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RESEARCH ARTICLE

The stability of rhythmic movement coordination depends on relative speed: the Bingham model supported

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Abstract Following many studies showing that the coupling in bimanual coordination can be perceptual, Bingham (Ecol Psychol in 16:45–53, 2001; 2004a, b) proposed a dynamical model of such movements. The model contains three key hypotheses: (1) Being able to produce stable coordinative movements is a function of the ability to perceive relative phase, (2) the information to perceive relative phase is relative direction of motion, and (3) the ability to resolve this information is conditioned by relative speed. The first two hypotheses have been well supported (Wilson and Bingham in Percept Psychophys 70:465–476, 2008; Wilson et al. in J Exp Psychol Hum 36:1508–1514, 2010a), but the third was not supported when tested by de Rugy et al. (Exp Brain Res 184:269–273, 2008) using a visual coordination task that required simultaneous control of both the amplitude and relative phase of movement. The purposes of the current study were to replicate this task with additional measures and to modify the original model to apply it to the new task. To do this, we conducted two experiments. First, we tested the ability to produce 180° visual coordination at different frequencies to determine frequencies suitable for testing in the de Rugy et al. task. Second, we tested the de Rugy et al. task but included additional measures that yielded results different from those reported by de Rugy et al. These results were used to elaborate the original model. First, one of the phase-driven oscillators was replaced with a harmonic oscillator, so the resulting coupling was unidirectional. This change resulted in the model producing less stable 180° coordination behavior beyond 1.5 Hz consistent with the results obtained in Experiment 1. Next, amplitude control and phase correction elements were added to the model. With these changes, the model reproduced behaviors observed in Experiment 2. The central finding was that the stability of rhythmic movement coordination does depend on relative speed and, thus, all three of the hypotheses contained in the original Bingham model are supported.

Keywords Coordination · Perception/action · Non-linear dynamics · Stability

Introduction

Rhythmic movement coordination in humans is specifically structured. Bimanual coordinative movements performed at preferred rates (≈ 1 Hz) and at 0° mean relative phase are maximally stable, while movements at 180° are less stable. Typically, a spontaneous transition from 180° to 0° occurs as movement frequency is progressively increased to >2.5 Hz (Kelso 1984; Kelso et al. 1986, 1987). Movements at relative phases other than 0° or 180° (e.g., 90°) are unstable without explicit training (Wenderoth et al. 2002; Wilson et al. 2010a, b; Zanone and Kelso 1992a, b, 1997). This structure, however, is not exclusive to intrapersonal movements (i.e., of a single person's limbs) and has been demonstrated in coordinations mediated by vision either between two people (de Rugy et al. 2006; Schmidt et al. 1990; Temprado et al. 2003; Temprado and Laurent 2004) or between a person and a computer display (Wimmers et al. 1992; Buekers et al. 2000; Wilson et al. 2005a, b).

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The stability pattern has also been exhibited by perceptual judgments performed using either vision (Bingham et al. 1999; Bingham 2001; Zaal et al. 2000) or proprioception (Wilson et al. 2003) to judge the movements. These findings along with others (Mechsner et al. 2001) show that the coupling of these movements can be perceptual and, thus, entail detection and use of information.

With this observation, Bingham (2001, 2004a, b) proposed a dynamical, coupled oscillator model of bimanual coordination that incorporated (and predicted) the results from both movement studies and judgment studies. The model is:

$$\begin{aligned} \ddot{x}_1 + b\dot{x}_1 + kx_1 &= c\sin(\Phi_2)P_{12} \\ \ddot{x}_2 + b\dot{x}_2 + kx_2 &= c\sin(\Phi_1)P_{21} \end{aligned} \tag{1}$$

where

$$P_{12} = \mathrm{sgn}(\sin(\Phi_1)\sin(\Phi_2) + \alpha(\dot{x}_1 + \dot{x}_2)^3 N_t) \tag{2}$$

In this model, the movement of each damped mass-spring oscillator is driven by a term representing the perceived phase ($\boldsymbol{\phi}$) of the other oscillator modulated by a coupling term (**P**) representing perceived relative phase. As shown in Bingham (2001, 2004a, b), the driver is simply a normalized velocity,[1] that is, a signed speed. The model contains the hypothesis that relative phase is specified by relative direction of movement: Relative movement always in the same direction yields 0° phase and relative movement always in opposite directions yields 180° phase. Thus, this term is simply a sign (±1) because sign on velocity represents direction of motion. The coupling term indicates whether the oscillators are moving in the same ($\mathbf{P} = +1$) or opposite ($\mathbf{P} = -1$) directions and is the sign of the product of the phases (normalized velocities) of each of the two oscillators, incremented by a Gaussian noise term (N_t) with a variance that is proportional to the cubed velocity difference between oscillators. This last term, the noise term, represents the ability to resolve or discriminate relative direction of motion perceptually. Psychophysical investigations reveal that this ability is a function of the relative speeds of motion; that is, relative direction of motion is easy to see at moderate relative speeds and difficult to see at high speeds (DeBruyn and Orban 1998).

So the hypotheses contained in this model are (1) that being able to produce stable coordinative movements is a function of the ability to perceive relative phase; (2) that the information to perceive relative phase is the relative direction of motion; and (3) that the ability to detect relative direction of motion depends on relative speed. As relative speed differences between oscillators increase, it becomes more difficult to detect the relative direction of the oscillators and, consequently, to perceive relative phase. Therefore, as relative speed differences increase, it becomes more difficult to stably produce well-coordinated movements.

All three of the hypotheses contained in the Bingham (2001, 2004a, b) model have been examined in one way or another. Wilson et al. (2010a) tested the first hypothesis, namely that being able to produce stable coordinative movements is a function of the ability to perceive relative phase. They investigated whether stable movements can be acquired by improving perceptual ability. This was done by training a group of participants to visually discriminate 90° perceptually from other, similar phases. In a two-alternative forced choice task, participants identified a target phase of 90° in a pair of displays and were given feedback about their performance. The basic result was that improved perceptual discrimination of 90°, as shown by decreased thresholds for perceiving 90°, led to improved performance in the movement task at 90° with no training in the movement task. This observation well supports the first hypothesis of the Bingham model.

