kelso 1995; Kelso et al. 1991; Kelso and Jeka 1992; Swinnen et al. 1998).

There are, however, other studies—using the same basic methodology as Mechsner et al. (2001)—that suggest a role for anatomical constraints in bimanual coordination (e.g., Li et al. 2004; Riek et al. 1992). In Riek et al. (1992), the posture of the forearm was varied so that flexion produced movement either toward or away from the body's midline. When the posture of the two forearms was the same, transitions were always observed from spatial anti-phase to spatial in-phase. However, when they were positioned differently, transitions were observed from spatial in-phase to spatial anti-phase. Transitions always favored the co-activation of homologous muscle groups. Using bimanual horizontal abduction–adduction movements of the wrists along with manipulations of forearm posture, Li et al. (2004) similarly found that coordination accuracy and stability were maximized when there was a simultaneous activation of homologous muscles. Moreover, they noted the recruitment of additional degrees of freedom (simultaneous vertical flexion–extension movements of the

wrist), accompanying the destabilization of coordination in the horizontal dimension, which assisted in producing the required horizontal movements.

Although Li et al. (2004) demonstrated a tendency towards coactivation of homologous muscles, their observation that additional degrees of freedom were recruited when forearm posture was altered led them to conclude that such manipulations may change the entire movement system, making neat distinctions between spatial and anatomical constraints difficult. This suggestion was consistent with other studies that demonstrated that both spatial and anatomical constraints operate in bimanual coordination dynamics (e.g., Mitra et al. 1997; Park et al. 2001; Swinnen et al. 1997). In two of those studies, participants swung hand-held pendulums about the wrist in the coronal plane in order to dissociate spatial and anatomical definitions of relative phase (Mitra et al. 1997; Park et al. 2001). In the sagittal plane, contracting homologous muscles in in-phase (anti-phase) causes the pendulums to move in-phase (anti-phase). However, in the coronal plane, contracting homologous muscles in in-phase (anti-phase) causes the pendulums to move in anti-phase (in-phase). In both Mitra et al. (1997) and Park et al. (2001), ϕ_{dev} (attractor location) was a function of the spatial definition of ϕ while $SD\phi$ (strength of the attractor) appeared to be a function of the anatomical definition. Mitra et al. (1997) proposed modeling such results in the manner of Schöner and Kelso (1988a, b) by adding an additional 2π periodic term to Eq. 1:

$$\dot{\phi} = \Delta\omega - a \sin \phi - 2b \sin 2\phi - c \sin(\Gamma - \phi) + \sqrt{Q}\zeta_r. \quad (3)$$

The term Γ represents the relative phase in a spatial frame of reference. In most cases, when the spatial and anatomical definitions of relative phase are identical, the additional term goes to zero, effectively reducing this model to Eq. 1. However, in cases where the spatial and anatomical definitions differ, this additional term alters the strength but not the location of attractors. In the experimental task used by Mitra et al. (1997), this additional term strengthened the attraction to whatever anatomically defined relative phase produced spatial in-phase. Such data and modeling suggest that both spatial and anatomical constraints superimpose in determining the observed coordination dynamics.

Overview

Past research provides conflicting conclusions regarding the influence of spatial and anatomical constraints on the dynamics of coordinated bimanual rhythmic movements. In the present experiment, participants swung hand-held

pendulums about the wrist while attending to visual feedback about ϕ (a phase plot of each pendulum) displayed on a screen. We hope to inform the debate over the roles of spatial and anatomical constraints by investigating the effects of visually perceiving $\phi = 0^\circ$ or 180° while actually performing $\phi = -180^\circ$ to $+180^\circ$. Spatial and anatomical constraints were dissociated by introducing a phase shift in the visual display so that visual feedback differed from the movements being performed by the participants in 15° increments from -180° to $+180^\circ$. Because the actual movements of the pendulums were different from those presented visually (a fact that could presumably be detected haptically), a complete dissociation between spatial and anatomical constraints was not possible in this case; therefore, interpretation is limited to the roles of visual-spatial and anatomical constraints on the dynamics of relative phase. If visual-spatial constraints dominate, then the resulting coordination dynamics were governed primarily by the relative phase of the visual display. If anatomical constraints dominate, then the resulting coordination dynamics were governed primarily by the relative phase being performed by the limbs. The third possibility—that visual-spatial and anatomical constraints co-operated in this task—was evaluated by comparing the observed results to the predictions from Eq. 3.

Method

Participants

Sixteen (5 male, 11 female) students at Arizona State University participated in this study in order to fulfill the course requirements of Introduction to Psychology. Participants were asked whether they consider themselves right- or left-handed, and all but one female participant reported being right-handed.

Design

Participants were instructed to swing two pendulums at a self-selected frequency while watching a display (superimposed phase plots each pendulum) that provided visual feedback about their movements. Visual feedback was offset from performed ϕ in 15° increments from -180° to $+180^\circ$ (in randomized order). Participants were instructed to swing the pendulums so that the visually displayed ϕ was either 0° or 180° . In this fashion, participants received visual feedback specifying either $\phi = 0^\circ$ or 180° (a visual-spatial constraint) while actually performing a range of ϕ from -180° to $+180^\circ$ (an anatomical constraint). The two main factors in the analyses, then, were intended visual phase (ϕ_{vis} , maintaining either visual in-phase or visual

anti-phase) and intended performed relative phase (ϕ_{int} , the relative phase that they would need to perform in order to maintain ϕ_{vis} ; there were 24 levels from -180° to $+180^\circ$ in 15° increments). The extent to which behavior reveals an influence of visual–spatial or anatomical constraints will be reflected in the significance of those two factors, respectively. The movement trajectories of each hand were recorded and analyzed to determine the cycling frequency, amplitude, and relative phase.

