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Proprioceptive Perception of Phase Variability

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Abstract

Previous work has established that judgments of relative phase variability of two visually presented oscillators co-vary with mean relative phase. 90° is judged to be more variable than 0° or 180° , independently of the actual level of phase variability. Judged levels of variability also increase at 180° . This pattern of judgments matches the pattern of movement coordination results. Here, participants judged the phase variability of their own finger movements, which they generated by actively tracking a manipulandum moving at 0° , 90° or 180° and with one of four levels of Phase Variability. Judgments co-varied as an inverted U-shaped function of mean relative phase. With an increase in frequency 180° was judged more variable while 0° was not. Higher frequency also reduced discrimination of the levels of Phase Variability. This matching of the proprioceptive and visual results, and of both to movement results supports the hypothesized role of on-line perception in the coupling of limb movements. Differences in the two cases are discussed as due primarily to the different sensitivities of the systems to the information.

Introduction

Relative phase (ϕ) is a measure of coordination in studies of human rhythmic limb movement. Bingham, Zaal, Shull & Collins (2000) investigated the perception of mean relative phase and phase variability. Participants judged the degree of coordination in the movement of two visually presented oscillating dots. On average, judgments of mean relative phase were accurate. Judgments of phase variability, however, varied in an asymmetric inverted U-shaped function of mean relative phase. A mean relative phase of 180° was judged to be intrinsically more variable than a mean relative phase of 0° , and 90° was judged to be the most variable mean relative phase. The asymmetry was magnified by increasing the frequency of the oscillators from 0.75Hz to 1.25Hz, which increased judged variability at 180° but not at 0° . Bingham and Collins (submitted) replicated the frequency results using frequencies ranging from 1Hz to 3Hz, and showed that the variability in judgments of both mean relative phase and of phase variability was also an inverted U-shaped function of mean relative phase. Bingham, Schmidt and Zaal (1999) replicated these results by using oscillators driven by actual human movement. Zaal, Bingham and Schmidt (2000) used dots oscillating in both the fronto-parallel plane and in depth, and showed that the levels of phase variability were discriminated best at 0° , then 180° , and not at all at 90° .

The overall pattern of the judgments, then, is an asymmetric inverted U-shaped function, with 90° judged to be inherently noisy and 180° to be noisier than 0° and in response to an increase in frequency, 180° was judged to be increasingly noisy while 0° was unaffected. This pattern mirrors three characteristic phenomena from the movement coordination literature. First,

participants can spontaneously (without training) produce only two stable states: 0° (in-phase; both oscillators at the same point in their cycle at a given time) and 180° (anti-phase; the two oscillators at opposite points in their cycle at a given time; Kelso, 1984, 1995). This is reflected in the judgment studies by participants judging relative phases other than 0° and 180° to be inherently noisy. Second, 0° is more stable than 180° ; movement at 180° is characterized by higher phase variability (Kelso, 1984). This is reflected in the judgment studies by participants judging 0° to be less variable than 180° . Third, increased frequency yields increased phase variability at 180° but not 0° . Under an instruction of non-interference, this eventually leads participants to spontaneously transition from 180° to 0° . There is no spontaneous tendency to switch in the reverse direction, from 0° to 180° , with changes in frequency - 0° remains stable while 180° destabilizes (Kelso, 1984; Kelso, Scholz & Schöner, 1986; Kelso, Schöner, Scholz & Haken, 1987). This is reflected in the judgment studies by their judgments at 0° being unaffected by the frequency manipulation, but not the judgments made at other mean relative phases which were judged to be more variable at higher frequency.

This pattern of results in the movement literature persists even when the coupling is visual, for instance when a participant is coordinating with either another person (Schmidt, Carello, & Turvey, 1990) or with a simulated oscillator (Wimmers, Beek & van Wieringen, 1992). The similarity between our visual results and the movement results suggests that the movement phenomena may be due in part to differential stability in the perception used to couple (and hence coordinate) oscillating limbs. The movement phenomena are all based on a person rhythmically moving two of their own limbs. In this case, the coupling could either be understood at an informational (proprioceptive) level of analysis or at a neural level of analysis,

that is, as some kind of neural crosstalk (the latter motivating several modeling efforts, e.g. Beek, Peper & Daffertshofer, 2002; Cattaert, Semjen & Summers, 1999).¹ The previous visual results were interpreted in the context of a visual informational coupling, and the current study was designed to test a proprioceptive informational coupling.

We had one immediate problem. The movement literature has all demonstrated that people are unable to spontaneously produce mean relative phases other than 0° and 180°. To investigate proprioceptive perception of relative phase, we needed participants to generate reasonably stable movements at other mean relative phases. To enable them to do this, we designed a haptic tracking task, which would produce proprioceptive perceptual information about the state of the limbs being moved. Haptics entails active movement with contact between skin and environmental surfaces (Gibson, 1966)². Participants actively tracked two haptic stimulators (platforms) with their fingers moving at three relative phases with four levels of phase variability. It was uncertain whether in fact participants would be able to do this. Nevertheless, the goal was for participants to produce appropriate movements and therefore be able to make judgments of phase variability on the basis of the proprioceptive information generated by those movements. The tracking aspect of the task also allowed us to separate information about the coordination (proprioceptive judgment task) from the actual production of the coordination (haptic movement task). If we replicated the visual judgment results, this would support a hypothesis about an informational component in the performance of (non-haptic) coordination tasks.

More specifically, we report results from experiments with one (1Hz) and three (1Hz, 2Hz and 3Hz) frequencies. We tested three mean relative phases (0° , 90° and 180°). We only dared to test movement at 90° in addition to 0° and 180° . Because there were only three levels of mean phase, there was no point in testing judgments of mean phase. Participants made judgments of phase variability. We predicted that we would find the pattern from the visual judgment studies now using proprioception, specifically that judgments of phase variability would follow an asymmetric inverted U-shaped function of mean relative phase, and that participants' ability to discriminate various levels of phase variability would be a function of both mean relative phase and frequency.

Experiment One – 1Hz only

Method

Participants

Seven students at Indiana University participated. They were aged 18-39. All were free of motor disabilities, and were paid \$7 for participation. Each session lasted about 1hr.

