Exp Brain Res (2005) 164: 517–528
DOI 10.1007/s00221-005-2272-3

RESEARCH ARTICLE

Andrew D. Wilson · David R. Collins
Geoffrey P. Bingham

Perceptual coupling in rhythmic movement coordination: stable perception leads to stable action

Received: 5 August 2004 / Accepted: 23 December 2004 / Published online: 11 May 2005

Abstract Rhythmic movement coordination exhibits characteristic patterns of stability, specifically that movements at 0° mean relative phase are maximally stable, 180° is stable but less so than 0°, and other coordinations are unstable without training. Recent research has demonstrated a role for perception in creating this pattern; perceptual variability judgments covary with movement variability results. This suggests that the movement results could be due in part to differential perceptual resolution of the target movement coordinations. The current study used a paradigm that enabled simultaneous access to both perception (between-trial) and movement (within-trial) stability measures. A visually specified 0° target mean relative phase enabled participants to produce stable movements when the movements were at a non-0° relationship to the target being tracked. Strong relationships were found between within-trial stability (the traditional movement measure) and between-trial stability (the traditional perceptual judgment measure), suggestive of a role for perception in producing coordination stability phenomena. The stabilization was incomplete, however, indicating that visual perception was not the sole determinant of movement stability. Rhythmic movement coordination is intrinsically a perception/action system.

Keywords Rhythmic movement coordination · Perception/action · Perceptual coupling

A. D. Wilson · G. P. Bingham (✉)
Department of Psychology, Indiana University, 1101 E10th St, Bloomington, IN 47405-7007, USA
E-mail: gbingham@indiana.edu

D. R. Collins
Department of Neurological Surgery, Washington University School of Medicine, St. Louis, MO, USA

Introduction

Human rhythmic movement coordination is a common research paradigm for investigations of perception/action systems within a dynamic systems framework. The measure used is relative phase (ϕ), which describes the relative positions of two oscillators within their cycles. Kelso (1984) established the characteristic phenomena, which were described in the Haken–Kelso–Bunz model (Haken et al. 1985). Without special training, the only stable coordinative patterns are mean relative phases of 0 and 180°. 180° is less stable than 0° (movement is more variable and, with increases in frequency, tends to exhibit spontaneous transitions to 0°). Other relative phases are unstable without practice. Research has focused on establishing why different relative phases show different stabilities.

The first research in this area involved people rhythmically moving two of their own limbs (e.g. Kelso et al. 1986, 1987). There have consequently been several hypotheses that proposed the differential stabilities were due to interference between efference copies of motor commands (e.g. Cattaert et al. 1999) or to the non-linear interactions between two neural oscillators driving the limbs (e.g. Beek et al. 2002. The phenomena persist, however when the coupling is between two people (Schmidt et al. 1990; Temprado et al. 2003) or between a person and a computer display (Buekers et al. 2000; Wimmers et al. 1992). These latter studies eliminated the possibility of the above kind of neural interactions, but all entail the need to detect information about the oscillators to be coupled. They therefore suggest that the coordination phenomena may be more generally due to differential stability in the ability to detect the information used to couple and hence coordinate oscillating limbs. More recent work has therefore investigated the role of perception more directly.

The standard measure in the movement studies is within-trial variability, while the perceptual studies rely on between-trial variability—these latter studies generally entail judgments and there is no within-trial variability measure. The logic of this perceptual measure is simple; if participants are producing different judgments of mean phase or phase variability from trial to trial, this shows that they are having difficulty perceptually resolving the target phase. A correlation between within- and between-trial variability is suggestive evidence of a role for perception in producing the movement phenomena for the following reason. If perception of 90° is variable, for instance, this would explain why movement at 90° is variable; the person is unsure of when they are moving correctly or incorrectly and is hence slow to perform corrections to maintain the required steady state. When the person drifts to a phase that is clearly perceived (like 0°), they then recognize that they are producing an inappropriate phase and act to make a correction. The net result is that the mean relative phase will drift backward and forward between the target phase and a more stable phase, increasing the measured movement variability.

In a number of studies, participants have made judgments of mean relative phase and phase variability, judging oscillations presented either visually (Bingham 2004b; Bingham et al. 1999, 2000; Zaal et al. 2000) or proprioceptively (Wilson et al. 2003). Judgments of phase variability varied as an asymmetric inverted U-shaped function of mean relative phase (as did the variability of the judgments of mean phase and phase variability). Non-0° phase relations were judged to be intrinsically more variable than 0°, maximally so at 90°, with 180° judged to be intermediate between these extremes. These results were interpreted to suggest one reason for poor within-trial movement stability at 90° in movement studies is because participants are unable to detect deviations from this intended mean phase, and hence unable to perform corrections quickly. It was also found that increases in frequency made non-0° phase relations look more variable, and added phase variability was only readily distinguished at 0°. In other words, many of the characteristics of human movement coordination are apparent in human perception of both their own or another's coordinated movements.

This match between the perceptual and movement results suggests a role for perception in the production of the coordination phenomena. The immediate objection to this interpretation is that the perceptual and movement measures are not the same. The former entails (between-trial) judgment variability and the latter (within-trial) movement variability. The goal of the current study is to explore a new methodology that explicitly produces directly comparable movement measures of between-trial (perceptual) and within-trial (movement) variability within the same perception/action task and person. This will enable direct comparison of these measures for the first time.

To be clear, the within-trial measure of movement variability is the traditional measure of movement stability. The between-trial measure of variability in mean movement state for each trial is a measure of the relative ability to perceive the intended target phase. If the intended movement target were well known and perceivable, but movement was just unstable at that target, then between-trial variability would be low despite high within-trial variability. They would simply vary around the clearly specified intended target. For example, take the case of trying to balance a broomstick on your finger—the target state ("upright") is never in question, but the execution of a given movement will be noisy. Between-trial variability for successful balancing acts will be low (success means getting it upright) but the within-trial variability would be high (as the broom moves around the upright mean state). On the other hand, if the instability of movement during a trial were related to the inability to detect and identify the target, then the two types of variability should be comparable in terms of both relative amount (qualitative patterns of variation) and absolute amount (quantitative values).

We are not arguing that the movement phenomena simply reduce to perceptual effects, as suggested by Mechsner et al. (2001) and Meschner and Knoblich (2004). For instance, Temprado et al. (2003) found that non-isodirectional movement (180°) was less stable than isodirectional movement (0°), even if the former entailed using homologous muscle groups. However, movements that were comparable directionally were always stabilized when using homologous muscles. While all movement indeed entails perception, movement is still of actual oscillating limbs that have very specific dynamic properties. Human rhythmic movement of a single limb exhibits the characteristics of a non-linear autonomous oscillator (Kay et al. 1987, 1991), and the coordination phenomena must emerge from the coupling of two such oscillators. The research described above simply suggests that the coupling is well described as perceptual (informational) and another goal of this study is to explicitly relate perceptual manipulations to movement consequences.

The visual and proprioceptive studies described were judgment studies. In the study of perception/action systems, action measures are preferable (Pagano and Bingham 1998). Liao and Jagacinski (2000) manipulated the relationship between the control (movement) and input (perceptual) signals in a movement-coordination task. Participants controlled (with a joystick) either the position or velocity of a dot on the screen, and had to either pursue another dot at a mean relative phase of 0° or compensate for the movement of their dot by moving at 180° to it. In the pursuit/position control condition participants had to move at 0° to their dot to produce 0° between the dots on the screen; in the pursuit/velocity condition participants had to move at 90° to their dot to produce 0° between the dots on the screen; and in the compensatory condition participants had to move at 180° to their dot to keep it in a constant location. Performance was quite good in the pursuit tasks—participants were able to move at both 0° and 90° relative to the dots to produce 0° between the dots on the screen. They were also able to move at 180° relative to their dot in the compensatory condition, but only when controlling position. In other words, participants were able to use the stable control information (the 0° relationship between the dots on the screen) to coordinate and control movements that were at a non-0° phase relation to the dot being tracked.