Apparatus

The apparatus is depicted in Fig. 1. Participants sat on a chair with their feet planted firmly on the floor and their forearms resting parallel to each other in the sagittal plane on armrests. Their wrists extended beyond the end of the armrest to allow unobstructed wrist movements. Participants held identical pendulums in each hand, composed of a 50 cm wooden dowel (diameter 12 mm) with a 50 g mass attached securely to the distal end. A ski-pole handle was used to ensure a firm grip. The participants swung the pendulums from front to back in the sagittal plane without lifting their forearms from the armrests. Each pendulum had a natural frequency of 0.80 Hz.

The movement trajectories of the two pendulums were recorded with an Optotrak 3020 motion analysis measurement system (Northern Digital Inc., Waterloo, Canada) that was located 3.30 m in front of the participant and 0.75 m off of the ground. The Optotrak recorded the three-dimensional positions (50 Hz; chosen in order for the

calculations of actual and transformed relative phase to be completed within one sample) of two infrared light-emitting diodes (IREDS) attached 5 cm apart above the mass on each pendulum. Pendulum angles were calculated based on the positions of the two IREDS in the participant's sagittal plane.

Visual feedback was provided continuously in the form of phase angles on a standard VGA color monitor (800×600 pixels, 256 colors; Visiontek NV9960 32 MB AGP video card) that was situated 2 m in front of the participant. Software was developed in our lab to calculate pendulum angles, angular velocities, and phase angles using an Intel Pentium III 800 MHz CPU computer. For the purposes of calculating phase angles for this display, pendulum angle, x , and the angular velocity of x , \dot{x} , were plotted on orthogonal axes and normalized to be more symmetric (i.e., distributed approximately as a unit circle) around zero in this phase plane. Normalization was accomplished using three steps (a slightly different procedure was used to normalize phase angles after data collection was complete for data analysis): (1) The mean of the first 50 samples of x and \dot{x} (taken both at the beginning of the familiarization period and again at the beginning of the 60 s data collection period) were subtracted from each subsequent value to center each time series around zero; (2) A mean amplitude for both x and \dot{x} was estimated by calculating the mean of the absolute values of the minimum and maximum for the first 50 samples; (3) Each data point in the centered time series was divided by this estimated mean amplitude. This normalization procedure carried the assumption that the midpoint, amplitude, and minimum and maximum velocity of each cycle were roughly stable over the course of a trial. Using the normalized values of x and \dot{x} , the phase angle of each hand was calculated as $\theta = \arctan(\dot{x}/x)$. The phase angles of the two hands were displaced from each other by an amount equal to the relative phase offset for the trial. The current phase angle of each pendulum was displayed as a ball (green for the left hand and red for the right hand) traveling around a circular track (diameter 10 cm). The two balls were superimposed so that they were on top of each other during in-phase oscillations and on opposite sides of the circular track during anti-phase oscillations.

Procedure

Participants were seated in the chair and instructed to swing the two hand-held pendulums back and forth continuously using only their wrists. They were shown how movements of each pendulum translated into movements of the red and green balls on the screen; each cycle of the pendulum from front to back to front caused the corresponding ball to traverse one cycle around the circular

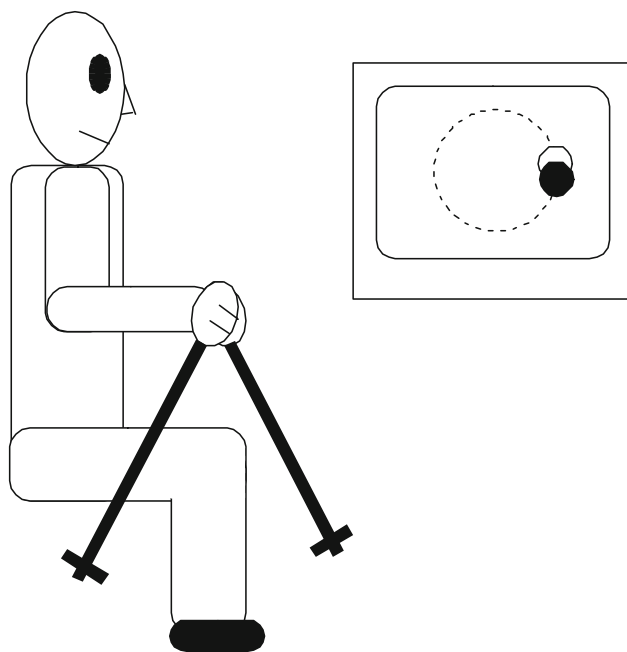


Fig. 1 Apparatus and display used in the present experiment

track. The only degrees of freedom in the visual display were the phase angles of each pendulum; i.e., the balls only moved along the track and never deviated off of the track, even if the participant were to alter the amplitude of the pendulum oscillations. Participants were allowed to familiarize themselves with the equipment and to explore the relationship between the pendulums and the visual display prior to the session. Although the task required the participants to attend to the visual display, their hands were not occluded. At the beginning of each trial, the participant began swinging the pendulums while viewing the display. Once the participant reported that they had settled into a comfortable and stable pattern (usually after about 5 s), the 60 s of data collection began. Participants were informed that they should expect a brief (1 s) interruption in the visual display while the computer reset some parameters and were instructed to maintain their pattern until the display returned. Participants were allowed to rest between trials.

The session consisted of two blocks of 24 randomly ordered trials. During one block of trials, participants were instructed to oscillate the pendulums to maintain $\phi_{\text{vis}} = 0^\circ$; during the other block, they were instructed to maintain $\phi_{\text{vis}} = 180^\circ$. The order of blocks was randomized. Participants were free to elect their own frequency of oscillation and were instructed to choose a comfortable moderate pace. Prior to the start of each block, participants were instructed that, in order to perform the desired task, they might have to offset the motion of the two pendulums to varying degrees because, on each trial, a phase shift would be introduced. On each trial, phase shifts were introduced in 15° increments from -180° to $+180^\circ$. The order of offsets was randomized and participants were not informed about the magnitude of the offset on any trial. Participants were allowed to rest between trials. All procedures were carried out according to the principles of the Helsinki Declaration and the American Psychological Association and were approved by the Institutional Review Board of Arizona State University.