Design

There were two within-subject factors, Mean Relative Phase (3 levels; 0° , 90° , 180°) and Phase Variability (4 levels; 0° , 5° , 10° , 15°). Phase Variability was added to the signal using three different Methods (described below) for each trial type, making a total of 36 trials per subject. We obtained measures of mean relative phase and phase variability for both judgments and the participant's actual kinematics for each trial as they tracked the presented signal.

Apparatus and Stimuli

The system used to generate the movements to be tracked by participants consisted of a generic 486 personal computer, custom microcontroller and servoamplifier circuits, and, as actuator, the head positioning motor from a Micropolis 1355 hard disk drive. This system flexed and extended the index finger of each hand about the metacarpal phalangeal (knuckle) joint. A lever arm (normally horizontal) was mounted to the motor's rotor. A 1.4cm x 1.9cm finger plate was mounted to the distal arm end, and a plastic washer was glued to it. This washer served as the finger rest. Rotor-to-plate separation was 9.4cm. The plate moved primarily in the vertical direction, with a maximum plate displacement of about 5cm. A positional error feedback servoamplifier was used to control the actuator. Absolute position was obtained by connecting the slider of a high quality linear potentiometer (ETI LCP-12A-25) to the arm. As the motor moved, the potentiometer generated a feedback signal that caused deviations in the movement waveform (due to loading) to be compensated for by additional opposing force. Additional details of the construction and capabilities of the system may be found in Eberhardt, Bernstein, Barac-Cikoja, Coulter and Jordan (1994).

The trajectories of the two finger-plates were generated through numerical simulation. Two aspects of their relative motion were manipulated. First, the plates could move with a mean relative phase of 0°, 90° or 180°. Second, at each level of relative phase, four levels of phase variability were determined in terms of standard deviations of relative phase equal to 0°, 5°, 10°, and 15°.

Variability of relative phase was produced by slowing down and speeding up the individual oscillators. This was accomplished by manipulating the size of the time steps in the numerical simulations. A time step longer than a nominal time step (i.e. a time step appropriate for the display rate) would advance an oscillator, and a time step shorter than a nominal time step would delay an oscillator. By differentially changing the time steps of the two oscillators, their difference in phasing, and hence their relative phase, was perturbed.

The time steps were determined as follows. The time t_i of each oscillator i at time step n was the time at the previous time step plus a modified (shortened or lengthened) new time step;

$$t_i(n) = t_i(n-1) + (1 + N^*_{i,t})\delta t, \quad (2)$$

where δt is the nominal time step of 0.03s. The temporal noise $N^*_{i,t}$ had two components:

$$N_i = A_{N,i} \cos(\omega_N t) + 0.1 A_{N,i} \xi_t, \quad (3)$$

$$N^*_{i,t} = [-0.95 < N_i < 0.95]. \quad (4)$$

First, the noise consisted of an oscillating component with a frequency ω_N of 1, 0.5, or 0.25 times the frequency of plate oscillation ($\omega_p = 1\text{Hz}$). This component had amplitude $A_{N,i}$, that when combined with a smaller Gaussian component was appropriate to introduce a specific relative-phase difference between the two oscillators, that is, an amplitude such that over the entire trial the standard deviation of relative phase was 0° , 5° , 10° or 15° . The oscillating component was combined with a smaller Gaussian component (ξ_t is Gaussian white noise of unit variance), with the restriction that the total advance or delay in timing of the oscillator was smaller than 0.95 times a nominal time step. The phase $\phi_i(n)$ of each oscillator at each time step then was

$$\phi_i(n) = \omega_p t_i(n) + \Delta \phi_{i,t}. \quad (5)$$

where $\Delta\phi_i$ is an initial phase offset to introduce differences in mean relative phase. Finally, the motion of each oscillator was generated as

$$X_i(n) = A_p \cos(\phi_i(n)), \quad (6)$$

Where A_p is the amplitude of the plate motion.

In producing each level of variability in relative phase (standard deviation of 0° , 5° , 10° , or 15°), we added the noise to the oscillators in one of three different ways to ensure that the phase variability was not confounded with specific kinematic characteristics, such as the timing of the end points in the oscillation. As a first method, noise signals of equal amplitude and opposite phase were added to each oscillator. A second method was to add noise signals with equivalent phase but with one amplitude triple the other. Third, a noise signal could be added to only one of the oscillators. We used a constrained random procedure to determine which oscillator received the larger perturbation in the second and third methods, so that each received it equally often.

Procedure

Refer to Figure 1. Participants were brought into the lab and shown the manipulandum. The way the plates could move was demonstrated, and participants were instructed to rest their fingers on the finger-plates and actively track the movement with their eyes closed, without resisting or pulling on the plates. Active tracking was crucial – good proprioceptive perception requires active movement (e.g. Pagano & Turvey, 1996, Paillard & Brouchon, 1968, 1974; see also Clark & Horch, 1986 for a review). The active tracking restriction was monitored in three ways. First, the manipulandum platforms were slightly elastic. If participants did not actively move their fingers, the platforms would simply press against the fingers rather than move them. Second, if

this occurred, a light went on that told participants they were not tracking the platforms correctly. The experimenter monitored this light. Third, we measured the participants' kinematics for later analysis – this measurement (of the participants' movements, not the motor's activity) revealed that they were indeed moving appropriately (see below).

Three instances of each combination of mean relative phase and phase variability were presented, yielding 36 trials per session. A single trial consisted of an 8s movement. Participants were instructed to actively track the movement of the device and then indicate their judgment of phase variability by making a mark on an unscaled line, left being minimum and right being maximum variability.

Mean relative phase was then explained and demonstrated. Participants were shown examples of the plates moving at 0° , 90° and 180° (with no phase variability). Phase variability was then explained, and demonstrated (15° phase variability at 0° , 90° and 180° mean relative phase). Participants were instructed that their task was to judge variability. To make their judgments, participants marked a line on a piece of paper (one per trial). The line represented a scale, with far left being no phase variability and far right being maximum phase variability. To get an intuition for this range, participants received 12 practice trials; 0° , 90° and 180° mean relative phase with 10° ("a medium level"), 0° ("a low level"), 15° ("the highest level"), and 5° ("a different medium level") phase variability. All trials were at 1Hz. Each judgment sheet was taken and the location of the subject's judgment measured to the nearest millimeter as a distance from the left end of the line. A higher value, therefore, indicates a judgment of higher variability.