Other studies have investigated the effect of manipulating perceptual information on movement coordination. Bogaerts et al. (2003) showed that 180° movements were stabilized when visual feedback about the movement was altered to show 0°. Byblow et al. (1999) stabilized both symmetric and asymmetric circular movements with linear feedback that was directionally compatible with the movements. These studies demonstrate that a stably perceived control signal can be used to stabilize movements that would otherwise be unstable. Movement stability in each case was a function of perceptual stability.

The overall goal of the current study was to more explicitly investigate the role of perception in the production of coordinated rhythmic movements. Participants moved a joystick to control a dot on a screen. Their task was to track a computer-controlled oscillating dot to produce one of three (visually defined) mean relative phases while we independently manipulated the phase relationship between the joystick and the dot being tracked. We predicted that movement would be maximally variable for visual phase relations other than 0°, but that a 0° visual target would help stabilize movements that were at a non-0° phase relation to the dot being tracked. The variability judgment experiments described above found that phase variability was resolved best at 0°. This suggests that when the task is to produce 0° on the screen, people may be able to use this better resolution to detect when their movements are variable, even when the movement is actually at a non-0° phase relation to the dot being tracked.

Experiment 1

Materials and methods

Participants

Three groups of eight students at Indiana University participated. They were aged 18–39. All were free of motor disabilities, and were paid $10 for participation. Each session lasted about 1 h. The experimental procedures were approved by Indiana University's Committee for the Protection of Human Subjects and performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Design

Refer to Fig. 1. Two phase relations were independently manipulated within subject—the target visual (unimodal) phase relation between the two dots (0°, 90° or 180°), and the visual-proprioceptive (cross-modal) phase relation between the joystick and the computer controlled dot (0°, 90° or 180°). This allowed us to create five phase conditions: three consistent (0:0, 90:90 and 180:180) and two inconsistent (0° visual target; 0:90 and 0:180). The labeling convention is target visual phase:cross-modal phase. Frequency was manipulated between groups of participants, and was set to 1, 1.5 or 2 Hz.

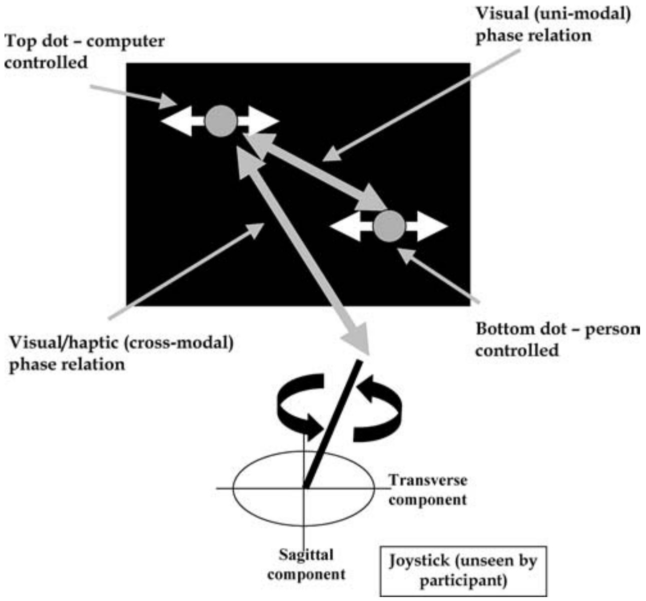


Fig. 1 Schematic diagram of experimental setup

Procedure

Refer to Fig. 1. Participants sat in front of a Dell Optiplex GX110 PC, which was connected to a Microsoft force-feedback joystick. The force feedback was disabled, which minimized the resistance of the joystick and eliminated any spring or viscosity. The joystick sat in a box with the open side facing the participants, who sat so that they could comfortably use the joystick but not see it. The computer presented a display of two dots, white on a black background, one above the other. Displays were generated using ExpLib, a free C++/Direct X based suite (http://people.umass.edu/alc/explib/start.htm). The screen refresh rate was 85 Hz, and each trial was 60 s long. Each dot was 40×40 pixels (approximately 15 mm in diameter), traversed a path 300 pixels across (approximately 115 mm) and was viewed from approximately 630 mm.

The top dot was under the control of the computer, and it oscillated from side to side at one of the three frequencies. The bottom dot was controlled by the participant, using the joystick. This dot could be made to move from side to side by moving the joystick in a smooth, circular movement. The joystick had a plastic cuff at its base, which participants could use to ride the joystick frame. This ensured movements were full circles, and smooth. The movement could be either clockwise or counter-clockwise, but participants were instructed not to change direction within a trial. The computer recorded the *x* and *y* coordinates of the joystick and computed the angle ($\tan^{-1}(y/x)$) at each time step. This angle is the measure of an oscillator's location within a cycle, and was then used to specify the location of the bottom dot within its side-to-side cycle. Using the joystick's location to specify the dot's location enabled us to manipulate the cross-modal phase relation directly, as described below. (Using a circular movement rather than a linear movement was required to implement this manipulation; A.D. Wilson et al., submitted, for an investigation of the consequences of this configuration.)

Participants were instructed to produce one of three visual target phases between the two dots for as much of each 60-s trial as possible. Trials were blocked in expected order of difficulty. Participants were first instructed to produce 0°. There were three practice trials (one each of 0:0, 0:180 and 0:90). For the next three trials the cross-modal phase relation was set to 0° (0:0). This was followed by a block of six trials with the cross-modal phase relation set to 90° (0:90). This was achieved by adding 90° to the phase computed from the joystick's position, and meant that in order to produce the 0° visual target the participant had to set the cross-modal phase relation to 90°. The next six trials set the cross-modal relation to 180° (0:180), followed by three more 0:0 trials (the two 0:0 blocks were combined for all analyses). Finally, there were two blocks of four trials in which the instructions were to produce either 180° or 90° visually. The cross-modal phase relation was not altered, and so to produce 90°, for instance, the participant had to set the cross-modal phase relation to 90°. Hence, these trials are designated 90:90 and 180:180.

Data processing

Only the first four trials from 0:0, 0:90 and 0:180 were analyzed, to keep the number of trials the same as 90:90 and 180:180. Each dot's position time series was filtered using a low-pass Butterworth filter with a cut-off frequency of 10 Hz, differentiated and filtered again to produce velocity signals. The continuous relative phase between the two dots was computed as the difference between the arctangent of each dot's velocity over position.

Relative phase is a circular variable, i.e. its distribution of possible values lies on a circle. This creates a problem for calculating basic descriptive variables. For instance, taking the "normal" mean of 1 and 359° yields 180°, which is a vector pointing in the direction opposite to the actual mean direction, namely 0° (or 360°). Also, any two angles separated by 360° are the same position on that circle, and they hence indicate the same relative phase.