Analysis

Amplitude, A , was calculated as the angular distance between the maximum forward and backward extension in a cycle. For the purposes of the remaining data analysis, pendulum angle, x , and its angular velocity, \dot{x} , were normalized to be more symmetric (i.e., distributed approximately as a unit circle) around zero using the following two steps: (1) the mean of each series was subtracted from each data point in the series to center the time series around zero; (2) each data point in the centered time series was divided by the mean of the absolute values of the minimum and maximum for each series. (The

normalization procedure differed slightly from that used to produce the visual feedback because the mean, maximum, and minimum values of each entire time series were not available during the trial.) Using the normalized values of x and \dot{x} , the phase angle of each hand at sample i , θ_i , was calculated as $\theta_i = \arctan(\dot{x}_i/x_i)$. The cycle frequency of each hand, ω , was then calculated by transforming the first time derivative of θ into Hz (cycles/s) by multiplying by 50 (samples/s)/ 2π (rad/cycle). Relative phase, ϕ , was calculated by subtracting θ_i for the right hand (RH) from θ_i for the left hand (LH) (i.e., $\phi = \theta_{\text{LH}} - \theta_{\text{RH}}$). Means were calculated across both the A , ω , and ϕ time series to yield the summary statistics of mean amplitude, A_{ave} , mean cycle frequency, ω_{ave} , and mean relative phase, ϕ_{ave} . The standard deviation of the ϕ time series (i.e., the within-trial standard deviation), $\text{SD}\phi$, served as the measure of relative phase variability.

Results

Frequency and amplitude

A repeated measures analysis of variance (ANOVA) of ω_{ave} as a function of hand (LH and RH), ϕ_{vis} , and ϕ_{int} was conducted. As expected, there was no main effect of hand, $F(1, 23) < 1$, ns, $\eta^2 = 0.02$, and no significant interactions involving hand, all $\eta^2\text{s} < 0.1$, indicating that participants successfully performed the task of swinging the two pendulums at the same frequency. The main effect of ϕ_{int} was significant, $F(23, 345) = 2.96$, $p < 0.05$, $\eta^2 = 0.17$, as was the interaction of ϕ_{int} with ϕ_{vis} , $F(23, 345) = 1.74$, $p < 0.05$, $\eta^2 = 0.1$. This interaction is depicted in Fig. 2. As can be seen in this figure, participants swung the pendulums most slowly around $\phi_{\text{int}} = 0^\circ$ and 180° . A simple effects analysis revealed, however, that this effect of ϕ_{int} on ω_{ave} existed only when participants intended to maintain $\phi_{\text{vis}} = 0^\circ$, $F(23, 345) = 3.23$, $p < 0.05$, $\eta^2 = 0.18$; there was no effect of ϕ_{int} on ω_{ave} when participants intended to maintain $\phi_{\text{vis}} = 180^\circ$, $F(23, 345) = 1.08$, ns, $\eta^2 = 0.07$. None of the other effects were significant, all $\eta^2\text{s} < 0.11$.

A repeated measures ANOVA of the standard deviation of ω ($\text{SD}\omega$) as a function of hand, ϕ_{vis} , and ϕ_{int} was conducted. The three main effects were all significant, but there were no significant interactions, all $\eta^2\text{s} < 0.07$. The significant main effect of hand indicated that variability was greater for the LH (0.85 Hz) than it was for the RH (0.72 Hz), $F(1, 15) = 4.87$, $p < 0.05$, $\eta^2 = 0.25$. The significant main effect of ϕ_{vis} indicated that variability was greater at $\phi_{\text{vis}} = 0^\circ$ (0.93 Hz) than at $\phi_{\text{vis}} = 180^\circ$ (0.64 Hz), $F(1, 15) = 10.37$, $p < 0.05$, $\eta^2 = 0.41$. The main effects of ϕ_{vis} and ϕ_{int} are shown in Fig. 3. As can be

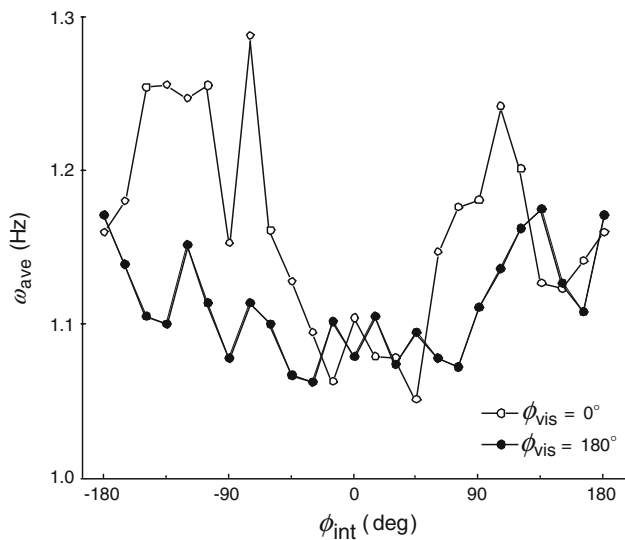


Fig. 2 Mean frequency of oscillation (ω_{ave}) as a function of ϕ_{int} and ϕ_{vis}

seen in this figure, the effect of ϕ_{int} was such that participants exhibited the least variability in ω_{ave} when performing around $\phi_{int} = 0^\circ$ and 180° , $F(23, 345) = 4.92$, $p < 0.05$, $\eta^2 = 0.25$.