The session then proceeded in two parts. In the first part, 36 trials were blocked by Mean Relative Phase as practice trials. The second part consisted of 36 trials completely randomized. The data reported are from this second session.

We recorded a position signal for each hand, for each trial and from each subject. Each position signal was filtered (using a low pass Butterworth filter with a cutoff at 10Hz), rescaled such that the values matched the amplitudes of the movements (in mm), differentiated to yield a velocity signal, and filtered again. These signals were used to compute a phase angle time series for each trial, using the Matlab atan2 function. A relative phase time series for each trial was produced by subtracting the phase of the right hand from the phase of the left. These relative phase time series were averaged over the three methods used to generate phase variability, and a mean relative phase and mean phase standard deviation were calculated for each Phase by Phase Variability trial.

Results and Discussion

There were three questions to be addressed. First, we intended to replicate the signal used in Zaal et al (2000), in which there was no Phase x Phase Variability interaction – did we actually make the manipulandum move in this fashion? To address this, we ran the manipulandum in a baseline (unloaded) condition and measured the kinematics of the device. Second, how well could the participants track whatever the manipulandum was doing? This was equally crucial, as it was this tracking that was to be the basis for participants' judgments of phase variability, and it was intended that there be no Phase x Phase Variability interaction in these movements. To address this, we compared the kinematics from the unloaded condition to the kinematics from the

participants. Third, how did this tracking relate to participants' judgments about phase variability in the signal? In particular, had we replicated the Phase x Phase Variability interaction in the judgment data? To address this, we compared the judgment data to the kinematics (using z-scores).

1. Manipulandum Kinematics.

We ran the manipulandum unloaded (no participant, although we placed two quarters on each platform to dampen jitter at each peak flexion and extension point) through a full set of trials and measured its movements under each Phase and Phase Variability condition. Figure 2a illustrates the comparison between the mathematical signal (the dotted lines) and the kinematics of the unloaded manipulandum (solid lines). As is illustrated by the dotted lines, the intention was to produce the four different levels of Phase Variability constantly over changes in Mean Relative Phase. This was trivial to achieve in Zaal et al (2000) – the stimuli were merely dots on the screen. However, we had to pass this signal into the manipulandum, a device with its own dynamic properties. As can be seen in Figure 2a, we came close to reproducing the signal in the 10° and 15° conditions, but we did less well at 0° and 5°. The device added some phase variability to the 0° and 5° Phase Variability trials.

2. Participant Kinematics

The second question was how well did the participants' track this manipulandum output? As shown in Table 1, participants successfully reproduced the three levels of mean relative phase, 0°, 180°, and even the potentially problematic 90°. This allowed us to include data from the 90° trials in our analyses.

As can be seen in Figure 2b, participants (solid lines) reproduced the manipulandum output (dotted lines) with reasonable fidelity, although less well at 0° and 5° Phase Variability. We computed difference scores, subtracting the standard deviations of the unloaded manipulandum from the standard deviations of the participants' movements. There was extra noise at lower levels of intended Phase Variability, but this peaked at only around 2.5°. A repeated measures ANOVA revealed a significant effect of Phase ($F(2,30) = 10.99, p < 0.01$; % variance = 12.3%), and of Phase Variability ($F(3, 45) = 25.14, p < 0.01$, % variance = 79.89%) but no significant interaction. This lack of an interaction and the fact that most of the variance is captured by the intended separation between levels of Phase Variability suggests that participants successfully reproduced an adequate version of the intended signal.

We then wished to examine the participants' movements in more detail, to ensure that they had indeed reproduced the manipulandum movements and had not introduced any significant Phase x Phase Variability interaction.

As shown in Figure 2b, participants also produced four levels of phase variability, although levels that were slightly different than intended. While four levels of Phase Variability were generally discriminable, they were less separated and somewhat greater at low levels of Phase Variability when the Mean Relative Phase was 90° or 180°. We performed a repeated measures ANOVA on the mean relative phase standard deviations (phase SDs). There was a significant main effect of Phase, $F(2,18)=15.47, p < 0.01$, % variance = 5.4% and of Phase Variability,

$F(3,27)=312.37$, $p<0.01$, % variance = 93.1%. There was also a significant interaction, $F(6,54) = 7.00$, $p<0.01$, % variance = 1.5%.

Simple effects showed that the main effect of Phase was present at all levels of Phase Variability (all $p < .05$). Post-hoc Scheffé tests revealed that the significant effect of Phase was due to the variability of movements at 0° being significantly different from variability at 90° and 180° , and movements at 90° being more variable from those at 180° (all $p<.05$). This implied problems for interpreting the predicted Phase effect in the judgment data. This issue will be addressed more directly in Section 4 below.

Simple effects demonstrated that the main effect of Phase Variability remained significant at all levels of Phase (all $p<.01$). Pair-wise t-tests revealed that the only means not significantly different from each other were the means for 0° versus 5° Phase Variability at 180° Phase.

These results suggested that the various levels of phase variability were successfully separated in the movements being judged, which in turn suggests that any absence of this discrimination in the judgments would not be a signal based artifact. The significant Phase x Phase Variability interaction, although small, needed to be accounted for to determine whether it was responsible for any effects found in the judgments. Section 4 deals directly with this issue.

3. Participant Judgments of Phase Variability

There were three replications of each Phase x Phase Variability trial. A mean judgment and a judgment standard deviation was computed for each Phase x Phase Variability cell, collapsing over Method.

Refer to Figure 3, and compare it to Figure 2b (the kinematic 'signal' being judged). Phase variability was judged overall to be highest at 90°. The various levels of Phase Variability were not uniformly discriminated from one another; this discrimination changed with level of Phase, getting worse at 90° as compared to 0° and 180°. These results exhibit the inverted U-shaped function predicted, but not the predicted asymmetry between 0° and 180°. A repeated measures ANOVA was performed on the mean judgments of phase variability. There was a main effect of Phase, $F(2,18) = 18.19$, $p < 0.01$, % variance = 61.26, as well as a main effect of Phase Variability, $F(3,27) = 29.96$, $p < 0.01$, % variability = 34.25. There was also a significant Phase x Phase Variability interaction, $F(6,54) = 2.65$, $p < 0.05$, % variability = 4.47% (as compared to 1.5% in the kinematics). Post-hoc Scheffé tests revealed that overall, judgments of phase variability at 90° were significantly higher than judgments at 0° ($p < 0.001$) and 180° ($p < 0.01$) but that there was no significant difference between judgments at 0° and 180°.