Batschelet (1981), Fisher (1993), Mardia (1972) and Jammalamadaka and SenGupta (2001) provide trigonometric methods for computing circular equivalents of the mean and standard deviation, and for performing basic statistical tests. The mean vector θ is the direction of the resultant vector obtained by summing the relative phase vectors from each time step. The normalized length of this vector (mean vector length; MVL) is the measure of within-trial stability (subsequently denoted $\mathrm{MVL_W}$). We computed the mean direction of the mean vectors for the trials in each Frequency×Phase condition, and the normalized length of this vector (mean direction MVL; subsequently denoted $\mathrm{MVL_B}$) is the measure of between-trial stability. The MVL statistic (Eq. 1.3.8; Batschelet 1981) ranges from 0 (indicating minimum stability, i.e. a uniform circular distribution) to 1 (indicating maximum stability, i.e., no variability). If MVL is not significantly different from 0 (using the Rayleigh test for randomness; Batschelet 1981) the mean vector for that data set is uninterpretable. (Note that the computation of the $\mathrm{MVL_B}$ in the following "Results" sections will exclude any non-significant θ values for this reason.)

Results and discussion

Mean performance

Refer to Fig. 2. Mean performance was close to target in all phase conditions, although slightly low with a non-0° target visual phase. This reflects the fact that when participants were not on-target it was because they had slipped into a more stable mode, generally 0°. On average, however, participants were able to perform the consistent task. The 0° visual target condition's performance was closest to target at 1.5 Hz (which turned out to be a comfortable speed to do this task) and slightly U-shaped in the other frequencies. This suggests a 0° visual target phase was more difficult to maintain in the 0:90 condition than the 0:0 or 0:180 cases.

No circular multi-factor repeated measures ANOVA is available. This meant we were unable to directly analyze the directional data. Instead we concatenated the relative phase time series for the first four trials of each Frequency×Phase condition into one single vector

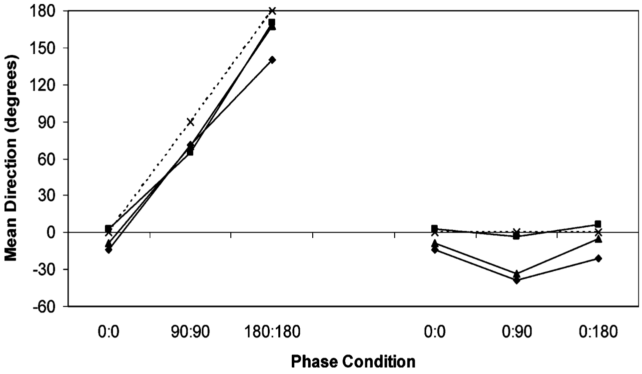


Fig. 2 Mean direction for Experiment 1 in degrees. *Filled diamond* = 1 Hz, *filled square* = 1.5 Hz, *filled triangle* = 2 Hz. *Dotted line* target (visual) phase. Confidence intervals not shown, as they are too small to be clear

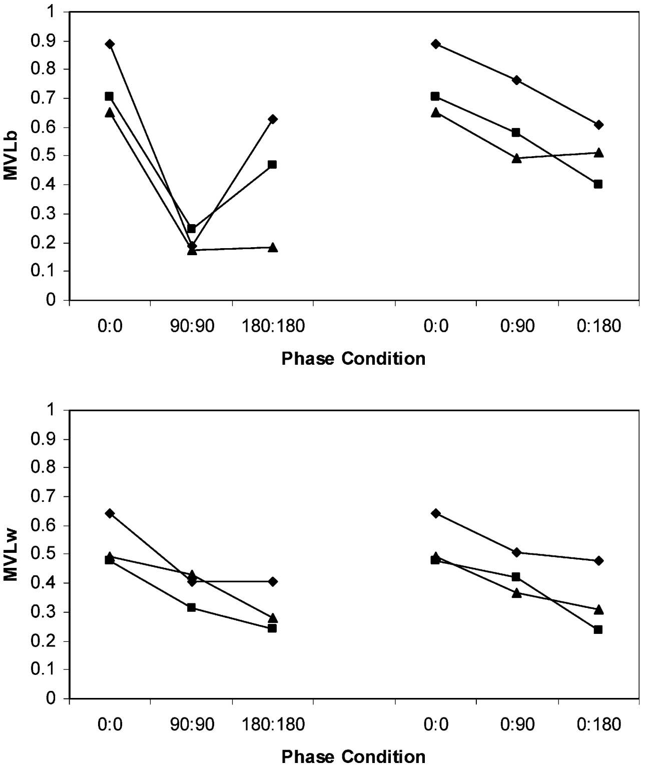


Fig. 3 The *top panel* shows between-trial stability, measured by mean direction MVL. The *bottom panel* shows within-trial stability, measured by mean MVL. *Filled diamond* = 1 Hz, *filled square* = 1.5 Hz, *filled triangle* = 2 Hz

for each participant. For each vector, we computed θ and its associated confidence interval. This was computed using a circular resampling bootstrapping algorithm (Algorithms 1–4, Section 8.3.5, Fisher 1993) implemented in MATLAB and computed using Indiana University's Research Computing cluster. Finally, we computed the circular mean of the estimates of θ for each subject, resulting in a single estimated θ for each Frequency×Phase condition. The confidence intervals were very small because of the large volume of data. All values of θ were therefore significantly different from each other.

Within- and between-trial stability

As described in the "Introduction", evidence for a perceptual component to the movement phenomena comes from establishing a relationship between the between (perceptual) and within (movement) stability.[1]

Each trial produced a mean direction θ and an MVL_W. We averaged the MVL_W values for each trial to obtain a mean within-trial MVL (Fig. 3). Within each Frequency×Phase condition, we computed a circular mean and MVL of all the legitimate mean directions. This mean direction MVL (MVL_B) is a measure of the mean between-trial stability (Fig. 3).

Refer to Fig. 3, top. As noted, no circular multifactor repeated measures ANOVA is available, which meant no direct analysis of $MVL_B$was possible (each data point on the graph is a single value). The confidence interval procedure described above also yields estimates of MVL, but again the intervals are so small that all estimates are significantly different from all the others. However, Fig. 3 clearly shows the predicted qualitative pattern—a U-shaped relationship between stability and phase in the consistent conditions and an increase in between-trial stability in the 0° visual target conditions. This increase does not bring 0:90 and 0:180 up to the level of 0:0—the stabilization seems incomplete and the non-0° cross-modal relationship was having an effect in proportion to its magnitude, rather than as the expected U-shaped function of phase. In other words, it was behaving less like a phase relationship and more like an inconsistency effect (i.e. scaling with the magnitude of the difference).

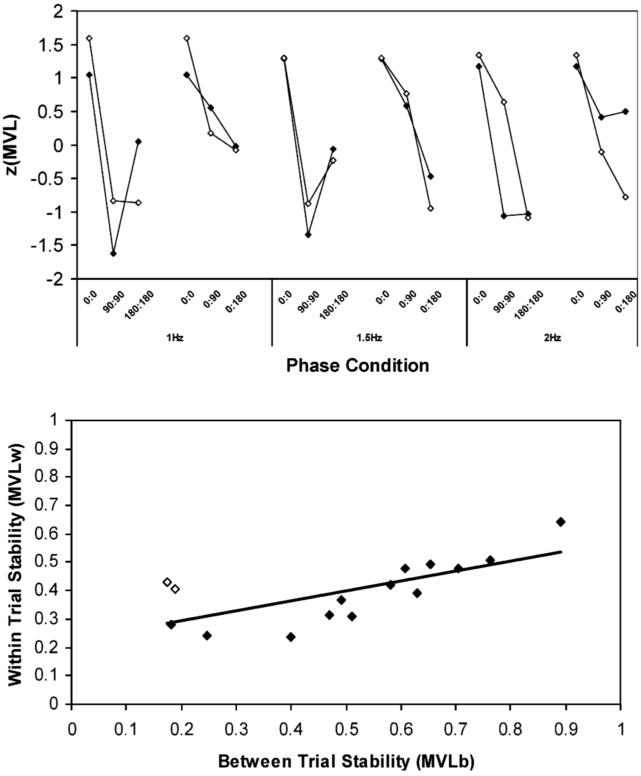


Fig. 4 The *top panel* compares the *z*-transformed within (*open diamond*) and between (*filled diamond*) trial stability measures. The *bottom panel* plots the regression of within vs between trial stability measures. The *solid line* is the regression excluding the outliers (*open diamond*)