Wilson and Bingham (2008) tested the second hypothesis contained in the Bingham (2001, 2004a, b) model; that is, they tested whether the information to perceive relative phase is relative direction of motion. They did this by using a perturbation method to explore the identity of the perceptual information being used. Specifically, Wilson and Bingham selectively perturbed relative position, relative speed, and frequency as participants identified the mean relative phase (0° or 180° with untrained observers; 90° with trained observers) under these perturbation conditions. Wilson and Bingham found that discrimination of 0° and 180° was unperturbed, while discrimination of 90° was entirely disrupted by the position perturbation (and somewhat impaired by the frequency perturbation). Wilson and Bingham concluded that the information used to perceive 0° and 180° was relative direction, but that this was not the information used to perceive 90°. They further concluded that the Bingham model was limited to modeling untrained observers (i.e., those who are not trained 90° observers) because the model successfully describes the information underlying performance at 0° and 180° but does not account for the performance of trained 90° observers.

de Rugy et al. (2008) tested the third hypothesis, namely that coordination stability is dependent on relative speed.

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[1] By normalized velocity, we mean one that is dimensionless and of relative magnitude in the range ±1. This is appropriate for optical information specifying visual events in terms of visual angle per second. Angular measure (radians or degrees) is dimensionless. Relative magnitudes are required because optical velocities vary independently of event velocities as the viewing distance changes and thus, for a given event, the absolute speeds are arbitrary although their pattern of variation is not. Event motions are visually identifiable whether viewed up close or from afar as long as they are visible i.e. above threshold (Bingham 1995).

They selectively manipulated movement amplitude, holding frequency constant, to manipulate relative speed during a unimanual visual coordination task. This resulted in three key conditions: 0° where the oscillators had equal amplitudes, 180° where the oscillators had equal amplitudes, and 0° where the computer-controlled oscillator had an amplitude three times larger than the person-controlled oscillator, that is, 0° equal amplitudes, 180° equal amplitudes, and 0° unequal amplitudes, respectively. The major predictions generated by de Rugy et al. were that if the stability of relative phase depends on relative speed, there would be (1) a difference between the 0° equal amplitudes and 0° unequal amplitudes conditions and (2) no difference between the 180° equal amplitudes and 0° unequal amplitudes conditions. The reason for the latter prediction was that the speed difference at peak speed should be the same in the 180° equal amplitudes and 0° unequal amplitudes conditions. However, de Rugy et al. reported that neither prediction was supported; that is, that relative phase variability was affected only by phase and frequency, in the usual way, but unaffected by the amplitude manipulation. Therefore, they claimed that the stability of rhythmic movement coordination does not depend on relative speed, and thus, the Bingham (2001, 2004a, b) model was not supported. They further concluded that the coupling term in the model does not reflect the coupling that occurs in human rhythmic visual coordination.

So it seems that the Bingham (2001, 2004a, b) model is limited on two accounts: (1) It does not account for the performance of trained 90° observers and (2) it appears not to account for de Rugy et al.'s (2008) finding that rhythmic movement coordination stability does not depend on relative speed. As for the first limitation, it is unsurprising that the model does not account for trained 90° observers' performance; this is because the model was designed to capture the untrained coordination pattern and it, therefore, purposely produces highly variable performance in simulations of judgments and movements at 90°. Wilson and Bingham (2008) suggested that the model would have to be revised to account for trained performance at 90° by incorporating a different information variable than the one in the original model of untrained performance. Further work is required to revise the model to account for perceptual learning of new information variables.

Further work is also required to account for de Rugy et al.'s (2008) results. The Bingham (2001, 2004a, b) model was created to capture the dynamics of bimanual, not visual, coordination. The coupling term in the model is bidirectional; both of the oscillators are affected by the coupling term. In visual coordination tasks like that in the de Rugy et al., this condition is not met. One oscillator, the computer-driven one, displays simple harmonic motion and is not coupled to the other oscillator. Only the participant-controlled oscillator is affected by the participant's perception of the computer-controlled oscillator. One of the possible repercussions of this change is that the stability is different for visual coordination as compared to bimanual coordination. Given the unidirectional coupling, it would be expected to be less stable, and the scaling of frequency would affect movement stability in this task more than in the bimanual version. Examination of de Rugy et al.'s data, which shows very high variability of 180° at 1.75 Hz, suggests that this is the case.

The Bingham (2001, 2004a, b) model in its original form is not entirely suitable as a model of visual (unimanual) coordination; but, then again, it was not designed to be. We feel that there are some straightforward modifications of the original Bingham model that could make it suitable. de Rugy et al. (2008), however, contend that the mechanism by which the Bingham model constrains relative phase production is incorrect and, therefore, even in the best case, substantial modifications including eliminating the dependence on speed are required. In the worst case, no modifications will make the model suitable for visual coordination. In this paper, we investigated whether it was possible to make modifications to the Bingham model, while preserving its essence, to make it suitable as a model of visual coordination. To do this, we performed two experiments testing visual coordination behaviors. One replicated the task used by de Rugy et al. where we report additional measures of the results to better evaluate the performance of participants. Then, we made a series of modifications to the original Bingham model and compared the model simulations to the results from our experiments and those from de Rugy et al.