A repeated measures ANOVA of A_{ave} as a function of hand, ϕ_{vis} , and ϕ_{int} was conducted. As expected, there was no main effect of hand, $F(1, 15) < 2.47$, ns, $\eta^2 = 0.14$. In fact, the only significant effect involving hand was the interaction of hand and ϕ_{int} indicating that A_{ave} for the RH was significantly greater than A_{ave} for the LH at a few levels of ϕ_{int} around $\phi_{int} = 180^\circ$ ($\phi_{int} = -165^\circ, -150^\circ, 105^\circ, 120^\circ$, and 150°), $F(23, 345) = 2.51$, $p < 0.05$, $\eta^2 = 0.14$. The effects of ϕ_{vis} , and ϕ_{int} are depicted in

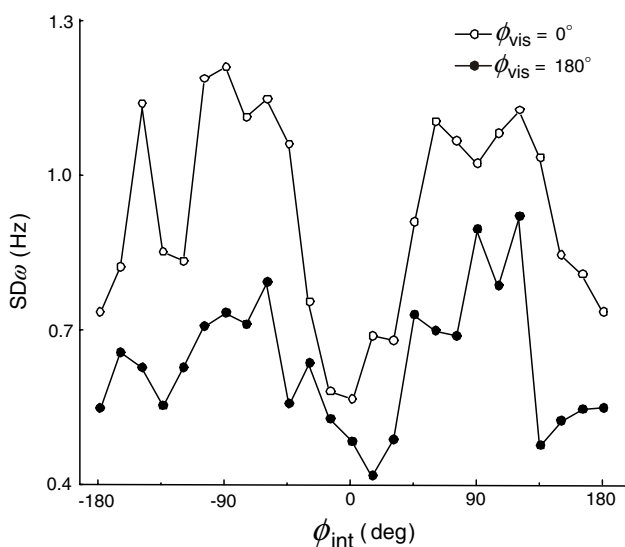


Fig. 3 Variability of frequency ($SD\omega$) as a function of ϕ_{int} and ϕ_{vis}

Fig. 4. As can be seen in this figure, A_{ave} was greater when participants intended to maintain $\phi_{vis} = 180^\circ$, $F(1, 15) = 30.96$, $p < 0.05$, $\eta^2 = 0.67$. There was also a significant main effect of ϕ_{int} in which A_{ave} was greatest when performing around $\phi_{int} = 0^\circ$ and 180° , $F(23, 345) = 4.86$, $p < 0.05$, $\eta^2 = 0.25$. None of the other effects were significant, all η^2 s < 0.09 .

Relative phase

A repeated measures ANOVA of ϕ_{ave} as a function of ϕ_{vis} and ϕ_{int} was performed. Those effects are depicted in Fig. 5. If participants accurately performed ϕ_{int} , then there should be no difference as a function of ϕ_{vis} (i.e., all of the data should lie along the dotted line in Fig. 5). There was no effect of ϕ_{vis} , $F(1, 15) = 3.61$, ns, $\eta^2 = 0.19$, but a significant effect of ϕ_{int} , $F(23, 345) = 518.59$, $p < 0.05$, $\eta^2 = 0.97$, indicating that participants were performing the task by roughly matching ϕ_{int} . Two important features in Fig. 5 are the curvature of the functions relating ϕ_{ave} to ϕ_{int} and the significant interaction between ϕ_{vis} and ϕ_{int} , $F(23, 345) = 2.16$, $p < 0.05$, $\eta^2 = 0.13$. The curvature of the functions suggests that, although they generally matched ϕ_{int} , participants tended to actually perform ϕ_{ave} closer to either 0° or 180° . This can be seen in Fig. 5 in the roughly three data points ($\pm 45^\circ$) on either side of $\phi_{int} = 0^\circ$ or 180° where participants continued to perform either $\phi_{ave} = 0^\circ$ or 180° . In the language of coordination dynamics, values of ϕ in the vicinity of $\phi_{int} = 0^\circ$ or 180° were attracted towards $\phi = 0^\circ$ or 180° . The significant interaction of ϕ_{vis} and ϕ_{int} suggests that this tendency was stronger while maintaining $\phi_{vis} = 180^\circ$.