Post-hoc analysis of the main effect of Phase Variability revealed that judgments of phase variability co-varied with actual Phase Variability but that not all levels of Phase Variability were discriminated from each other. Judgments of phase variability in the 0° and 5° Phase Variability trials were not significantly different from each other ($p > 0.5$), but judgments of 0° trials were different from those of 10° ($p < 0.01$) and 15° ($p < 0.01$). Judgments of 5° were also different from 10° ($p < 0.05$) and 15° ($p < 0.01$).

Simple effects revealed a significant effect of Phase Variability at all levels of Phase (all $p < 0.05$). This suggested that at all levels of Phase the different levels of Phase Variability were being discriminated from each other. However, pair-wise comparisons revealed that the significant effect of Phase Variability at 90° Phase reflected only a difference between 15° Phase Variability and all other levels of Phase Variability (which were not significantly different from each other). In other words, the only level of Phase Variability discriminated at 90° Phase was 15°. This is still noteworthy, however, in contrast to the visual discrimination performance at 90°, in which no levels of Phase Variability were discriminated (Zaal, Bingham and Schmidt, 2000).

Simple effects also revealed a significant effect of Phase at all levels of Phase Variability (all $p < 0.01$). Regardless of the level of phase variability, 90° was judged to be more variable than 0° or 180°.

The pair-wise comparisons did reveal a portion of the predicted asymmetry between 0° and 180°. At 0° Phase, 15° Phase Variability trials were judged to be significantly more variable than the other three levels, and 10° Phase Variability trials were judged more variable than both 5° and 0°. However, at 180° Phase, 10° and 15° Phase Variability were not discriminated from each other, nor were 0° and 5°. This pattern in participants' ability to resolve the levels of Phase Variability as a function of Phase is consistent with previous results in the literature.

We have a strong test case for the hypothesis that the judgment results are a perceptual effect – the 0° Phase Variability trials, where there was intended to be no phase variability in the signal to be judged. The variability in the manipulandum movements was not 0°, but it was quite low (see Figure 2a and 2b). In this case subjects still judged 90° to be more variable. We performed an ANOVA on the judgments of phase variability using the data from the 0° Phase Variability condition only (see Figure 3, filled diamonds). There was a significant main effect of Phase, $F(2,22) = 4.50$, $p < 0.05$. Post-hoc Scheffé tests revealed that judgments of phase variability at 0° were significantly lower than those at 90° ($p < 0.05$) but were not different from those at 180°. Judgments at 90° and 180° were not significantly different. This is the predicted inverted U-shaped function but again without the predicted asymmetry between 0° and 180°.

4. Z- Score Difference Analysis

Given the presence of a significant main effect of Phase in the kinematic data, we performed an analysis designed to factor out the effect of the kinematics from the judgments, and then re-test to see whether the key effects (especially the main effect of Phase) remained in the judgment data. We transformed the kinematics and judgments into z-scores and computed a difference score, judgments minus kinematics. Z-scores were used to bring the kinematics and judgments onto the same scale. If the judgments were a perfect report of the kinematic signal, we would expect the differences of z-scores to all come out to 0. Positive z-score differences would reflect a tendency to over-estimate the relative amount of phase variability (the judgment z-score is relatively larger than the kinematic z-score); conversely, a negative z-score difference would reflect a relative underestimation of phase variability.

As shown in Figure 4, judgments of movements at 90° Phase generally over-estimated phase variability relative to judgments at the two other Mean Relative Phases. We performed a repeated measures ANOVA on the difference scores, with Phase and Phase Variability as within-subject factors. All three effects remained significant. There was a main effect of Phase, $F(2,18) = 6.25$, $p < 0.01$, % variance = 29.6%, and of Phase Variability, $F(3, 27) = 28.88$, $p < 0.01$, % variance = 65.2%, and a significant Phase x Phase Variability interaction, $F(6,54) = 2.33$, $p < 0.05$, % variance = 5.2%. The key finding remained, namely the main effect of Phase. Post-hoc Scheffé analysis showed that, averaging over Phase Variability, judgments of phase variability at 90° significantly overestimated the amount of phase variability as compared to judgments at 0° ($p < .05$) and 180° ($p < .05$). This is again the predicted inverted U-shaped function. Once the effects in the kinematic data have been accounted for, the effect of the perception of phase remains - 90° is judged as inherently more noisy.

Experiment Two – 1, 2 and 3Hz

The results of the first experiment replicated the key results from the visual tasks. Participants successfully produced appropriate movements, but when judging those movements, 90° was judged to be more variable than 0° or 180°. The levels of Phase Variability in the signal were not all discriminated at 90°, implying that 90° is already perceived as inherently variable.

This second experiment was a replication of Experiment 1, with the addition of a frequency manipulation. Here, we intended to replicate the differential effect of frequency on phase in the proprioceptive discrimination of phase variability. Again, we analyzed the kinematics of the subjects, as well as their judgments of phase variability. We predicted a) to replicate the main

effect of Phase on judgments of phase variability, specifically the asymmetric inverted U-Shaped function with a peak at 90° , and b) a Frequency x Phase interaction, such that an increase in Frequency from 1Hz to 3Hz would differentially affect judgments of phase variability at the different levels of Phase. Specifically, judgments of phase variability made at the stable 0° Relative Phase would be relatively unaffected by Frequency. Judgments of phase variability made at the less stable 180° and unstable 90° would become higher with an increase in Frequency. The increase may be more noticeable at 180° due to a ceiling effect caused by 90° being judged to be noisy to begin with. This would replicate the asymmetric stability of 0° versus 180° commonly found in the movement and phase perception literature.