---

[1] Having to rely on circular statistics such as MVL means that the discussion of results will be reversed from what is usual in the movement coordination literature. Instead of "variability" (which increases with standard deviation) we will instead use "stability", which increases with MVL. This should be kept in mind when comparing this data with previous results. Transforming the data by ln(1/MVL) rescales MVL to more closely resemble a standard deviation, however, we wished to minimize the number of data transformations we performed

Refer to Fig. 3, bottom. We performed two separate repeated measures ANOVAs on the MVL$_W$ data. First, we analyzed the MVL$_W$ data from the consistent conditions (0:0, 90:90, 180:180; refer to the left hand side of Fig. 3, bottom). There was a main effect of phase condition ($F_{(2,186)} = 29.4$, $P < 0.01$) and of frequency ($F_{(2,93)} = 4.7$, $P < 0.05$) as well as an interaction between phase condition and frequency ($F_{(4,186)} = 3.119$, $P < 0.05$). Pairwise comparisons indicated that the main effect of phase condition was due to within-trial stability at 0:0 being higher than the other two conditions ($P < 0.01$), while the main effect of frequency was due to stability being higher at 1 Hz ($P < 0.01$). On average, 90:90 and 180:180 were not different from each other, indicating there was no U-shaped function of phase in the stability data. This was probably because stability was higher than expected in the 90:90 case, and was addressed using the regression analysis shown in Figs. 4 and 5 (see below for details). The interaction was because of the higher than expected stability at 2 Hz, 90:90, which inverted the shape of the function as compared to the other two frequencies. This point is a distinct outlier, however, and is accounted for in the regression analysis detailed below (and in Fig. 5).

Second, we analyzed the MVL$_W$ data from the 0° visual target conditions (0:0, 0:90, 0:180; refer to the right hand side of Fig. 3, bottom). The analysis revealed a main effect of phase condition ($F_{(2,186)} = 28.4$, $P < 0.01$). Pairwise comparisons showed that the main effect of phase condition was due to within-trial stability at 0:0 being higher than the other two conditions and 0:90 being more stable than 0:180 (both P values < 0.01). As in the between-trial data, stability decreased linearly with increase in the cross-modal phase relation, and not in a U-shape. There was no interaction between phase condition and frequency ($P > 0.1$). The 0° visual target helped stabilize the movement. However, the main effect of phase reveals that this within-trial stabilization was incomplete—stability was not increased to the level of 0:0. The (non-0°) cross-modal phase relationship was still having an effect (albeit linear) on movement stability.

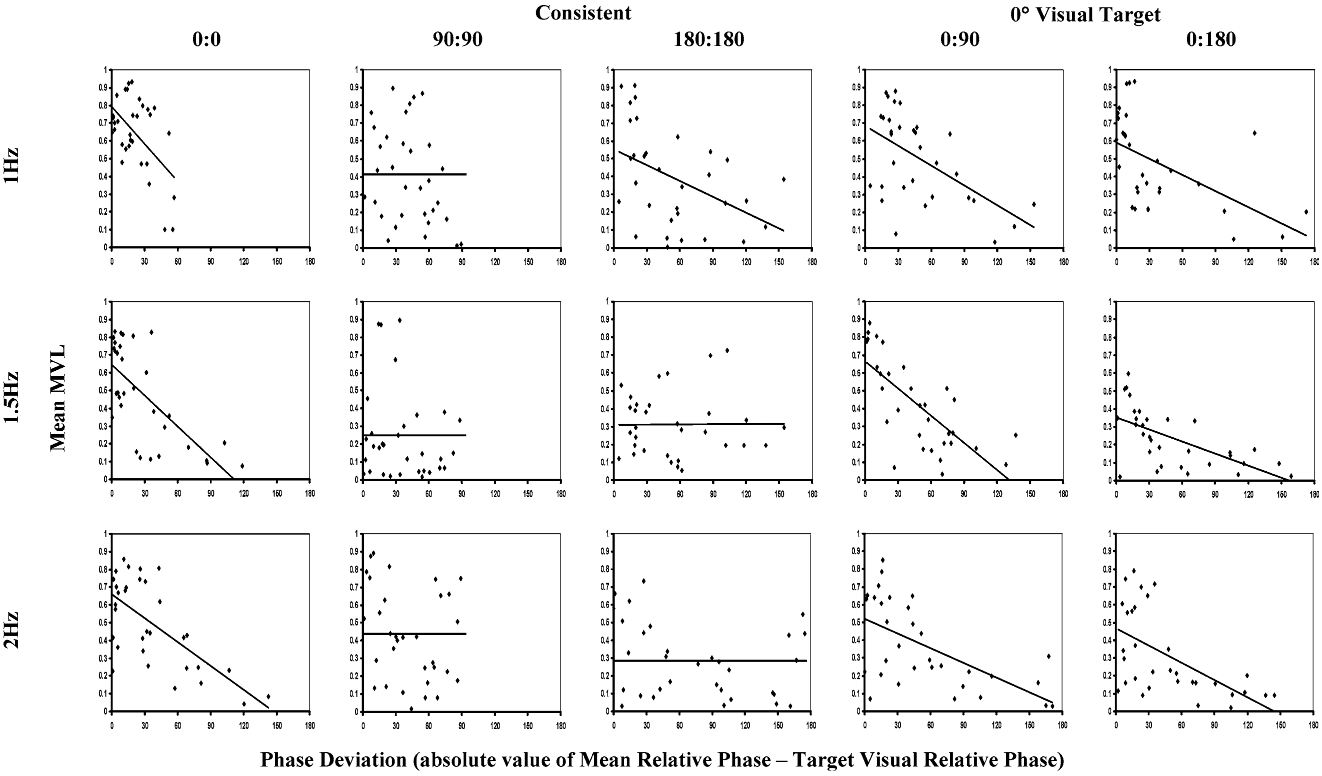


Fig. 5 Scatterplots for each frequency (*rows*) and phase (*columns*) condition, plotting absolute phase deviation vs mean within trial stability. Non-significant regression lines have been set to slope 0, intercept at the mean MVL for that condition

Because we were unable to perform ANOVAs on the between-trial stability data, we regressed it on the within-trial stability data on which we were able to do ANOVA. A correlation between the between-trial stability (Fig. 3, top) and the within-trial stability (Fig. 3, bottom) would support the above interpretation of Fig. 3, top. We looked for this relationship here.

We plotted the MVLs two different ways. Figure 4, top, shows the z-transformed data sorted by frequency and phase condition (the z-transform takes the difference in the spread of the two data sets into consideration, making the data more directly comparable. If the data sets were identical relative to their spread, the lines would be on top of each other). The patterns of within- and between-trial stability are indeed very similar, with several notable exceptions (2 Hz, 90:90, for instance). The fact that the two stability measures are so comparable in scale is significant evidence in support of the role of perception in producing the movement stability data. To quantify this match we regressed the between- and within-trial MVLs (Fig. 4, bottom) which yielded $R^2 = 0.49$. The fit is not particularly impressive, however, examination of the scatter plot revealed two noticeable outliers (1 Hz 90:90 and 2 Hz 90:90; the unfilled diamonds in Fig. 4, bottom). In these conditions, participants had a marked tendency across trials to either:

- perform close to the target phase with resulting low within-trial stability, or
- be unable to maintain the target phase and slip into a more stable mode, with resulting high within-trial stability.