Experiment 1: the relative stability of 180° visual coordination

In Experiment 1, we evaluated the stability of our visual coordination task at 180° and at increasingly higher frequencies under non-interference instructions. This experiment was necessary because there is a need to establish an appropriate range of frequencies to test in the de Rugy et al. (2008) task and to simulate using the model. We noted that de Rugy et al.'s participants exhibited exceptionally high variability in 180° coordination performance at 1.75 Hz. This result was a bit surprising given that previous work from Wimmers et al. (1992) demonstrated that unimanual/visual coordination is relatively stable until about 2.0 Hz. We suspected that de Rugy et al.'s participants were highly variable at 180° at 1.75 Hz because they were required to produce this directly in each separate trial, without the benefit of having frequency scaled within a trial (as was the case in Wimmers et al. experiment). This requirement probably made the production of the target phase (180°) more difficult.

So the first purpose of this experiment was to determine how difficult it is to produce 180° (especially at 1.75 Hz and above) without having frequency scaled within a trial. The second purpose was to provide a measure of the extent to which participants would have to be performing phase corrections as a function of the different frequencies of movement; frequencies that require constant corrections would not be appropriate for subsequent testing (see later discussion of the dual-task nature of the de Rugy et al. (2008) task). Although we gave non-interference instructions (participants were not to correct to return to performing 180° if they switched to 0°), this task was not the standard phase switching paradigm. First, different frequencies were tested in separate trials. Second, we used a time-on-task measure that was introduced by Wilson and collaborators (Wilson et al. 2010a, b). This measure provided the requisite measure of the extent to which participants would need to perform corrections at each frequency.

Methods

Participants

Ten adults (22–54 years old) participated in this study. All were right-handed, had normal or corrected-to-normal vision, and were free from any known neurological defects or motor disabilities. Ethical approval was granted by the Institutional Review Board at Indiana University, Bloomington.

Procedure

Participants sat at a desk 70 cm in front of a Power Mac G4 that was connected to a Logitech Force 3D Pro joystick (the force feedback feature was disabled). The joystick sat on a keyboard tray that was mounted under the desk, so that participants could use the joystick but not see it. The computer presented a display of two white dots, one above the other, moving horizontally across a black background (screen refresh rate 60 Hz, resolution 1,024 × 768). The vertical position of both dots was fixed. The top dot was under the control of the computer and oscillated at a predetermined frequency and amplitude (7.9 cm). The participant used the joystick to control the horizontal position of the bottom dot. The mapping of joystick to screen amplitude was set, so that required amplitude on the screen did not entail hitting limits of the joystick range of movement. The computer recorded the position of the joystick- and computer-controlled dots.

Participants were shown an 8-s demonstration of 180° relative phase. Participants then performed two blocks of seven trials of 20-s duration moving the bottom dot at 180° relative to the top dot. The first trial was performed at 0.5 Hz and the frequency in each successive trial increased by 0.25 Hz. Participants were instructed to move the joystick in a smooth, side-to-side movement to produce 180°; they were additionally instructed that if they spontaneously switched from 180° to 0°, they were not to try to correct to return to performing 180° (non-interference instructions).

Data analysis

A 60-Hz position time series for both the computer- and person-controlled dots was recorded. The time series data were filtered using a low-pass Butterworth filter with a 10-Hz cut-off frequency and numerically differentiated using a central difference method to produce a velocity time series. For each trial, a continuous relative phase time series was computed as the difference between the arctangent of each dot's velocity divided by position with requisite corrections for the quadrants of the phase plane. From each relative phase time series (trial), we computed *proportion of time on task*. Proportion of time on task is the proportion of each continuous relative phase time series (trial) that fell within the range of the target phase ± a tolerance (set to 20°); it measures within-trial stability at the required relative phase, i.e., how well the participant is able to move as requested (Wilson et al. 2010a, b). We then averaged proportion of time on task, for each participant, over the trials performed in a given condition.

Results

Figure 1a shows the proportion of time spent on task (180° ± 20°) as frequency increased from 0.5 to 2.0 Hz, by 0.25-Hz steps. Participants did not well produce 180° past $\approx$1.25 Hz. These results indicate that participants are not able to consistently produce 180° at higher frequencies (i.e., 1.75 Hz) at least not without frequency scaling within a trial; therefore, performance at such frequencies simply cannot be usefully tested. In addition, when required to produce 180° at frequencies approaching 1.75 Hz, it is clear that participants must perform phase corrections increasingly frequently in order to produce 180°. In fact, it would be possible that the beginning of such a trial would be a series of attempted phase corrections to actually produce 180°. This, in turn, could potentially interfere with a participant's ability to produce the required movement amplitude.

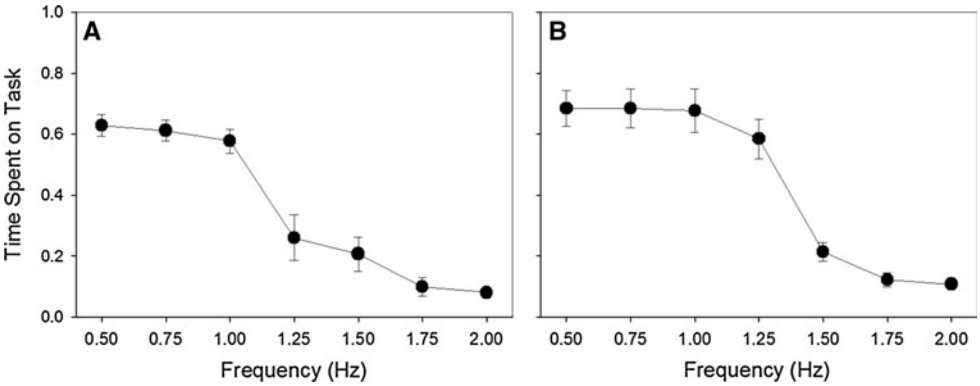

Fig. 1 Proportion of time spent on task (180° ± 20°) for **a** participants performing 180° under non-interference instructions and **b** model simulations of 180°. Frequency increased trial-by-trial from 0.5 to 2.0 Hz by 0.25-Hz increments. Participants exhibited phase switching (from 180° to 0°) at 1.25 Hz, and the model simulations showed phase switching was exhibited at 1.5 Hz

Experiment 2: required amplitudes and phase corrections

de Rugy et al. (2008) selectively manipulated oscillator movement amplitude to manipulate relative speed during a unimanual visual coordination task. This resulted in three key conditions: 0° equal amplitudes, 180° equal amplitudes, and 0° unequal amplitudes. In Experiment 2, we replicated these conditions; however, given the results obtained in Experiment 1, we reduced the maximum frequency which participants were required to produce to reduce the need for phase corrections somewhat and to make it more likely that participants might successfully perform the task. In addition, we also report phase error and movement amplitude. We report these measures because they provide important information regarding the performance of the de Rugy et al. (2008) task and, thus, are important for the modeling effort.