Method

Participants

Sixteen students at Indiana University participated. Seven of the participants were the same as those from Experiment 1, with nine additional subjects. They were aged 18-35. All were free of motor disabilities, and were paid \$7 for participation. Each session lasted about 1hr.

Design

There were three within-subject factors. As before, we manipulated Mean Relative Phase (3 levels; 0° , 90° , 180°) and Phase Variability (4 levels; 0° , 5° , 10° , 15°). We also manipulated Frequency (3 levels; 1Hz, 2Hz, and 3Hz). We obtained measures of phase variability both for judgments and for the participant's kinematics as they tracked the presented signal.

Apparatus, Stimuli and Procedure

The device used and the signal generation were the same as reported in Experiment 1, with the exception that we now produced signals at each of the three Frequencies for each combination of Mean Relative Phase and Phase Variability. This was achieved by increasing the speed of the manipulandum – in all cases the signal sent into the device was the same as in Experiment 1. The Procedure was the same as Experiment 1, with the frequency manipulation described verbally but not demonstrated.

Results and Discussion

As before, we performed three separate analyses. First, we analyzed the movements of the manipulandum and of the participants. Here, as in Experiment 1, we were dealing with a manipulandum with its own dynamic properties, as well as the need for participants to be actively tracking the device. We were concerned that adding the Frequency manipulation would exacerbate any problems the manipulandum or participants might have had at 90° or 180°. We needed to ensure that the kinematic signal being judged was still an adequate version of the signal, and if not, be able to control for its effects in our analyses. Second, we analyzed participants' judgments of phase variability, made on the basis of their active tracking of the signal from the manipulandum. Third, we analyzed the judgments after controlling for the kinematics, to ensure that our results from the second analysis remained.

1. Manipulandum Kinematics

To address the first question, we ran the manipulandum unloaded through a full set of trials as before, and measured its movements under each Frequency x Phase and Phase Variability condition. Figure 5a illustrates the comparison between the mathematical signal (dotted lines)

and the kinematics of the unloaded manipulandum (solid lines). As is illustrated by the dotted lines, the intention was to produce the four different levels of Phase Variability consistently over changes in Frequency and Mean Relative Phase. As can be seen in Figure 5a, across levels of Frequency, we came close to reproducing the signal in the 10° and 15° conditions, but we did less well at 0° and 5°; the device added some phase variability to these trials. Trials at 1Hz and 2Hz show essentially the same pattern – however, the problems at 0° and 5° Phase Variability become even worse at 3Hz. Trials with an intended Phase Variability of 0° are actually closer to 5°, and those intended to be at 5° are closer to 8°.

2. Participant Kinematics

The second question was how well did the participants' track this manipulandum output? As can be seen in Figure 5b, participants reproduced the manipulandum output reasonably, although less well at 0° and 5° Phase Variability and with increasing difficulty with these lower levels of Phase Variability at 3Hz as compared to 1Hz and 2Hz. Frequency, while having no overall effect, did exacerbate the effects of Phase, Phase Variability, and their interactions on participants movements. An ANOVA on the difference scores, subtracting the standard deviations of the unloaded manipulandum from the standard deviations of the participants' movements, confirmed these results. Phase ($F(2,30) = 8.75, p < 0.05$), and Phase Variability ($F(3, 45) = 38.68, p < 0.01$) both affected participants' ability to track the manipulandum, but not Frequency ($p > 0.1$). All interactions were significant: Frequency interacted with the effect of both Phase ($F(4, 60) = 5.00, p < 0.05$) and Phase Variability ($F(6, 90) = 4.78, p < 0.01$). Frequency also interacted with the Phase x Phase Variability interaction ($F(12, 180) = 3.92, p < 0.01$).

We tested the participants' kinematics in more detail to test whether the movements (the basis of the judgments) were an adequate version of the pure signal. We were especially interested in the various effects that included Frequency, because our design goal was to minimize these in the kinematics. As suggested by the above analysis, we had not been entirely successful. To establish the extent of Frequency related effects, we computed a movement phase SD for each Frequency x Phase x Phase Variability condition by collapsing across the three methods of introducing variability to the signal and calculating a cell mean and SD.

As shown in Table 2, participants were again able to reproduce the intended Mean Relative Phase, at all Frequencies. As shown in Figure 5b (solid lines), the four levels of Phase Variability were also reproduced successfully by participants, although the lower levels were more variable than intended. There was also a tendency for the movements to become more variable with changes in Phase and Frequency. The effect of Frequency was primarily due to movements at 3Hz, which were quite noisy. However, the effect of Phase on the pattern of movements remained the same across all levels of Frequency.

We performed a repeated measures ANOVA on the kinematic phase SD data, with Frequency, Mean Relative Phase and Phase Variability as within-subject factors. Frequency ($F(2,30) = 75.48$, $p < 0.01$, % variance = 1.23%), Phase ($F(2,30) = 287.25$, $p < 0.01$, % variance = 5%) and Phase Variability ($F(3,45) = 1760.16$, $p < 0.01$, % variance = 93.75%) were all significant, as was the Frequency x Phase Variability ($F(6, 90) = 22.79$, $p < 0.01$, % variance = 0.03%) and Phase x Phase Variability ($F(6,90) = 30.78$, $p < 0.01$, % variance = 1.3%) interactions. The significant effects of Frequency were a potential problem for the interpretation of our judgment results,

although the low percentage of variance explained indicated there was unlikely to be a major problem. By design, we wanted no effects of Frequency in the movements. Post-hoc analysis showed that there was no difference in the movements at 1Hz versus 2Hz, but that 3Hz was responsible for the main effect and the interaction term. Figure 6 illustrates this effect of Frequency. Note that the phase variability is appropriate (a little above the expected average of 7.5° that we obtained by collapsing over Phase Variability) and almost identical for 1Hz and 2Hz (the design intention) but jumps at 3Hz to an average of around 10° (as shown with the solid line). Accordingly, we performed an analysis on the judgment data (below) that excluded the 3Hz trials.

One noteworthy result was the non-significant Frequency x Phase interaction ($F(4,60) = 1.14$, $p > 0.1$). This matched the (by design) non-significant Frequency x Phase interaction in the signal. In other words, the effect of Phase was not changing over levels of Frequency in the movements people were making.