The latter was more common, elevating the average within-trial stability, but lowering the between-trial stability.[2] A regression conducted without these two data points yielded an $R^2 = 0.83$. So, allowing for the two exceptions, there is a clear relationship between the between- and within-trial stability measures.

The cause of the outliers hinted at further interesting structure in the stability data. An important aspect of this task was that participants attempted to generate the visual target phase relation but only succeeded to varying degrees. Not all 90:90 trials, for instance, produced a mean direction of 90°, and the MVL_W for a given trial was related to the mean direction for that trial. If a participant was able to maintain a mean direction of 90° on one trial but not the next, perhaps producing a mean direction of 0°, then the mean stability would be low for the first trial and high for the second, and medium on average. This average would then not be a good estimate of the within-trial stability for movements at the target phase. Additionally, between-trial stability would be low and decorrelated from the within-trial stability.

To address this, we regressed the mean within-trial stability (MVL_W) against the absolute mean relative phase deviation for each phase condition. Absolute phase deviation is computed by subtracting the target phase from the mean direction for a given trial, and taking the absolute value of the result. This places the target phase on the *y*-axis of the plots on Fig. 5. The slope of the regression line through this transformed data is an estimate of the between-trial stability. It is improbable that mean performance would cluster around more than one part of the space, and hence any spread will be more evenly distributed. If mean performance is spread out across the space of possible relative phases, then the slope will be low because of the constraint of the size of the space. The intercept of the regression line is an improved estimate of the within-trial stability at the target visual phase. If the regression line is significant, this suggests that stability was indeed varying as a function of performed phase and that a mean of all the variability would be reduced by trials in which mean performance deviated from the target. The intercept is the predicted level of within-trial stability at the target phase, which is at the *y*-axis after the transformation.

Refer to Fig. 5. Each graph is a scatter plot of MVL_W vs the absolute phase deviation for a given Frequency×Phase condition. Displaying the data this way makes several general patterns quite clear. The data is indeed significantly spread out, and MVL_W is negatively related to deviation from target visual phase (at least in the 0° visual target conditions). As frequency increases, both the slope and the intercept tend to go down; both within- and between-trial stability decreases. 0:0 is clearly more stable than the other conditions; the intercept is higher and the data is much less scattered.

Compare the consistent (90:90 and 180:180) conditions to the inconsistent, 0° visual target conditions (0:90 and 0:180). The stabilizing effect of the 0° visual target is clearly illustrated by the fact that all the regression lines in these latter conditions had significant slopes ($P < 0.05$). When participants were successfully moving to create a mean relative phase of 0° between the two dots, their movements were more stable, even if this entailed moving with a 90° or 180° cross-modal phase relationship. The intercepts are generally lower than those for 0:0, i.e., the movement was not stabilized to the same level as 0:0 trials. This shows again that the cross-modal relationship was still having an effect.

In the consistent plots, 0 on the phase deviation axis corresponds to a mean direction of 90° or 180°, respectively. The lack of significant slopes in several of these conditions demonstrates that correctly performing the target visual phase did not improve movement stability (unsurprising, given that the target visual phases, 90 and 180°, are both less stable). It also indicates that performing closer on average to 0° instead of 90° or 180° did not consistently stabilize movement. Low within-trial stability while moving at 0° on average suggests participants trying to comply with the instructions; they can see they are moving incorrectly and trying (unsuccessfully) to correct. The net result is low between-trial stability and slightly elevated within-trial stability.

The results of the regression are summarized in Fig. 6. The slopes (between-trial stability) and intercepts (within-trial stability) were *z*-transformed and again show strong covariation (compare this to Fig. 4, top). Again the scale of the two stability measures was very similar. Regression of the slopes and intercepts yielded an $R^2 = 0.83$, the same as the regression that excluded the outliers. These points were no longer outliers in the scatterplot. This confirmed that the relationship between MVL_W and mean direction, which the regression analysis was designed to account for, was indeed the cause of the outliers.

Experiment 1 replicated several basic movement coordination phenomena, lending support to this methodology. First, most participants were able to do

---

[2] This effect can clearly be seen in Fig. 2—the predicted U-shaped function is pronounced in the between-trial data but absent in the within-trial data. In the 90:90 condition, participants spent time at more stable relative phases, elevating the within-trial stability to be similar to that at 180:180, and lowering the between-trial stability

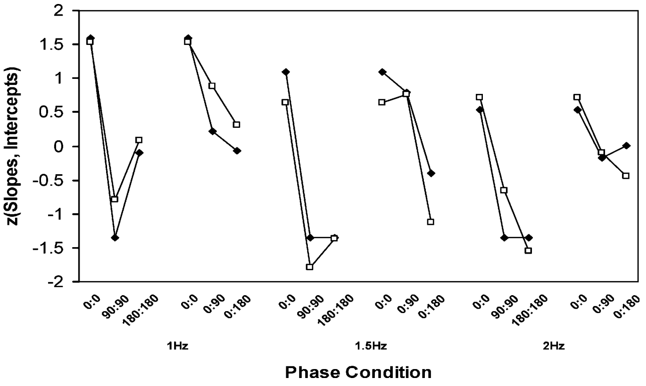


Fig. 6 *z*-Transformed slopes (between-trial stability; *filled diamond*) and intercepts (within-trial stability; *open square*) from analysis depicted in Fig. 5

the task on average (Fig. 2). Second, performance in the consistent conditions was qualitatively comparable to the analogous movement or judgment study conditions typically studied (Fig. 3; Bingham et al. 2000; Bingham 2004b; Wilson et al. 2003; Zaal et al. 2000). Third, a clear relationship existed between within- and between-trial stability (Figs. 4, 5 and 6), supporting the hypothesized role of perception in producing the movement coordination results. As noted, the matching scale of the two measures is evidence supporting the hypothesis that the differential movement stability is being caused by the differential perceptual stability.

The main new result is that the 0° visual target stabilized movements that were at a non-0° phase relationship to the dot being tracked. Two questions remain: why were the movements not stabilized all the way to the same level as 0:0, and why was the effect of the cross-modal phase relationship linear? The linearity suggests the cross-modal relationship was having an effect in proportion to the magnitude of the inconsistency. Experiment 2 replicated the five conditions from Experiment 1 and added two new conditions—90:0 and 180:0—to test this magnitude hypothesis directly.

Experiment 2

Materials and methods

Participants

Eight different students at Indiana University participated. They were aged 18–24. All were free of motor disabilities, and were paid $10 for participation. Each session lasted about 45 min.

Procedure

We replicated the five phase conditions from Experiment 1, and added two additional inconsistent, non-0° visual target conditions, 90:0 and 180:0. Four trials of each of the seven conditions were presented to all subjects, blocked, in the following order—0:0, 90:90, 180:180, 0:90, 90:0, 0:180, 180:0. All trials were at 1.5 Hz. The procedure was otherwise identical to that of Experiment 1.

Results and discussion

Mean performance

Refer to Fig. 7, which shows participants' mean performance (with the target phase for comparison). The first five conditions replicate the results from Experiment 1, in which mean performance was close to the target phase. Mean performance was poor, however, in the new inconsistent conditions 90:0 and 180:0. The non-0° visual target impaired performance and the 0° cross-modal phase relationship had no stabilizing effect.