The de Rugy et al. (2008) task was different from those used in previous research investigating the Bingham (2001, 2004a, b) model in one important way. Effectively, the de Rugy et al. task was a dual task because participants were required to produce a prescribed movement amplitude and to simultaneously produce a target phase. Each of the two subtasks entails perception and perceptually guided action. Perception and control of movement amplitude is required to generate required movement amplitude. Perception and control (i.e., correction) of relative phase is required to produce required relative phase. Dual tasking places a burden on the system likely resulting in a decrement in the performance of at least one aspect of the task. As shown in Experiment 1, producing a required phase particularly at higher frequencies involves (frequent) phase correction. This, in turn, may make it difficult to produce the required amplitude because attention would be distracted away from that aspect of the task. With loss of attention to amplitude, the natural tendency might be to allow amplitudes to become more similar simply because it would make the task easier to perform. In fact, other research has shown that this is exactly what happens when participants are asked to perform rhythmic coordinated movements with unequal amplitudes. The amplitudes are attracted toward one another (Kovacs and Shea 2010; Buchanan and Ryu 2006; Spijkers and Heuer 1995).

So if participants are unable to produce the required amplitudes, then the required speed differences will, likewise, not be produced. If participants fail to produce the required speed differences, then certain conditions would become more or less similar with respect to their relative stabilities. That is, 0° unequal amplitudes and 0° equal amplitudes conditions would be more similar, while 180° equal amplitudes and 0° unequal amplitudes conditions would be less similar. Thus, contrary to de Rugy et al.'s predictions, we do not expect the 180° equal amplitudes and 0° unequal amplitudes conditions to be equally stable. The difficulty of the latter, but not the former, can be voluntarily reduced by reducing the difference in amplitude.

Methods

Participants

The same ten adults as in Experiment 1 participated in this study.

Procedure

The instrumentation was the same as in Experiment 1 except for one change. In this experiment, an amplitude was prescribed by two thin vertical lines between which the participants were instructed to oscillate (see Fig. 2); these are the same instructions used by de Rugy et al. (2008). In this experiment, participants performed in three conditions (0° relative phase and equal amplitudes, 0° relative phase and unequal amplitudes, and 180° relative phase and equal amplitudes), each at three different frequencies (1.0, 1.25, and 1.5 Hz). As in the de Rugy et al.'s study, the amplitude of the participant-controlled oscillator was always 3.4 cm and was specified by two vertical lines on the computer

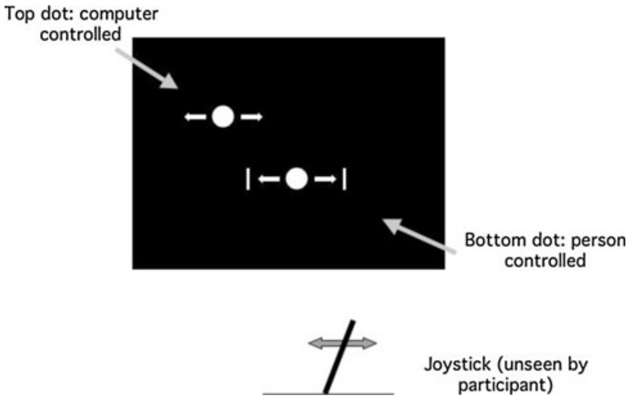

Fig. 2 Schematic diagram of the movement task setup

screen. The amplitude of the computer-controlled oscillator was either 3.4 cm (equal amplitudes condition) or 10.2 cm (unequal amplitudes condition). Also as in the de Rugy et al.'s study, the middle frequency was 1.25 Hz. However, because the results from a pilot study, from Experiment 1, and from de Rugy et al. indicated that participants would generally perform poorly at 1.75 Hz, we restricted our highest frequency to 1.50 Hz. Trials were blocked by condition and frequency. Each block of trials began with an 8-s demonstration of the to-be-produced pattern and a 20-s practice trial (not analyzed). The blocks of trials were counterbalanced between participants.

Data analysis

Data analysis was similar to that in Experiment 1 except that, for each relative phase time series (trial), we also computed SDψ, phase error, and movement amplitude. SDψ is the measure of within-trial uniformity or variability used by de Rugy et al.; so, to compare our results to theirs, we replicated their analysis. To find SDψ, uniformity U was calculated according to Fisher (1993). This measure was then transformed into a linear variable that varies between 0 and infinity by the following transformation:

$$\mathrm{SD}\psi = (-2\log_e U)^{1/2}$$

To find phase error, we computed the difference between the target relative phase and the mean direction of the mean vector θ (which is the direction of the resultant vector obtained by summing the relative phase vectors from each time step) for each trial according to Batschelet (1981). Movement amplitude was found by determining the maximum difference in displacement in each half cycle and averaging over half cycles within trials. Movement amplitude was then normalized to the required amplitude, so that if participants were accurately producing the required amplitude, the average amplitude would be equal to one; producing smaller amplitudes than required yielded values less than one and producing larger amplitudes yielded values greater than one.