3. Participant Judgments of Phase Variability

The previous results indicated that the actual movements which were to serve as the basis for people's judgments of phase variability were in most important respects an adequate version of the intended signal. The next step was to see if we had replicated the key Frequency x Phase interaction in the judgment data.

We computed a mean judgment of phase variability for each trial, collapsing across the three methods of introducing variability to the signal. As shown in Figure 7a, judgments of phase

variability reproduced the predicted asymmetric inverted U-shaped function of Mean Relative Phase. Phase variability was discriminated best at 0° Mean Relative Phase and 1Hz, with the discrimination getting worse with an increase in Frequency. This effect was also present at the other levels of Mean Relative Phase, but less so due to the levels of Phase Variability being less discriminable initially at 90° and 180°. We performed a repeated measures ANOVA with Frequency (all three frequencies at this point), Mean Relative Phase and Phase Variability as within-subject factors. There was no main effect of Frequency ($F(2,30) = 1.34, p=0.28$), but the other two main effects were significant (Phase, $F(2,30) = 61.45, p<0.01, \% \text{ variance} = 83.37$; Phase Variability, $F(3, 45) = 23.42, p<0.01, \% \text{ variance} = 11.55\%$). The only significant interaction was the predicted Frequency x Phase ($F(4,60) = 4.32, p<0.01, \% \text{ variance} = 3\%$).

Figure 7b illustrates judgments of phase variability about visually perceived oscillators for comparison (from Bingham and Collins, submitted). At 1Hz, the levels of phase variability were discriminated best at 0°, discriminated somewhat at 180° and not discriminated at all at 90°. Judgments were highest at 90° and lowest at 0°. This asymmetry is magnified by the Frequency manipulation (although note that while Frequency reduces participant's ability to resolve levels of phase variability at 0°, judgments are still lower than at the other two mean relative phases). Judgments at 180° become more similar to judgments at 90° with an increase in Frequency. Compare this to Figure 7a. The judgments about the proprioceptively perceived oscillators follow the identical pattern – the levels of Phase Variability were discriminated best at 0° Mean Relative Phase and 1Hz, but overall this discriminability decreases with Frequency.

We repeated the ANOVA on judgment data of movements at 1Hz and 2Hz only, because the kinematics analysis had revealed that we had failed to eliminate Frequency effects at 3Hz (as shown in Figure 6). The Frequency x Phase interaction remained significant ($F(2,30) = 5.84$, $p < 0.01$, % variance = 3.02%), and all the other results remained the same as the 3Hz analysis. We therefore continued analyzing the 1Hz and 2Hz data only.

Simple effects tests from the 1Hz and 2Hz analysis revealed that judgments of phase variability became higher with an increase in Frequency at 90° ($F(2,32) = 5.05$, $p < 0.05$) and at 180° ($F(2,32) = 5.03$, $p < 0.05$) but not at 0° ($p = 0.99$). This is the predicted differential perturbation of stability that we predicted – Frequency did increase judgments of phase variability but only at 90° and 180° , the two less stable mean relative phases.²

We then analyzed the 1Hz and 2Hz data from the 0° Phase Variability trials, to see whether judgments of phase variability varied even with the lowest level introduced variability². See Figure 7a (0° Phase Variability is depicted with filled diamonds). Again, even in the 0° Phase Variability trials, 90° was judged to be more variable than either 0° or 180° . We performed a repeated-measures ANOVA, with Frequency and Phase as within-subject variables. There was a main effect of Phase only ($F(2, 32) = 48.26$, $p < 0.01$).

4. Z-Difference Score Analysis

As in Experiment 1, we wished to confirm that the results obtained in the judgments were not the result of an accurate judgment of a distorted signal. The analysis on the kinematics did reveal a main effect of Phase and an interaction between Phase and Phase Variability, but not the

Frequency x Phase interaction. In the latter case, at least, the judgment results cannot be credited to the signal. To double-check the other results we performed an ANOVA on the difference scores between the z-transformed judgment and kinematic data (see Experiment 1's Results for details on this analysis).

As shown in Figure 8a, judgments of phase variability at 90° were overestimated as compared to judgments made at 0° and 180° Mean Relative Phase. A repeated measures ANOVA revealed a significant effect of Phase ($F(2,30) = 36.88, p < 0.01, \% \text{ variance} = 26.05\%$) and Phase Variability ($F(3,45) = 241.02, p < 0.01, \% \text{ variance} = 71.56\%$). There were two significant interactions: Frequency x Phase ($F(4,60) = 3.79, p < 0.01, \% \text{ variance} = 1.33\%$), and Phase x Phase Variability ($F(6, 90) = 4.26, p < 0.01, \% \text{ variance} = 1.77\%$). We repeated this ANOVA with the 1Hz and 2Hz data only, due to the problems in producing an adequate 3Hz signal (as discussed above). All significant effects remained significant.

Refer to Figure 8b, which plots the means for the Frequency x Phase interaction in the z-difference scores from the 1Hz and 2Hz data only. The predicted asymmetry between 0° and 180° is demonstrated here. Post-hoc pairwise t-tests revealed no significant differences at 0°, but significant differences at 90° and 180° across Frequency. Judgments were consistently overestimated at 90° as compared to judgments at 0° and 180°. Judgments became increasingly overestimated at 90° and 180° with the increase in Frequency, but not at 0°.

Discussion

The movement phenomena are all based on a person rhythmically moving and coordinating two of his or her own limbs. In cases where the coordination was between people, visual coupling reproduced all the effects. The question we addressed was, is the within-person coupling informational as well, that is, is the coupling proprioceptive as opposed to some other form of interaction best understood at a neural level of analysis? The current results tell us that proprioceptive information exhibits all of the same characteristics as the visual case and the within-person coupling might indeed be understood at a perceptual level of analysis. Participants' proprioceptively perceived their own movements and made judgments about the phase variability of those movements. Judgments in both of the current experiments co-varied with Phase rather than simply Phase Variability - 90° was consistently judged to be the noisiest condition, even in the absence of actual phase variability. There was also a Frequency x Phase interaction in Experiment Two, such that increases in Frequency made mean relative phases other than 0° look increasingly noisy.