Within- and between-trial stability

Refer to Fig. 8, and compare these data with the 1.5 Hz data in Fig. 3. Figure 8,top shows MVL_B, and the qualitative pattern from Experiment 1 remains—stability is a U-shaped function of phase condition in the consistent conditions and a linear function of phase condition in the 0° visual target conditions. The two new inconsistent conditions show low, similar stability. The inconsistency seems to have combined with the non-0° visual target to make these trials especially difficult.

We performed three repeated measures ANOVAs on the MVL_W data. First, we analyzed the data from the consistent conditions (0:0, 90:90, and 180:180; refer to the left hand side of Fig. 8, bottom). The analysis revealed a main effect of phase condition ($F_{(2,62)} = 24.4$, $P < 0.01$). Pairwise comparisons showed that within-trial stability at 0:0 was higher than the other two conditions ($P < 0.01$), replicating Experiment 1.

Second, we analyzed MVL_W from the 0° visual target conditions (0:0, 0:90 and 0:180; refer to the middle of Fig. 8, bottom). The analysis revealed a main effect of

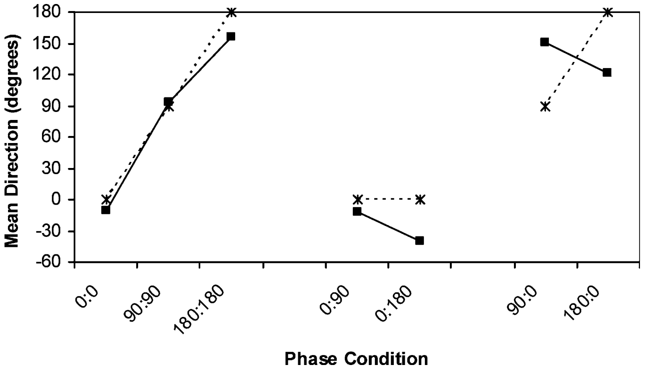


Fig. 7 Mean direction for Experiment 2 in degrees. = 1.5 Hz. *Dotted line* target (visual) phase

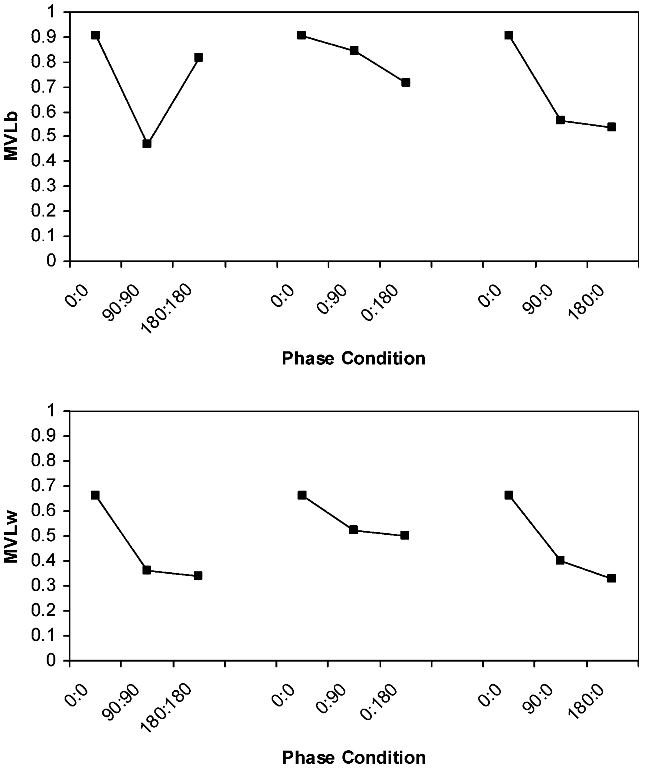


Fig. 8 The *top panel* shows between-trial stability, measured by mean direction MVL. The *bottom panel* shows within-trial stability, measured by mean MVL. =1.5 Hz

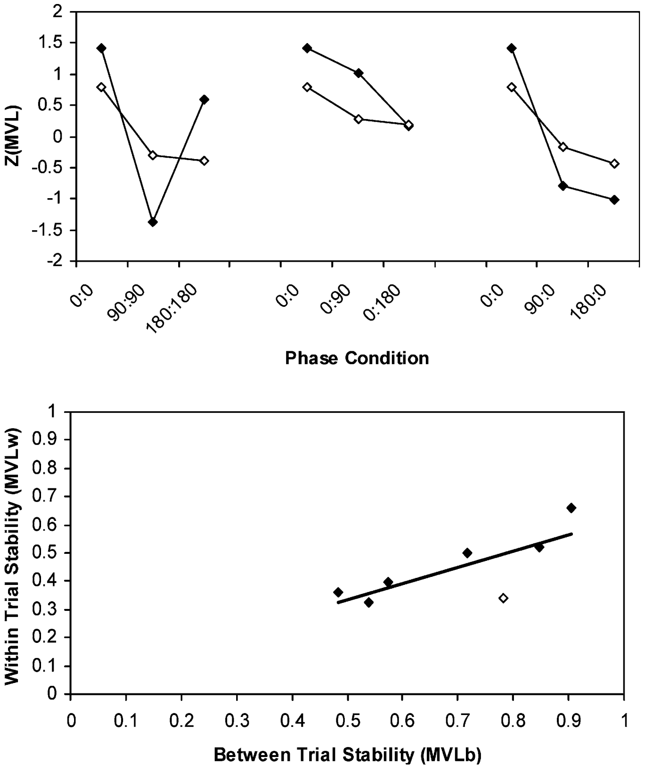


Fig. 9 The *top panel* compares the *z*-transformed within (*open diamond*) and between (*filled diamond*) trial stability measures. The *bottom panel* plots the regression of within vs between-trial stability measures. The *solid line* is the regression excluding the outlier (*open diamond*)

phase condition ($F_{(2,62)} = 7.2$, $P < 0.01$). Pairwise comparisons showed that within-trial stability at 0:0 was higher than the other two conditions ($P < 0.05$), replicating Experiment 1.

Third, we analyzed $\mathrm{MVL_W}$ from the inconsistent conditions (0:90, 0:180, 90:0 and 180:0; refer to the right hand side of Fig. 8, bottom). The analysis revealed a main effect of phase ($F_{(3,93)} = 5.8$, $P < 0.01$). Pairwise comparisons showed that the 0° visual target conditions were more stable ($P < 0.05$) than the non-0° visual target conditions (except 0:180 vs. 90:0, which failed to reach significance; $P = 0.07$). The 0° cross-modal relationship had no positive effect on movement stability; an ANOVA on the non-0° visual target conditions (90:90, 180:180, 90:0 and 180:0) revealed they did not differ in their stability ($F_{(3,93)} = 0.67$, $P = 0.57$).

To quantify the relationship between within- and between-trial movement stability, we again plotted the MVL data two different ways. Figure 9, top, shows the *z*-transformed data. The patterns are very similar, with the exception of 180:180 (again, note the matching scale). To quantify this match, we regressed these two measures, which yielded $R^2 = 0.57$ (although the fit improved to 0.89 with the removal of 180:180; refer to Fig. 9, bottom).