Time spent on task, SDψ, movement amplitude, and phase error were each averaged over the trials performed under the same conditions and analyzed separately using two-way repeated-measures analysis of variance (ANOVAs) with the following factors and levels: target frequency (1.0, 1.25, and 1.5 Hz) and condition (0° equal amplitudes, 0° unequal amplitudes, and 180° equal amplitudes). All post hoc analyses were performed using Duncan's multiple range test (MRT).

Results

First, as shown in Fig. 3, the pattern of results for SDψ is the same as was found by de Rugy et al. (2008); SDψ was not different for 0° with equal amplitudes versus 0° with unequal amplitudes. SDψ was different for 0° (with either equal or unequal amplitudes) versus 180° (with equal amplitudes). SDψ increased with movement frequency, at least for 180°. The ANOVA yielded a condition by target frequency interaction ($F_{(4,36)} = 4.69$, $P < 0.01$). There were also main effects of both target frequency ($F_{(2,18)} = 13.84$, $P < 0.01$) and condition ($F_{(2,18)} = 22.67$, $P < 0.01$). Post hoc analyses revealed that the 0° unequal amplitudes and 0° equal amplitudes conditions were equally variable and were less variable than the 180° equal amplitudes condition ($P < 0.05$).

Next, we checked mean phase error to see whether the participants were actually producing the assigned relative phase targets or were also spending time at relative phases other than those targeted. As shown in Fig. 4, mean phase

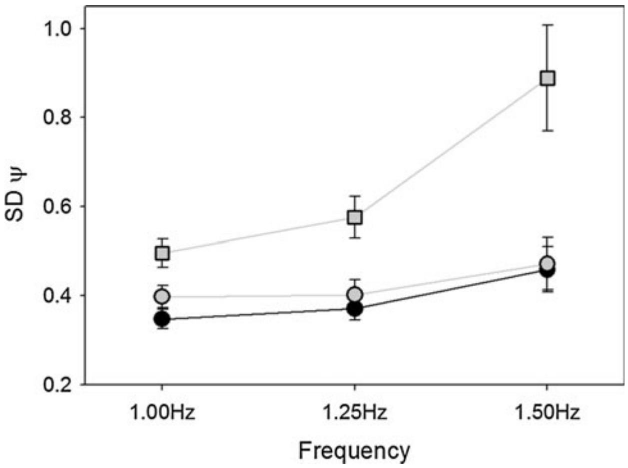

Fig. 3 SDψ as participants performed 0° = amplitudes (*solid line with filled circle*), 0° ≠ amplitudes, (*solid line with gray shaded circle*), and 180° = amplitudes (*solid line with gray shaded square*) conditions at 1.0, 1.25, and 1.50 Hz. There was an effect of phase but no effect of amplitude

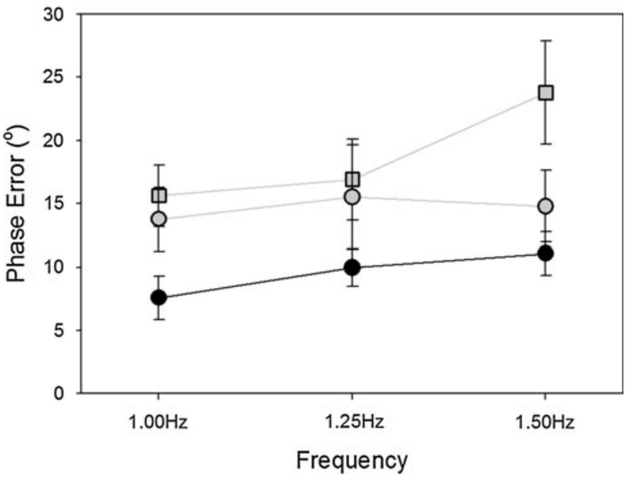

Fig. 4 Mean phase error as participants performed 0° = amplitudes (*solid line with filled circle*), 0° ≠ amplitudes (*solid line with gray shaded circle*), and 180° = amplitudes (*solid line with gray shaded square*) conditions at 1.0, 1.25, and 1.50 Hz. Participants were better able to perform 0° as compared to 180° movements

errors were all well above 0° especially for movements targeted to 180° relative phase. There was no condition by target frequency interaction ($F_{(4,36)} = 1.22$, $P > 0.05$), but there were main effects of condition ($F_{(2,18)} = 4.25$, $P < 0.05$) and of target frequency ($F_{(2,18)} = 4.29$, $P < 0.05$). These results show that participants were spending time at phases other than those targeted and increasingly often in the 0° unequal amplitudes and 180° equal amplitudes conditions. This trend was reflected in the overall mean phase errors: 9.54° for 0° equal amplitudes; 14.70° for 0° unequal amplitudes; and 18.78° for 180° equal amplitudes.

Next, we checked whether participants actually produced the assigned target amplitude. As shown in Fig. 5, movement amplitude was larger in the 0° unequal amplitude condition than in the remaining two (equal amplitude) conditions. The ANOVA yielded only a main effect of condition ($F_{(2,18)} = 32.61$, $P < 0.01$). Post hoc analyses revealed that movements of the joystick-controlled dot performed during the 0° unequal amplitudes condition were larger (by about 15–20%) than those performed during the 0° equal amplitudes or 180° equal amplitudes conditions ($P < 0.05$). That is, though participants were fairly accurate during the 0° equal amplitudes or 180° equal amplitudes conditions, they produced larger amplitudes than required during the 0° unequal amplitudes condition. This means that the amplitudes of the computer- and joystick-controlled movements were less different than intended by the design.

Finally, we turned to the time-on-task measure (Wilson et al. 2010a, b) that incorporates both precision and accuracy into the evaluation of stability. As shown in Fig. 6a, stability decreased over the conditions from 0° equal amplitude to 0° unequal amplitude and finally to 180° equal amplitude. In the ANOVA, there were main effects of both target frequency ($F_{(2,18)} = 9.98$, $P < 0.01$) and condition ($F_{(2,18)} = 13.91$, $P < 0.001$), but no interaction. Post hoc analyses revealed that the 0° equal amplitudes condition was more stable than the 0° unequal amplitudes condition, which was more stable than the 180° equal amplitudes condition ($P < 0.05$). This pattern of results indicates that the stability of these coordinated movements is affected by relative speed.