This pattern of results matches the relative stabilities of phase coordinations seen in the movement literature, in which 0° is the maximally stable (least variable) coordination and 180° is only stable at low frequencies. The pattern reported here reinforces the previous studies' conclusions that the ability to resolve phase variability may play an important role in determining the movement stability asymmetries.

As is often noted, moving at 90° is not a spontaneously stable coordination for people. Participants in our task, however, were indeed able to produce movements at 90° mean relative phase (refer to Tables 1 and 2). This was important for our analysis, as it enabled us to compare

judgment performance at three levels of mean relative phase and to replicate the finding that judgments of phase variability vary as an inverted U-shaped function of Phase. It is clear that the active tracking component of the task, which required participants to move so as to maintain constant pressure on the manipulandum from their fingers, made 90° relatively simple to produce. There is now additional and more general evidence that people can track movements to produce coordinations that they would not otherwise be able to produce spontaneously (Rosenbaum, 2002).

Our proprioceptive results replicated the pattern of the visual results in their similarity to the standard movement results. This replication of such a complex pattern of results in both visual and proprioceptive modalities was a remarkable result. To our knowledge, this has never been previously shown, and therefore the current results provide strong support for our hypothesis of a common informational basis for the performance of coordination tasks. The fact that the judgments are quite different from the actual pattern of the movements produced in the haptic tracking task indicates that efference copies of the motor commands cannot be the basis of the judgments. This is further supported by the visual judgment results where no motor commands were involved in producing actual limb movement patterns that were like the judgment patterns. Rather, in both the visual and the proprioceptive cases, further analysis must turn to a consideration of the information used to make the judgments and its relation to the movements so judged.

The proprioceptive results and the visual results are not absolutely the same in all respects, and this needs to be addressed. First, there was some ability, using proprioception, to resolve levels

of Phase Variability at a mean Relative Phase of 90° , even at higher frequencies. Compare the move from 1Hz to 2Hz in the visual data (figure 7b) as compared to the proprioceptive data shown in Figure 7a. In the proprioceptive case, the frequency increase did not completely eliminate the participants' ability to discriminate levels of phase variability. Second, in the visual data, judgments of phase variability at 180° rose with increase in frequency to be equal to judgments made at 90° . This did not occur in the proprioceptive judgments. Judgments made at 180° did increase with frequency, but the change was much less in the proprioceptive case than the visual. Overall, proprioceptive perception of phase variability at 180° was much more stable than visual perception.

One possible account for the differences is that the information may actually be different in the proprioceptive case as compared to the visual case. Bingham and Collins (submitted) hypothesized that the information about relative phase in the visual case is the relative directions of movement. The relative directions of movement are always the same in 0° mean phase and always the opposite in 180° mean phase (ignoring in either case the effect of phase variability). Visual psychophysical studies have shown that the perceptual ability to resolve directions of motion is conditioned by speeds of motion (De Bruyn & Orban, 1988; Snowden & Braddick, 1991). Resolution is good at medium speeds and poorer at slow and fast speeds. Bingham and Collins (submitted) have found evidence that resolution of relative phase and phase variability is a function of the relative speed of the oscillators' movements (that is, the difference in their speeds). Again, if the effect of phase variability is ignored, the relative speed is always the same at 0° mean relative phase, namely zero. In contrast, at 180° mean relative phase, the relative speed ranges from zero (at the endpoints, where both speeds are zero) to a maximum (midway

through a cycle where the speeds are maximum and oppositely directed). This means that the relative directions of movement and thus, the relative phase would be less well discriminated at 180° than at 0° mean phase. The relative direction is intrinsically more variable over the course of a cycle at 90° because the movements are in the same direction half the time and in opposite directions half the time. Bingham and Collins (submitted) hypothesized that these are the underlying causes of the judgment results they obtained, namely that 180° was judged to be more variable than 0° and only somewhat less variable than 90° . This pattern was not quite the same in our proprioceptive data. Judgments of phase variability at 180° mean phase were higher than at 0° mean phase, but only somewhat, and they were always lower than at 90° mean phase. It is possible that the proprioceptive system detects phase using different information than the visual system, and this information may show different stability properties. The differences are small, however, and minor quantitative differences are more likely to be the result of differences in sensitivity between the visual and proprioceptive systems. Proprioceptive perception is much more involved in our day-to-day rhythmic limb coordination tasks than vision. Most of these tasks also involve a mean relative phase other than 0° - walking, for instance. While these activities generally occur at preferred frequencies (around 1Hz), other frequencies are not uncommon. A higher tolerance for noise in the detection of phase variability would certainly be a useful trait of a system working to maintain stability under these conditions, and the system's regular coordination activity would frequently make the relevant perceptual information available to be learned. It may therefore be the case that the proprioceptive system is more sensitive and thus, better able to discriminate relative directions of motion under conditions of high relative speeds.

These results and the results of the previous experiments all emphasize the role of information in producing the phenomena associated with bimanual coordination tasks. They should not be construed as an attempt to explain the properties of rhythmic movement and its coordination as solely due to perception, however, as has been suggested by Mechsner, Kerzel, Knoblich and Prinz (2001). In movement, there are always actual oscillators involved. Some rhythmic movement properties (such as phase resetting after perturbations (Kay, Kelso, Saltzman & Schöner, 1987; Kay, Saltzman & Kelso, 1991) suggest that the oscillators must be modeled with a non-linear, autonomous dynamic. The relevant coordination phenomena are therefore the result of the coupling of two such oscillators. Some recent modeling efforts have focused on neural crosstalk (Cattaert, Semjen & Summers, 1999) or a combination of neural and oscillator dynamics (Beek, Peper & Daffertshofer, 2002) to produce these phenomena. The current results suggest that combining the role of perception with oscillator dynamics is also a viable modeling strategy. This conclusion is further supported by recent results showing that the passive movements of one limb (e.g. the left arm) affect the coordinated movements of two other limbs (e.g. right arm and leg) thus demonstrating a role of proprioception in the coupling of limb movements (Serrien, Li, Steyvers, Debaere & Swinnen, 2001). Furthermore, Peper and Carson (1999) showed that when cyclic isometric contractions of muscles in one arm are coordinated at 180° with oscillatory movements of the other arm, no phase transition results from increases in frequency as they normally do with oscillatory movements of both arms. This result implies that proprioceptive information about actual limb movement is an intrinsic component of these coordination phenomena. Thus, evidence is mounting that a perceptual level of analysis may be appropriate for an understanding of the coupling of rhythmic limb movements.