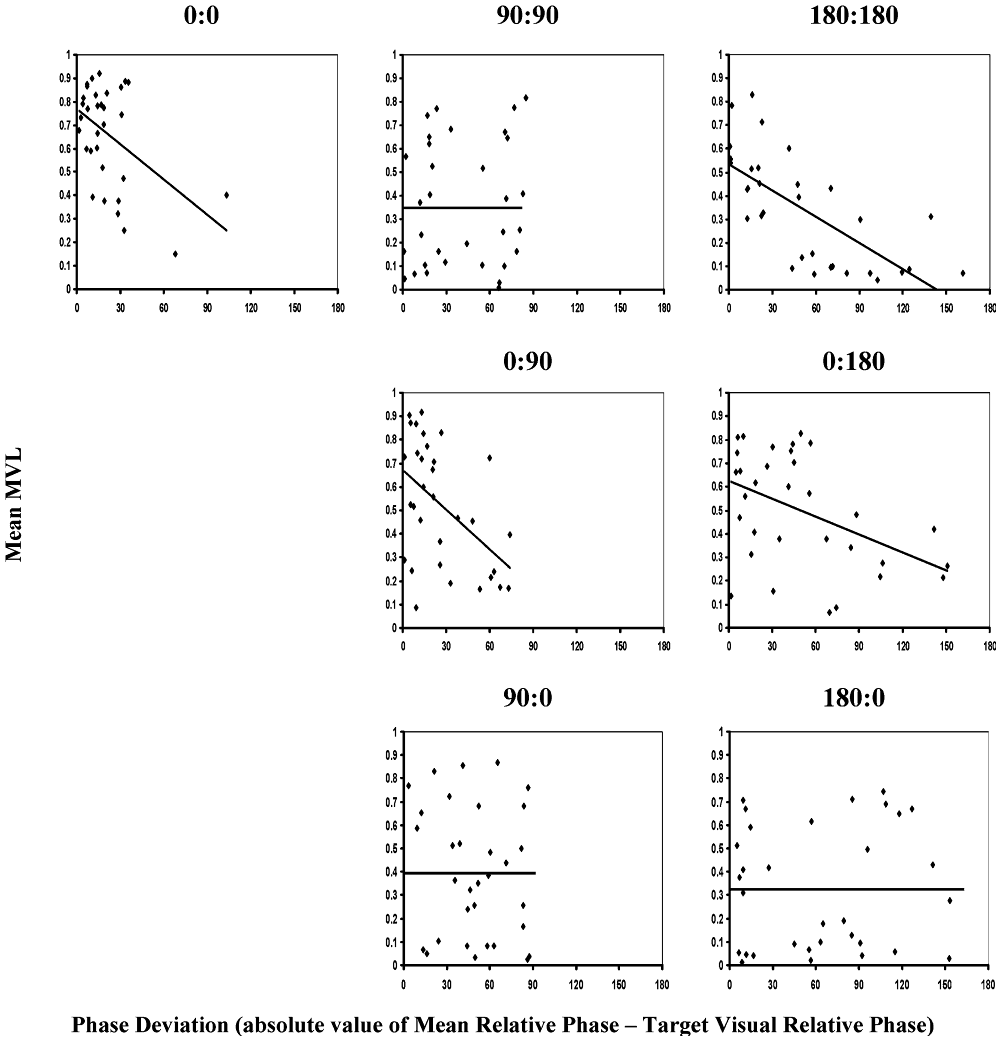
We repeated the within-trial stability versus absolute phase deviation analysis (refer to Fig. 10). First, examine the top five panels and compare them to the same conditions from Experiment 1 (Fig. 5, middle row). The overall pattern is replicated, although the regression for 180:180 is significant this time, confirming that the estimate of within-trial stability in Fig. 9, top, is indeed low. Neither regression line for the two new inconsistent conditions (90:0 and 180:0) was significant. The results of the regression are summarized in Fig. 11. The slopes and intercepts were *z*-transformed and again show strong covariation (compare this to Fig. 9, top, and once more note the matching scale). Regression of the slopes and intercepts yielded an $R^2 = 0.83$ (again very similar to the original within- vs between-stability regression).

Experiment 2 replicated the results from Experiment 1 and extended the results to two new inconsistent conditions. A 0° visual target stabilized performance, but a 0° cross-modal phase relationship did not—the visual target phase dictated performance. Mean stability when the visual target was 90° and 180° was again elevated due to time spent at more stable phases, and again this effect was more pronounced at 90°, causing stability in the 90° and 180° conditions to be similar.

General discussion

Human rhythmic movement coordination exhibits a characteristic structure that persists across a wide varietyof couplings (both within- and between-person).

Fig. 10 Scatterplots for each phase condition, plotting absolute phase deviation vs. mean within trial stability. Non-significant regression lines have been set to slope 0, intercept at the mean MVL for that condition



Previous research has strongly suggested the coupling is, in general, perceptual, or informational (e.g., Bingham et al. 2000; Wilson et al. 2003). By this interpretation, 0° is a stable movement coordination because it is perceptually very salient. Common movement is a powerful perceptual grouping principle (e.g. Johansson 1950). People can readily and accurately detect deviation from a mean relative phase of 0°, which enables them to quickly correct their movements for errors. The importance of this fact in creating the movement phenomena has been inferential up to this point—the perceptual and movement studies have always been separate. The current methodology was designed to explicitly manipulate both the information and the movement requirements within the same task to ask whether the perception–action system can use the stability of perception at 0° to coordinate movements at non-0° mean relative phases. This method also allows for direct, within-person comparisons of perceptual and movement stability.

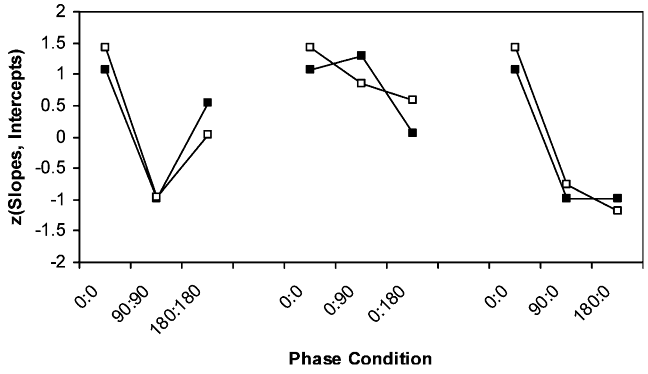


Fig. 11 *z*-Transformed slopes (between-trial stability;) and intercepts (within-trial stability;) from analysis depicted in Fig. 10

The results demonstrated a clear role of perceptual information in determining the characteristic movement phenomena. When the target visual phase was 0°, participants were able to improve the stability of their movements that were at 90° or 180° to the tracking target. Both within- and between-trial stability improved with the 0° visual target. In other words, it is not moving at a non-0° phase relation that is difficult per se, but it is made difficult (or easy) by the ability to resolve the information used to coordinate that movement. If the information is well resolved (i.e., at 0°, as in 0:90 and 0:180), the movement is stable; if it is poorly resolved (at non-0° values, as in 90:90 and 180:180) the movement is less stable.

Visual information did not completely determine performance—non-0° movements were not stabilized to the same level as 0° movements. Rhythmic movement coordination is intrinsically a perception–action system, and the states of the limbs must be taken into account (e.g., Byblow et al. 1999; Li et al. 2004; Serrien et al. 2001; Temprado et al. 2003), as well as the perception of those states. With that caveat, however, it is clear that in rhythmic movement coordination the coupling is informational and largely responsible for the stability of the coordination (see also Bogaerts et al. 2003).

The dominance of the visual phase relation is not surprising, given that the task was defined in terms of the visually defined phase relationship. If the task is defined purely cross-modally (i.e. participants can only see the dot to be tracked with the joystick) mean stability is qualitatively similar to the current results, but lower overall. 0° is relatively stable, while 90 and 180° are similar to each other. The cross-modal phase relation seems to be more difficult to perform but equally so across phase conditions (see Wilson et al. submitted, for details and an expanded analysis of this "visual dominance" effect).