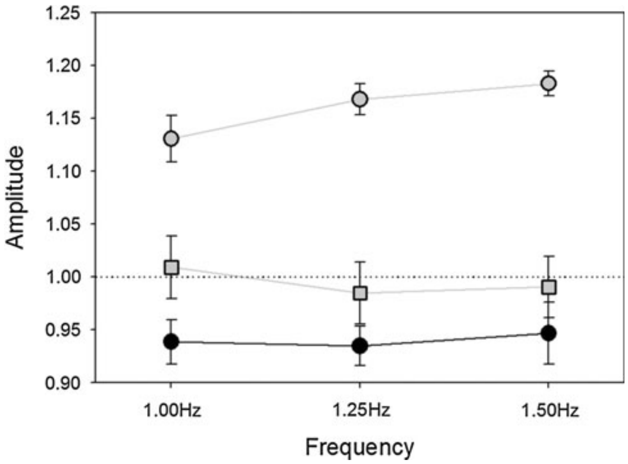

Fig. 5 Movement amplitude as participants performed 0° = amplitudes (*solid line with filled circle*), 0° ≠ amplitudes (*solid line with gray shaded circle*), and 180° = amplitudes (*solid line with gray shaded square*) conditions at 1.0, 1.25, and 1.50 Hz. Participants produced larger than required amplitudes in the 0° ≠ amplitudes condition

Modeling visual coordination

de Rugy et al. (2008) concluded that their results ruled out relative speed as the relevant noise term and, accordingly, suggested that the specific perception–action mechanism described by the Bingham (2001, 2004a, b) model was incorrect. Across the two present experiments, we not only replicated their key results using the SDψ measure, but also showed that (a) the highest frequency tested by de Rugy et al. was too high and (b) under the amplitude manipulation used, participants showed large phase errors and poor amplitude matching. SDψ was, therefore, measuring the stability of the incorrect movements produced and not the stability of the intended movements (see Wilson et al. 2005a, b). Reanalyzing the relative phase data using a measure of movement stability at the target phase, time on task, confirmed that performance varied as a function of the relative speeds, supporting the mechanism in the Bingham model. Here, based upon the results from Experiments 1 and 2, we make a series of modifications to the model, while

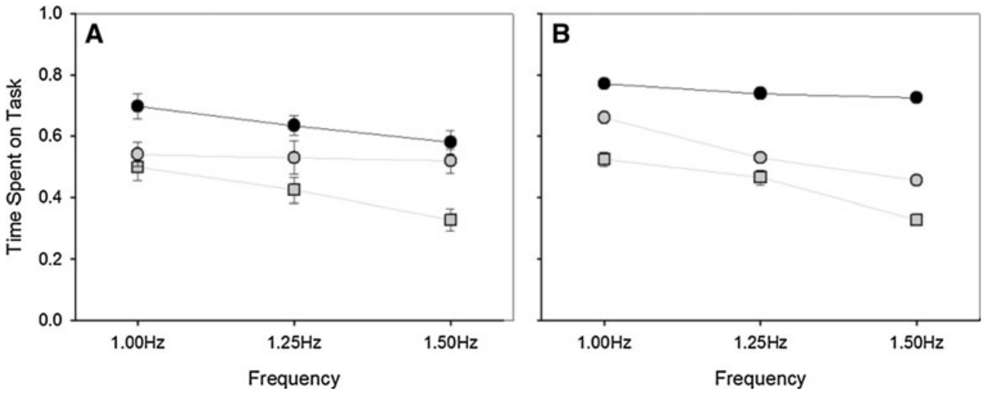

Fig. 6 **a** Proportion of time spent on task (target phase ± 20°) as participants performed 0° = amplitudes (*solid line with filled circle*), 0° ≠ amplitudes (*solid line with gray shaded circle*), and 180° = amplitudes (*solid line with gray shaded square*) conditions at 1.0, 1.25, and 1.50 Hz. 0° = amplitudes was more stable than 0° ≠ amplitudes which was more stable than 180° = amplitudes conditions. **b** Proportion of time spent on task (target phase ± 20°) for model simulations

preserving the basic mechanisms, to evaluate its suitability as a model of visual coordination.

180° visual coordination

In Experiment 1, we evaluated the stability of our visual coordination task at 180° at increasingly higher frequencies under non-interference instructions. We found that participants were unable to produce 180° consistently at higher frequencies (i.e., 1.75 Hz). The original Bingham (2001, 2004a, b) model, however, entailed bidirectional coupling and exhibited relatively stable 180° coordination until higher frequencies (>2.5 Hz). Here, we made two modifications to the original Bingham model that reflect the key differences between the unimanual and bimanual coordination tasks but preserve the nature of the model. We then compared the model simulations to the results from Experiment 1 (see Fig. 1).

First, to represent the computer-controlled dot, we substituted a harmonic oscillator for one of the phase-driven oscillators. Second, and accordingly, the coupling term (**P**) only affected the remaining phase-driven oscillator. Thus, the coupling was unidirectional. The adjusted model was:

$$\begin{aligned} &\ddot{x}_1 + b\dot{x}_1 + kx_1 = c\sin(\Phi_2)P_{12} \\ &\ddot{x}_2 + kx_2 = 0 \end{aligned} \tag{3}$$

where again

$$P_{12} = \operatorname{sgn}(\sin(\Phi_1)\sin(\Phi_2) + \alpha(\dot{x}_1 - \dot{x}_2)^3 N_t) \tag{4}$$

We used this to simulate the phase switching from Experiment 1, using 40 random seeds for N_t, the Gaussian noise, to generate 40 corresponding trials for each frequency plateau. The simulation results compared well with the results of the human participants. As shown in Fig. 1b, the model produced similar behavior to the participants in Experiment 1. The model was unable to produce 180° performance past ≈1.50 Hz.