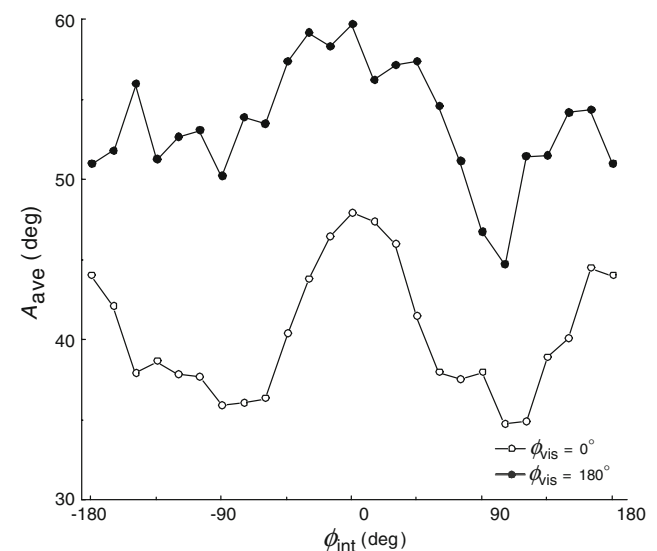


Fig. 4 Mean amplitude (A_{ave}) as a function of ϕ_{int} and ϕ_{vis}

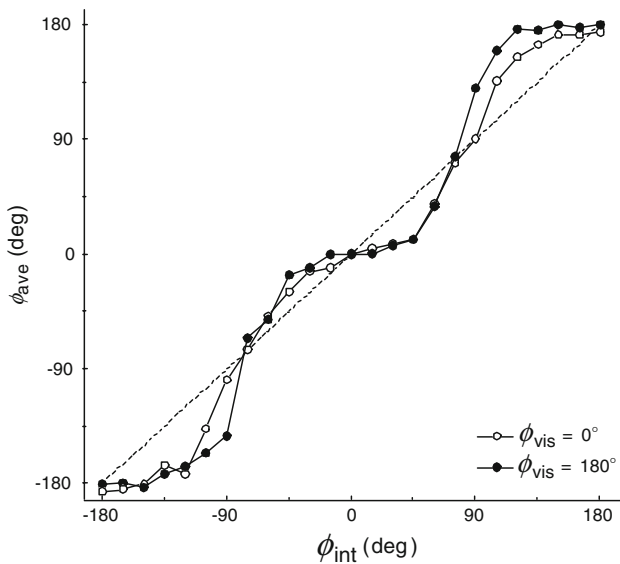


Fig. 5 Mean relative phase (ϕ_{ave}) as a function of ϕ_{int} and ϕ_{vis}

Both of the important features in Fig. 5 that were described above are better analyzed using the deviation of ϕ_{ave} from ϕ_{int} . A repeated measures ANOVA of ϕ_{dev} ($\phi_{ave} - \phi_{int}$) as a function of ϕ_{vis} and ϕ_{int} was performed. Those effects are shown in Fig. 6. The results of the statistical test were very similar to the ANOVA on ϕ_{ave} . Again, there was no main effect of ϕ_{vis} , $F(1, 15) = 3.61$, ns, $\eta^2 = 0.19$, but the main effect of ϕ_{int} was significant, $F(23, 345) = 24.62$, $p < 0.05$, $\eta^2 = 0.62$. The significant interaction of ϕ_{vis} and ϕ_{int} , $F(23, 345) = 2.16$, $p < 0.05$, $\eta^2 = 0.13$, suggests, again, that this tendency was stronger while maintaining $\phi_{vis} = 180^\circ$.

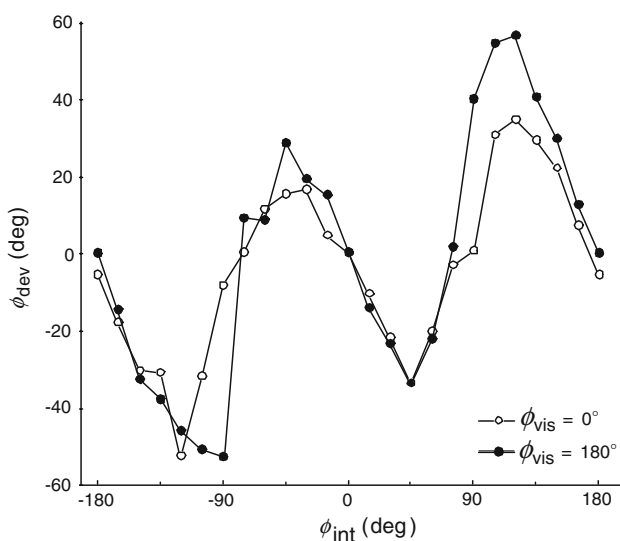


Fig. 6 Mean phase shift ($\phi_{dev} = \phi_{ave} - \phi_{int}$) as a function of ϕ_{int} and ϕ_{vis}

Despite the lack of a main effect of ϕ_{vis} in the ϕ_{dev} ANOVA (possibly due to $\phi_{dev} < 0$ canceling out $\phi_{dev} > 0$), it appears from Fig. 6 that participants performed closer to ϕ_{int} while maintaining $\phi_{vis} = 0^\circ$. To establish whether this effect was significant (as suggested by the previous significant interactions), an ANOVA of $|\phi_{dev}|$ as a function of ϕ_{vis} and ϕ_{int} was performed. All effects were significant. Most importantly, the main effect of ϕ_{vis} was significant, $F(1, 15) = 13.03$, $p < 0.05$, $\eta^2 = 0.47$, indicating that participants exhibited less of a shift away from ϕ_{int} while maintaining $\phi_{vis} = 0^\circ$ (29.32°) than they did while maintaining $\phi_{vis} = 180^\circ$ (36.37°). The significant main effect of ϕ_{int} , $F(23, 345) = 20.53$, $p < 0.05$, $\eta^2 = 0.58$, and the significant interaction between ϕ_{vis} and ϕ_{int} , $F(23, 345) = 2.25$, $p < 0.05$, $\eta^2 = 0.13$, represent the same effects described above in the analysis of ϕ_{dev} .

The functions depicted in Fig. 6 are suggestive of dynamical equations of motion indicating attractors around $\phi = 0^\circ$ and 180° and repellers around $\phi = \pm 90^\circ$. Attractive states are those in which the function crosses $\phi_{dev} = 0^\circ$ with a negative slope. The negative slope identifies the fact that ϕ_{ave} for all conditions along this slope are shifted towards the attractive state. Repelling states are those in which the function crosses $\phi_{dev} = 0^\circ$ with a positive slope. The positive slope identifies the fact that ϕ_{ave} for all conditions along this slope are shifted away from the attractive state. The strength of an attractive or repelling state is represented by the magnitude of the slope, with slopes further from zero indicating greater strength.

To assess the attractive strength of $\phi = 0^\circ$ and 180° for both $\phi_{vis} = 0^\circ$ and 180° , the negative slopes were estimated by regressing a line through $\phi_{dev} = f(\phi_{int})$ from -45° to $+45^\circ$ around 0° and 180° and a repeated measures ANOVA performed as a function of ϕ_{vis} and attractor (0° and 180°). Those data are shown in Fig. 7. Both main effects were significant. The significant main effect of ϕ_{vis} , $F(1, 15) = 9.38$, $p < 0.05$, $\eta^2 = 0.39$, indicates that the magnitude of the slopes was greater at $\phi_{vis} = 180^\circ$ (-0.82) than $\phi_{vis} = 0^\circ$ (-0.65). The significant main effect of attractor, $F(1, 15) = 5.02$, $p < 0.05$, $\eta^2 = 0.25$, indicates that the magnitude of the slopes was greater around 180° (-0.83) than 0° (-0.64). There was no interaction, $F(1, 15) < 1$, ns, $\eta^2 < 0.01$.