The fact that the perceptual information in question needs to be detectable by both the visual and proprioceptive systems constrains what that information could be, while the need for specific dynamic characteristics from the oscillators constrains what form the information could take. With these constraints in mind, Bingham (1995) and Bingham and Collins (submitted) have developed a model related to the model of Kay, Kelso, Saltzman & Schönner (1987) to explicitly represent the functional characteristics of the perception-action system. The model consists of two oscillators with a mass-spring dynamic derived from the equilibrium point-models of limb movement, coupled informationally by the perceived phase of the other oscillator. The perceived phases are ultimately represented in the model as the normalized velocities of the oscillators. This representation is both motivated and justified by the current findings and the visual results we have replicated – velocity is an information source detectable by both vision and proprioception. This information, used to drive the biologically motivated oscillators, successfully captures the key phenomena of bimanual coordination (see Bingham & Collins, submitted, for details of the model). Note that the properties of the oscillators are as important as the properties of the detected information in modeling the movement phenomena. Both perception and action are necessary to fully account for the phenomena of bimanual coordination in humans.

FOOTNOTES

1. Perceptual and neural are different levels of analysis that cannot be mixed in a single analysis. By definition, perception involves the nervous system and perceptual interactions thus entail neural interactions. So, as such, neural cross talk does not exclude the possibility of perceptual involvement and perceptual interactions. Furthermore, given the extensive role of sensory elements in all coherent motor activity as revealed for instance by recent accounts of severe somatosensory deficits (Cole, 1995) as well as the outcome of recent debates about CPG's (e.g. Pearson, 1985) it is unlikely that perception can be ruled out in neural level analyses of coordinated movement. In any case, perceptual and neural levels of analysis should not be confounded.

2. In this paper, "haptics" will refer to the tracking task, while "proprioception" will refer to the information about the coordinated limb movements and the systems detecting that information.

3. This is analogous to the visual case, where we were able to analyze the trials in which there actually was no variability present. The dynamics of the device made this impossible; however our kinematic analysis suggested we were close enough to make this analysis relevant.

TABLES

Mean Relative Phase	Phase Variability			
	0°	5°	10°	15°
0°	1.77	1.605	2.06	1.94
90°	92.29	94.01	92.29	93.44
180°	180.00	178.85	180.57	180.00

Table 1. Mean kinematic relative phases produced by participants in Experiment 1.

Mean Relative Frequency	Phase	Phase Variability			
		0°	5°	10°	15°
1Hz	0°	3.20	3.21	3.24	2.63
	90°	92.40	86.26	92.17	87.09
	180°	177.19	183.39	182.83	177.21
2Hz	0°	2.71	3.43	2.37	2.72
	90°	87.38	92.11	85.80	92.76
	180°	183.34	176.96	177.07	183.05
3Hz	0°	3.28	2.78	2.87	2.83
	90°	93.43	86.46	92.57	85.37
	180°	177.37	183.27	177.45	183.24

Table 2. Mean kinematic relative phases produced by participants in Experiment 2.

FIGURE CAPTIONS

1. Photograph of the manipulandum. The participant, eyes closed, actively tracked the manipulandum platforms (levers) with their index fingers. See text for more detail.

2. The top panel (2a) compares the phase variability of the signal (dotted lines) to the phase variability in the movement of the manipulandum (solid lines) in Experiment 1.

The second panel (2b) compares the phase variability in the movement of the manipulandum (dotted lines) to the phase variability in the movement of the participants tracking the manipulandum (solid lines). Diamond: 0° Phase Variability. Square: 5° Phase Variability. Triangle: 10° Phase Variability. Circle: 15° Phase Variability.

3. Mean judgments of phase variability in Experiment 1, expressed in mm (refer to text for details). Closed Diamond: 0° Phase Variability. Open Square: 5° Phase Variability. Open Triangle: 10° Phase Variability. Open Circle: 15° Phase Variability.

4. Z-score differences for Experiment 1 ($z(\text{Judgments}) - z(\text{Kinematics})$). Closed diamond: 0° Phase Variability. Open Square: 5° Phase Variability. Open Triangle: 10° Phase Variability. Open Circle: 15° Phase Variability.

5. The top panel (5a) compares the phase variability of the signal (dotted lines) to the phase variability in the movement of the manipulandum (solid lines) in Experiment 2.

The second panel (5b) compares the phase variability in the movement of the manipulandum (dotted lines) to the phase variability in the movement of the participants tracking

the manipulandum (solid lines). Diamond: 0° Phase Variability. Square: 5° Phase Variability. Triangle: 10° Phase Variability. Circle: 15° Phase Variability.

6. A plot of the Frequency x Phase (collapsed over Phase Variability) interaction in the participants' kinematic data from Experiment 2. Open Diamond: 1Hz. Open Square: 2Hz. Closed Triangle: 3Hz.

7. The top panel (7a) shows mean judgments of phase variability in Experiment 2, expressed in mm (refer to text for details). Closed Diamond: 0° Phase Variability. Open Square: 5° Phase Variability. Open Triangle: 10° Phase Variability. Open Circle: 15° Phase Variability.

The bottom panel (7b) shows mean visual judgments of phase variability, expressed as a number on a scale from 1-10 (adapted from Bingham and Collins, submitted). Closed Diamond: 0° Phase Variability. Open Square: 5° Phase Variability. Open Triangle: 10° Phase Variability. Open Circle: 15° Phase Variability.

8. The top panel (8a) shows the z-score differences for Experiment 2 ($z(\text{Judgments}) - z(\text{Kinematics})$). Closed diamond: 0° Phase Variability. Open Square: 5° Phase Variability. Open Triangle: 10° Phase Variability. Open Circle: 15° Phase Variability.

The bottom panel (8b) shows the Frequency x Phase interaction for the 1Hz and 2Hz z-score difference data. Closed Diamond: 1Hz. Closed Square: 2Hz.

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