Required amplitudes and phase corrections

In Experiment 2, we replicated the key tasks from de Rugy et al. (2008): 0° equal amplitudes, 180° equal amplitudes, and 0° unequal amplitudes. We obtained a similar pattern of results in the SDψ measure indicating that our participants and de Rugy's participants were exhibiting the same behaviors. We also found that participants were not accurately producing the required amplitude in the 0° unequal amplitudes condition but did so in the other conditions. These findings indicate that participants were able to (and did) control amplitude at least under some circumstances. Amplitude control, however, was not a feature of the original Bingham model or the modified model; amplitude was simply initially set using the parameter c, and simulations of the Bingham model exhibited the inverse frequency–amplitude relationship characteristic of human limb movements in the spontaneous switching tasks (Bingham 2004a). So we added an amplitude control feature to the model. We also added a phase correction feature. Phase correction was required because of the findings in Experiment 1: Without phase corrections, participants were not well able to produce at 180° at 1.25 Hz and above. Therefore, our participants and those in de Rugy et al. (2008) were performing phase corrections, so that they would be in compliance with task instructions (move so as to produce 0° or 180°).

Amplitude control and phase correction both entail perception. Perception of amplitude must be involved to control and to try to produce the required amplitudes. Perception of relative phase must be involved to be able to detect when the phase being produced has deviated from the targeted phase and thus, must be corrected. This latter factor introduces the question of how well and how quickly deviations from target phase might be detected and whether there might be a difference in the saliency and detection time for phase targets of 0° and 180°. This task gets very complicated, quickly. The original Bingham (2001, 2004a, b) model includes terms that reflect perception of amplitude and relative phase. Thus, we were able to develop a modification of the original coupled oscillator model that accommodated the additional constraints on coordination introduced by the de Rugy et al. (2008) task. The subtasks that this model handles are the following: (1) visual coordination, (2) amplitude control, and (3) phase correction.

Visual coordination

The modifications required to model the task in Experiment 1 (see Eqs. 3 and 4) were incorporated in this new version: One of the phase-driven oscillators was replaced with a harmonic oscillator. The phase-driven oscillator was coupled to and driven by the perceived phase of the harmonic oscillator multiplied by the coupling term resulting in unidirectional coupling only.

Amplitude control

Production of the prescribed amplitude required the addition of a function that both represents perceived amplitude and uses it to control amplitude. We accomplished this using as information the other polar coordinate on the phase plane as formulated in Bingham (2001, 2004a, b). Phase angle is one of the polar coordinates on the phase plane; the other coordinate is the radius, which is also a measure of the energy of movement. Hence, it is called '*e*', and it is determined as:

$$e_n = \sqrt{v_n^2 + x^2} \tag{5}$$

where v is the velocity and x is the position. An advantage of the Bingham model was that it included a parameter, c, on the phase driver that modulates the amplitude. So we modeled perceptual control of amplitude by scaling c as a function of the difference between required and perceived movement amplitude as follows:

$$c = c_0 + \gamma(a^* - e_n) \tag{6}$$

where a^* was the target amplitude and c_0 was the initial value for the amplitude parameter.

Phase correction

Production of a prescribed relative phase required the addition of a function for detection and correction of deviations from the prescribed phase. This correction requires the performer to perceive that the current phase is sufficiently different from the required phase to merit correction. This requires a criterion amount of error to merit correction. A possible response might be to speed up or slow down movement to re-establish target phase; however, what we observed participants to do was simply to stop moving, to position themselves at the endpoint of the movement and then, wait until the computer-controlled dot was either at the same end for 0° or at the opposite end for 180°, and then, begin movement again. Participants essentially just reset to the initial conditions. Therefore, we modeled phase correction by resetting the integrators to the initial conditions for the given targeted phase.

The Bingham (2001, 2004a, b) model included a representation of perceived mean phase, namely the coupling term, **P**, (representing relative direction) integrated over a nominal observation time, σ (a 1 s window).

$$P_{JM} = \frac{\int_{t-\sigma}^{t} P\mathrm{d}t}{\sigma} \tag{7}$$

This had been used to model results from previous perceptual judgment studies.

The question that remained was what criteria should determine that the current perceived relative phase was sufficiently different from the target phase to require correction. We noted that the mean phase deviations in Experiment 2 were different for targets at 0° versus 180°. The implication was that participants had greater difficulty discriminating deviations from a 180° target than from a 0° target. Therefore, we realized that the criterion should be asymmetric in this way. Then, we also noted that participants attempting to produce 180° often spontaneously transitioned to 0°, then detected this once it had happened, and corrected their relative phase back to 180°. Deviations from 0° are easier to detect as such. Accordingly, we used asymmetric correction criteria defined relative to 0°. For 0° target phase, correction was initiated if the moving average of relative phase reached $\geq$45°. For 180° target phase, correction was initiated if the moving average of relative phase reached $\leq$5° (i.e., 175° from the 180° target). These were used together with the information about relative phase and a pre-specified target phase to simulate detection of deviations from the target phase and consequent resetting of the integrators to initial conditions.

To perform simulations of each of the conditions in Experiment 2, we used 40 random seeds for N_t, the Gaussian noise in the coupling term, to generate 40 trials for each condition and frequency. Given the actual amplitude results in which the amplitude difference was smaller than required in the 0° unequal amplitudes conditions, we used a reduced amplitude difference in our simulations of that condition.

Figure 6b shows the results from these simulations analyzed in terms of the proportion of time-on-task measure for comparison to the results of Experiment 2 (compare to Fig. 6a). These simulations yielded stability differences between the 0° equal amplitudes and 0° unequal amplitudes and then, the 180° equal amplitudes conditions that replicated the pattern of results obtained in Experiment 2. In short, the results of our replication of the task used by de Rugy et al. (2008) were successfully predicted by an elaborated version of the original Bingham model. The model was supported by the results of this task, contrary to the conclusions of de Rugy et al.