Variability of relative phase

A repeated measures ANOVA was performed on $SD\phi$ as a function of ϕ_{vis} and ϕ_{int} . Those effects are shown in Fig. 8. All effects were significant. There was a significant main effect of ϕ_{vis} , $F(1, 15) = 39.70$, $p < 0.05$, $\eta^2 = 0.73$, indicating that participants were more variable at $\phi_{vis} = 0^\circ$ (48.68°) than at $\phi_{vis} = 180^\circ$ (30.77°). There was also a significant main effect of ϕ_{int} , $F(23, 345) = 17.47$,

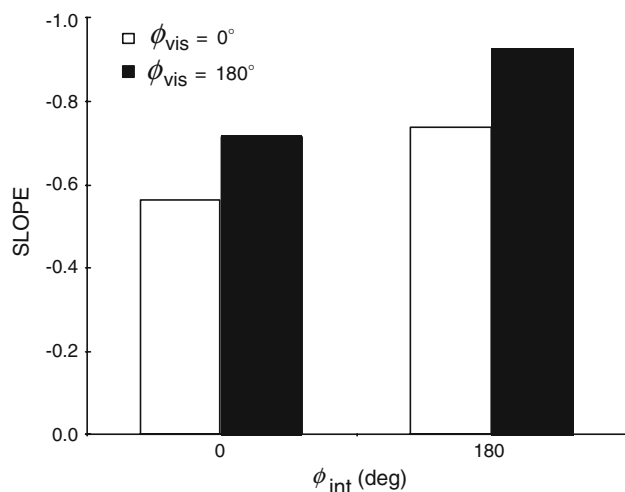


Fig. 7 Slope of the negative zero-crossings at $\phi_{\text{int}} = 0^\circ$ and 180° from Fig. 4

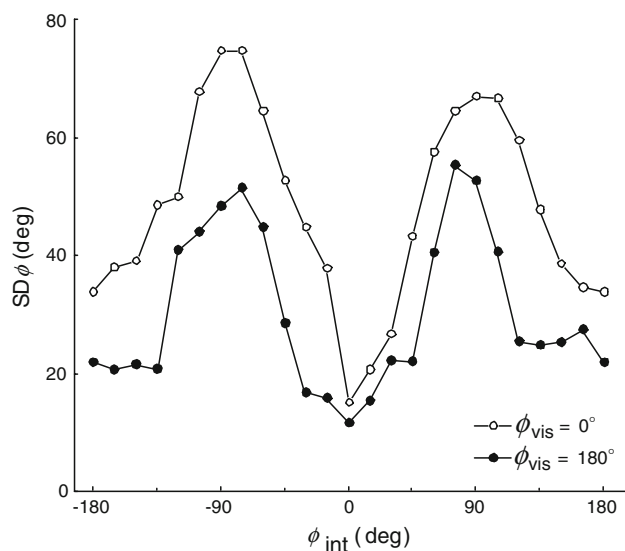


Fig. 8 Variability of relative phase ($\text{SD}\phi$) as a function of ϕ_{int} and ϕ_{vis}

$p < 0.05$, $\eta^2 = 0.54$, indicating that participants exhibited the least variability when performing around 0° and 180° . Lastly, there was a significant interaction between those two variables, $F(23, 345) = 1.63$, $p < 0.05$, $\eta^2 = 0.1$, indicating that the increased $\text{SD}\phi$ accompanying ϕ_{int} between 0° and 180° was more pronounced when participants maintained $\phi_{\text{vis}} = 0^\circ$.

Discussion

This experiment was designed to inform the issue of whether the relative phase dynamics of rhythmic bimanual coordination are governed more by spatial or anatomical

constraints. Participants coordinated rhythmic movements of their wrists while attending to visual feedback about relative phase. The task was to maintain in-phase or anti-phase coordination in the visual display by performing relative phases from -180° to $+180^\circ$. By comparing the observed patterns of coordination to what is currently known about an individual's intrinsic dynamics, we were able to assess how much the behavior reflected an influence of anatomical constraints (through the effects of ϕ_{int}) and how much it reflected an influence of visual-spatial constraints (through the effects of ϕ_{vis}).

Visual-spatial and anatomical constraints

Considered in isolation, there were results in the present experiment that could be taken as evidence in favor of either visual-spatial or anatomical constraints. With visual feedback, participants were able to perform relative phases across the entire range from -180° to $+180^\circ$. There was, however, an attraction towards $\phi = 0^\circ$ and $\phi = 180^\circ$. Not only were ϕ_{dev} and $\text{SD}\phi$ minimized at those values but participants continued to perform those preferred patterns across a range of ϕ_{int} approximately 45° above and below those values. Those effects of ϕ_{int} could be taken as evidence for anatomical constraints. Nevertheless, if coordination in the present task were governed solely by anatomical constraints, then differences should have emerged only as a function of ϕ_{int} . Any differences that emerged across ϕ_{vis} could not be explained purely on the basis of anatomical constraints. In fact, there were clear effects associated with the visual manipulation used in the present experiment that could be taken as evidence for visual-spatial constraints. Specifically, going from $\phi_{\text{vis}} = 0^\circ$ to $\phi_{\text{vis}} = 180^\circ$, there was an increase in $|\phi_{\text{dev}}|$ and a decrease in $\text{SD}\phi$. Participants were clearly influenced by anatomical constraints, but visual-spatial constraints played an important role as well.

Consistent with Li et al. (2004), we propose that the important question, then, is not whether anatomical or visual-spatial constraints dominate but, rather, how they may have combined and interacted in the present task. It appears that accommodating the visual-spatial constraints required participants to modulate, possibly by destabilizing, coordination at the anatomical level. There are two effects that support this interpretation. The first is that the strength of attraction was greater near $\phi = 180^\circ$ (see Figs. 6, 7), in contrast to previous studies that have demonstrated a clearly stronger attraction near $\phi = 0^\circ$ (Amazeen et al. 1996; Kelso 1984; Kelso et al. 1986, 1987, 1996; Sternad et al. 1996). Because the visual displays in the present experiment were designed to eliminate any attraction towards $\phi = 0^\circ$ or 180° , the observed attraction towards those values represents the residual effects of

anatomical constraints. Those findings suggest, then, anatomical constraints were stronger, and visual–spatial constraints weaker, in the vicinity of $\phi = 180^\circ$. The second effect is that the strength of attraction was greater for $\phi_{\text{vis}} = 180^\circ$ (see Figs. 6, 7), suggesting that anatomical constraints were stronger, and visual–spatial constraints weaker, for $\phi_{\text{vis}} = 180^\circ$.