This method presents some unique difficulties for data analysis and interpretation. The fact that participants were producing movements created a relationship between mean performance and mean within-trial stability that obscured the relationship between the within- and between-trial stability—however, the regression analysis clearly accounts for this structure. The circular nature of relative phase also constrains the types of analyses that are possible, specifically on mean performance and between-trial stability. However, any correlation between the analyzable within-trial stability and the between-trial stability suggests that the formal results from the within-trial data are indeed generalizable. Regarding interpretation, the coupling here is between the participant and a display, rather than within a person. This emphasizes the perceptual nature of the coupling, but does not rule out the possibility that the movement coordination phenomena seen within a person may be mediated more by nervous system interactions than by perception. Specifically, it has been proposed that the difficulties in producing non-0° phase relations in within-person coordination tasks is due to neural cross-talk (Cattaert et al. 1999), or some kind of interference between efference copies of motor commands (Beek et al. 2002). However, participants in Wilson et al. (2003) still judged 90° to be maximally variable even though they successfully moved at that relative phase by tracking a manipulandum. This mismatch ruled out motor commands (which were successfully producing the coordination) as the basis of the judgments (which were not reflecting the success of the movement). Instead, judgments were based on the perceived state of the fingers. These results indicate that perception is the right level of analysis to consider the coupling, which is the locus of the structure in human rhythmic movement coordination. Of course, the exact implementation of the coupling will certainly involve the nervous system; however, interference generated by the nervous system is unable to account for the entire scope of the movement coordination literature, and it seems plausible and parsimonious to suggest that the phenomena emerge from perception, the common denominator.

Visual information about relative phase was used to stabilize coordinated movements. Movements at 0° were generally more stable than at non-0° values (Figs. 5, 10), unless the target phase was not 0°, in which case moving at 0° was detected quickly as being inappropriate and brief, unstable correct movements were generated. The current study demonstrates that perception is a key player in determining the stability of a coordinated movement; future extensions of this paradigm will investigate its role in bimanual coordination. Another issue the current study leaves unresolved is the precise nature of the perceptual information. Bingham (2004a, b) proposed a model of bimanual movement coordination in which two non-linear oscillators are coupled informationally to each other via the perceived relative phase of the oscillators. Perceived relative phase is represented in the model as the relative direction of movement, with the ability to perceptually resolve this conditioned by the speeds of motion. Studies are in progress using this methodology to address explicitly the details of the information and its role in the control and coordination of the rhythmic movement perception/action system.

Acknowledgements We thank Joshua Isaacson for his help in collecting the data. The Indiana University super-computing cluster is supported by the National Science Foundation under Grant No. 0116050. Portions of this data were presented at the 3rd Annual Meeting of the Vision Sciences Society, Sarasota, FL, May 9–14 2003.

References

Batschelet E (1981) Circular statistics in biology. Academic, New York

Beek PJ, Peper CE, Deffertshofer A (2002) Modeling rhythmic interlimb coordination: beyond the Haken-Kelso-Bunz model. Brain Cogn 48:149–165

Bingham GP (2004a) A perceptually driven dynamical model of bimanual rhythmic movement (and phase perception). Ecol Psychol 16(1):45–53

Bingham GP (2004b) Another timing variable composed of state variables: phase perception and phase driven oscillators. In: Hecht H, Savelsbergh GJP (eds) Advances in psychology 135: time-to-contact. Elsevier, Amsterdam

Bingham GP, Schmidt RC, Zaal FTJM (1999) Visual perception of relative phasing of human limb movements. Percept Psychophys 61:246–258

Bingham GP, Zaal FTJM, Shull JA, Collins D (2000) The effect of frequency on visual perception of relative phase and phase variability of two oscillating objects. Exp Brain Res 136:543–552

Bogaerts H, Buekers MJ, Zaal FTJM, Swinnen SP (2003) When visuo-motor incongruence aids motor performance: the effect of perceiving motion structures during transformed visual feedback on bimanual coordination. Behav Brain Res 138:45–57

Buekers MJ, Bogaerts HP, Swinnen SP, Helsen WF (2000) The synchronization of human arm movements to external events. Neurosci Lett 290:181–184

Byblow WD, Chua R, Bysouth-Young DF, Summers JJ (1999) Stabilisation of bimanual coordination through visual coupling. Hum Mov Sci 18:281–305

Cattaert D, Semjen A, Summers JJ (1999) Simulating a neural cross-talk model for between-hand interference during bimanual circle drawing. Biol Cybern 81:343–358

Fisher NI (1993) Statistical analysis of circular data. Cambridge University Press, Cambridge

Haken H, Kelso JA, Bunz H (1985) A theoretical model of phase transitions in human hand movements. Biol Cybern 51:347–356

Jammalamadaka SR, SenGupta A (2001) Topics in circular statistics. World Scientific Publishing, NJ

Johansson G (1950) Configuration in event perception. Almqvist and Wiksell, Stockholm

Kay BA, Kelso JAS, Saltzman EL, Schöner G (1987) Space–time behavior of single and bimanual rhythmical movements: data and limit cycle model. J Exp Psychol Hum 13:178–192

Kay BA, Saltzman EL, Kelso JAS (1991) Steady-state and perturbed rhythmical movements: a dynamical analysis. J Exp Psychol Hum 17:183–197

Kelso JAS (1984) Phase transitions and critical behavior in human bimanual coordination. Am J Phys 15:R1000–R1004

Kelso JAS, Scholz JP, Schöner G (1986) Nonequilibrium phase transitions in coordinated biological motion: critical fluctuations. Phys Lett A 118:297–284

Kelso JAS, Schöner G, Scholz JP, Haken H (1987) Phase-locked modes, phase transitions and the component oscillators in biological motions. Phys Scripta 35:79–87

Li Y, Levin O, Carson RG, Swinnen SP (2004) Bimanual coordination: constraints imposed by the relative timing of homologous muscle activation. Exp Brain Res 156:27–38

Liao M, Jagacinski RJ (2000) A dynamical systems approach to manual tracking performance. J Motor Behav 32(4):361–378

Mardia KV (1972) Statistics of directional data. Academic, New York

Mechsner F, Kerzel D, Knoblich G, Prinz W (2001) Perceptual basis of bimanual coordination. Nature 414:69–73

Mechsner F, Knoblich G (2004) Do muscles matter for coordinated action? J Exp Psychol Hum 30(3):490–503

Pagano CC, Bingham GP (1998) Comparing measures of monocular distance perception: verbal and reaching errors are not correlated. J Exp Psychol Hum 24(4):1037–1051

Schmidt RC, Carello C, Turvey MT (1990) Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. J Exp Psychol Hum 16:227–247

Serrien DJ, Li Y, Steyvers M, Debaere F, Swinnen SP (2001) Proprioceptive regulation of interlimb behavior: interference between passive movement and active coordination dynamics. Exp Brain Res 140:411–419

Temprado JJ, Swinnen SP, Carson RG, Tourment A, Laurent M (2003) Interaction of directional, neuromuscular and egocentric constraints on the stability of preferred bimanual coordination patterns. Hum Mov Sci 22:339–363

Wilson AD, Bingham GP, Craig JC (2003) Proprioceptive perception of phase variability. J Exp Psychol Hum 29(6):1179–1190

Wimmers RH, Beek PJ, van Wieringen PCW (1992) Phase transitions in rhythmic tracking movements: a case of unilateral coupling. Hum Move Sci 11:217–226

Zaal FTJM, Bingham GP, Schmidt RC (2000) Visual perception of mean relative phase and phase variability. J Exp Psychol Hum 26:1209–1220