Discussion

The purpose of this study was to investigate whether it was possible to make modifications to the original Bingham model (2001, 2004a, b), while preserving its essence, to make it suitable as a model of visual coordination. Our first step was to eliminate the bidirectional coupling contained in the original model because the perceptual coupling in that version of the model is bidirectional but visual coordination entails no such bidirectionality (see Eqs. 3–4). The results from Experiment 1 confirmed that the relatively simple modifications to the original model allowed it to reproduce human visual coordination behavior under non-interference instructions.

Most visual coordination, however, is not performed under the non-interference conditions. When left to their own devices, participants will make corrections in order to produce the requested phase (usually 0°, 180°, or 90°). The key tasks implemented by de Rugy et al. (2008) and replicated here in Experiment 2 entailed visual coordination and the maintenance of a prescribed target phase and also required the production of specific amplitudes. These two additional constraints required the detection and correction of deviations in both amplitude and phase that, again, were not explicitly modeled by Bingham (2001, 2004a, b). We therefore revised the model to include these requirements (see Eqs. 5–7). The simulations of Experiment 2 confirmed that these additional modifications reproduced human visual coordination behavior with these additional constraints.

We, therefore, concluded that the coupling term in the new model reflects the coupling that operates in visual coordination. We should note that we had to make several decisions in the exact implementation of the model that remain to be tested. For example, we modeled amplitude control by assuming that amplitude was continuously perceived as the radius polar coordinate of the phase plane. The resulting model therefore predicts that this should be a perceptible property. Bingham (2004a, b) also hypothesized that this information variable is used to detect deviations from limit cycle stability (while maintaining the autonomy of the dynamic). Goldfield et al. (1993) have demonstrated that infants are able to bounce themselves at resonance, suggesting that they are sensitive to this energy coordinate; it remains for future investigations to test whether adults can use this variable in this task. Second, we implemented phase corrections as a simple reset to initial conditions when an error was detected (because this was observed as a common strategy used by participants). Not all phase corrections will be of this type—for example, participants might briefly speed up or slow down to return to the target relative phase if the error is detected quickly. It remains for future investigations to determine precisely when people use which strategy. Nevertheless, the simulation results show that the model is able to reproduce the behaviors exhibited by participants performing these new, complex tasks.

In sum, the results from human participants and model simulations support the hypotheses contained in the original Bingham model (2001, 2004a, b), namely that the information used to perceive relative phase is relative direction conditioned by relative speed. This conclusion, of course, is in opposition to that made by de Rugy et al. (2008). We believe that one of the sources of this disagreement lies in the difference between how coordination stability was assessed. de Rugy et al. assessed coordination stability using a measure of within-trial phase uniformity/variability (SDψ) where higher values (of SDψ) denote higher variability and lower values denote lower variability. SDψ is only interpretable if one can assume that mean direction and stability are independent of each another. However, the cardinal feature of coordinated rhythmic movement is that mean direction and stability in rhythmic movement coordination tasks are *dependent* on one another: 0° is more stable than 180° and both 0° and 180° are more stable than 90°. Consequently, coordination stability assessed only by SDψ can be misleading. For example, if one attempts to produce 30° but actually spends long periods of time producing another phase, such as 0°, SDψ values will be low and performance at 30° would be assessed as relatively stable. Low SDψ values in this example, however, simply reflect the failure to maintain the appropriate target phase. In sum, SDψ provides information about only one aspect of performance stability, consistency, but does not provide information about the other aspect, accuracy. This problem is generally addressed by also reporting the error of relative phase (usually absolute error); however, this only allows one to note whether or not SDψ is valid for that condition. We, however, adopted another measure, 'time on task.' As explained in Wilson et al. (2010a, b), this variable neatly summarizes the data of interest (consistency and accuracy) in a single, valid number. The task used by de Rugy et al. and thus in the current study requires production of a specific phase relation with execution of corrections if movement is perceived by a participant to deviate from the required relative phase. In view of this, for the performance of a given coordination pattern to be considered stable, the performance must be both consistent and accurate, that is, it must stably be at the target phase. Assessment of this requires the time-on-task measure.

Finally, it is worth discussing the importance of the Bingham model and reasons why its vindication is a useful outcome. A series of studies that preceded the formulation of the Bingham model showed conclusively that rhythmic coordinated movements were coupled perceptually (for example, see Schmidt et al. 1990; Wimmers et al. 1992; Byblow et al. 1999; Buekers et al. 2000). This meant that it was incumbent on researchers to discover the information that was used in these tasks to support the perceptual coupling. Non-linear coupled oscillator models had previously been formulated and much studied in the context of these tasks, in particular the well-known HKB model (Haken et al. 1985; Kay et al. 1987; Beek et al. 2002). However, none had included components representing hypotheses about the relevant perceptual information. The Bingham model was the first to do this. It is a true perception/action model. As had the previous models, it incorporated advances in action theory including mass-spring models of limb movement. However, it also introduced hypotheses about the perceptual information that were developed in light of extensive work in visual psychophysics. As already mentioned, the information for relative phase was hypothesized to be relative movement direction, and because the psychophysics had shown that the ability to resolve the direction of motion visually is limited by relative speeds of motion, relative speed was included in the model as the ultimate source of noise in the non-linear dynamics. This last feature was the unique contribution of the model to the advancing science. This feature is what marked this model as a perception/action model and it was this last feature that was challenged by de Rugy et al. (2008). However, this feature of the model was supported by the current studies and thus we find support for the mechanism by which the Bingham model constrains relative phase production. The Bingham model and the hypotheses contained within, therefore, have been vindicated and it remains as a point of reference for future research on coordination.

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