As a rule, when participants use visual information (i.e., when visual–spatial constraints become stronger), we should notice variations in their performance as they attempt to accommodate the task requirements. The $SD\omega$ data and the $SD\phi$ data both support this prediction. If, as was suggested above, the strength of attraction towards $\phi = 0^\circ$ and 180° is inversely related to the strength of the visual–spatial constraints, then we should observe greater change in performance for $\phi_{\text{vis}} = 0^\circ$ and when participants performed relative phases away from the attractors at $\phi = 0^\circ$ and 180° . Those predictions were supported in Fig. 3 for $SD\omega$ and in Fig. 7 for $SD\phi$; they were both surprising results considering that, ordinarily, $\phi = 0^\circ$ is less variable than $\phi = 180^\circ$.

In the modeling of Haken et al. (1985), both ω and A contribute to the stability of coordination: coordination becomes less stable as ω increases and A decreases (although see the results of Post et al. 2000, suggesting a subordinate role for A). The ω_{ave} and A_{ave} data both suggest, then, that the increased variability associated with accommodating the visual–spatial task requirements may be related to a decrease in stability at the anatomical level. Figure 2 shows that ω_{ave} varied as a function of ϕ_{int} only when participants maintained $\phi_{\text{vis}} = 0^\circ$. During $\phi_{\text{vis}} = 0^\circ$, ω_{ave} was minimized in the vicinity of $\phi = 0^\circ$ and 180° . In addition, whenever it was minimized, ω_{ave} was nearly identical when participants maintained $\phi_{\text{vis}} = 0^\circ$ as when they maintained $\phi_{\text{vis}} = 180^\circ$. The fact that participants modified ω_{ave} across ϕ_{int} while maintaining $\phi_{\text{vis}} = 0^\circ$ suggests that they adapted their coordination to the visual information; i.e., their performance was influenced by spatial constraints. When participants performed in the vicinity of 0° and 180° , however, there was no conflict between spatial and anatomical constraints and so the observed ω_{ave} was the same as it was when they maintained $\phi_{\text{vis}} = 180^\circ$, where anatomical constraints prevailed. Likewise, Fig. 4 shows that A_{ave} was minimized, suggesting that coordination at the anatomical level was destabilized, at $\phi_{\text{vis}} = 0^\circ$ and around $\phi_{\text{int}} = -90^\circ$ and 90° .

Although the preceding discussion has focused largely on the role of anatomical constraints in governing the relative strength of the visual–spatial constraints, perceptual characteristics of the present display may have played a role as well. Specifically, because the balls overlapped in $\phi_{\text{vis}} = 0^\circ$ —thereby making even small deviations from ϕ_{int} apparent—the information that was available in the

visual display may have been more salient to participants. In fact, research has shown that participants perceive anti-phase to be more variable than in-phase (Bingham et al. 1999, 2000; Wilson et al. 2003; Zaal et al. 2000), which suggests better attunement to the information in $\phi_{\text{vis}} = 0^\circ$. Although we cannot yet define the information variables in the present display, it seems reasonable to assume that any increased salience would effectively increase the strength of the visual–spatial constraints.

Modeling the coordination dynamics

The results in Figs. 6 and 7 along with the preceding suggestions regarding the contributions of visual–spatial and anatomical constraints in the present task are reflected in the motion equation of Eq. 3. Before we present this modeling approach, we wish to make clear that this is not the standard method of modeling ϕ_{dev} using the locations of the negative-sloped zero-crossings of $\dot{\phi} = f(\phi)$. Given the similarity of our task and results to those of Tuller and Kelso (1989) and Yamanishi et al. (1980) and the successful modeling of those data by Schöner and Kelso (1988a, b), the approach advocated by Schöner and Kelso would appear most appropriate. However, when we applied that model (using standard parameter values of $a = b = 1$, $c = 20$; Schöner and Kelso 1988a, b), we were able to generate the general pattern of ϕ_{dev} indicating attractors at $\phi = 0^\circ$ and 180° but were unable to capture the observation in Figs. 6 and 7 that the attraction to $\phi = 180^\circ$ was greater than the attraction to $\phi = 0^\circ$. An inability of Schöner and Kelso model to capture all of our results should not be taken to suggest that the present data reveal any limitations to that model or to that general approach. Rather, we will conclude below that the transformed visual feedback used in the present experiment created a task that was qualitatively different from the tracking task used by Tuller and Kelso (1989) and Yamanishi et al. (1980) in a way that is better represented using the motion equation in Eq. 3 (from Mitra et al. 1997).

Setting the parameters of Eq. 3 to be consistent with the interpretation described in the previous section yielded the predictions for $\dot{\phi}$ (corresponding to ϕ_{dev}) in Fig. 9. To generate those predictions, Γ (representing ϕ_{vis}) was set to 0 for $\phi_{\text{vis}} = 0^\circ$ and 180 for $\phi_{\text{vis}} = 180^\circ$. We suggested above that increased salience of $\phi_{\text{vis}} = 0^\circ$ in the present display may have strengthened the influence of the spatial constraints and so c was set to +2 for $\phi_{\text{vis}} = 0^\circ$ and -1 for $\phi_{\text{vis}} = 180^\circ$. To capture the suggestion that the anatomical constraints were stronger during $\phi_{\text{vis}} = 180^\circ$, b and a were set to 1 and 0.5 for visual anti-phase ($b/a = 2$) and 0.5 and 1 for visual in-phase ($b/a = 0.5$), respectively. A comparison of the model predictions in Fig. 9 to the actual data in Fig. 6 suggests that this model was able to successfully

capture the spatial and anatomical contributions to the relative phase dynamics in the present experiment.

The slopes of ϕ_{dev} through $\phi_{\text{int}} = 0^\circ$ and 180° were used to estimate the relative strengths of the anatomical contributions to the bimanual coordination dynamics. Predictions of those results can be obtained by evaluating λ at each of the values of ϕ . Those predictions are shown in Fig. 10. Again, a comparison of the model results in Fig. 10 to the actual data in Fig. 7 suggests that Eq. 3 was able to successfully capture the observed results of an increased attraction to $\phi = 180^\circ$ and an increased attraction to both $\phi = 0^\circ$ and $\phi = 180^\circ$ at $\phi_{\text{vis}} = 180^\circ$.

Although equating $\dot{\phi}$ with ϕ_{dev} is not a standard approach, the two variables share a similarity—namely, both reflect the change in ϕ that would be expected given a particular value of ϕ_{int} . The difference is that $\dot{\phi}$ indicates how ϕ will change as it approaches an attractor whereas ϕ_{dev} generally represents the distance between the attractor and ϕ_{int} . In the studies of Yamanishi et al. (1980), participants performed the patterns from memory after receiving instruction with visual metronomes. The ability to perform relative phase patterns other than $\phi = 0^\circ$ and 180° from memory suggests that a new attractor had been formed, consistent with the modeling approach of Schönner and Kelso (1988a, b). In the present experiment, there was no such instruction, only the altered visual feedback of the limbs. Perhaps no new attractors were formed, but with attractors at $\phi = 0^\circ$ and 180° only, observed performance may have resulted from the interaction of forces drawing coordination towards one of the attractors based on $\dot{\phi}$ at ϕ_{int} and an effort on behalf of participants to match ϕ_{int} using altered visual feedback. That possibility can be tested in future research by eliminating the visual display and

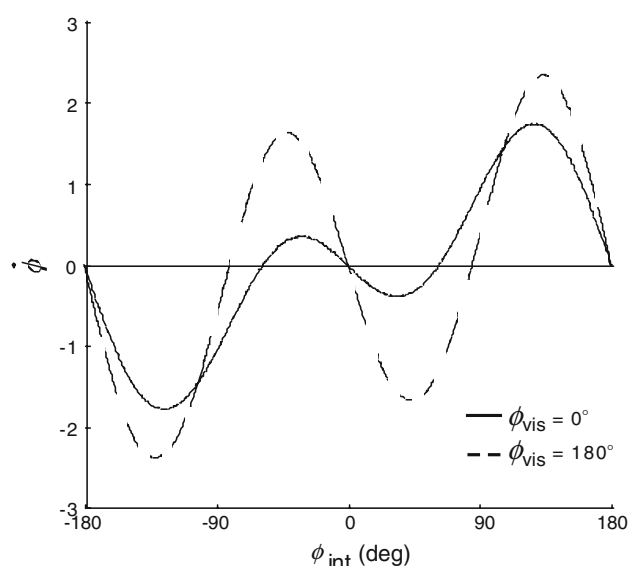


Fig. 9 Predictions for $\dot{\phi}$ as a function of ϕ_{int} and ϕ_{vis} from Eq. 3

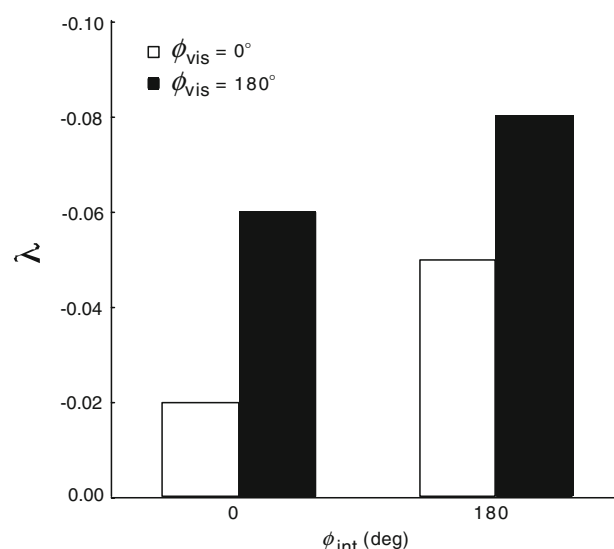


Fig. 10 Predictions for λ at $\phi_{\text{int}} = 0^\circ$ and 180° as a function of ϕ_{vis} from Eq. 3

asking participants to continue performing ϕ_{int} without the altered visual feedback. Based on the hypothesis presented, we would expect no change in the attractor layout; i.e., the results should be captured fully by the model in Eq. 1.

Conclusions: constraints and information

The results of the present study are consistent with previous research (Mitra et al. 1997; Park et al. 2001; Swinnen et al. 1997) suggesting that spatial and anatomical constraints interact in the relative phase dynamics of rhythmic bimanual coordination. Mechsner et al. (2001) argued for a different distinction—one between perceptual and motoric contributions to bimanual coordination—that is not appropriately applied to these data because participants in this experiment had access to haptic information specifying the actual motions of the wrists. Insofar as both visual–spatial and anatomical constraints contributed to bimanual coordination, then, we must conclude that participants likely used both visual and haptic information about limb movements.

The design of the present experiment associated visual information with a spatial definition of ϕ and haptic information with an anatomical definition. In fact, the methods used in many of the experiments cited in this article manipulated information in ways that would leave the haptic information about the anatomical definition of coordination intact. The data from Mitra et al. (1997), though, show that these roles are not privileged: participants may use haptic information to specify a spatial definition of coordination, even when that specification is at odds with a simultaneous specification of an anatomical

definition by the same modality. Fully distinguishing the roles of visual and haptic information—or perceptual and motoric control—in bimanual coordination will require altering or eliminating haptic information about the limbs. Such methods are difficult to implement (see discussion in Swinnen et al. 2003) and research suggests that even without sensory feedback from the limbs, participants may retain some awareness of the limb's location in space via effortful or dynamic touch (Carello et al. 2006).

The visual–spatial information used by the participants in this study came in the form of superimposed phase plots depicting the motions of the wrists. Such a display offers information that may be similar, but is certainly not identical to the information gained from viewing the hands directly (see Swinnen et al. 2003). Nevertheless, participants clearly incorporated this visual–spatial information into their coordination so that their behavior reflected a combination of visual–spatial and anatomical constraints. The dynamical model in Eq. 3 captured this combination. Specifically, it appeared that coordination was destabilized at the anatomical level to accommodate the visual–spatial constraints. This leads to the conclusion that anatomical constraints exist whenever we coordinate our limbs and they form the context within which spatial constraints exert an influence.

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