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The Effects of Feedback Format, and Egocentric & Allocentric Relative Phase on Coordination Stability

John Pickavance[1]

Arianne Azmoodeh[1]

&

Andrew D Wilson[1*]

[1] Psychology, School of Social Sciences, Leeds Beckett University, Leeds, UK

* Corresponding Author

Email: a.d.wilson@leedsbeckett.ac.uk / DrAndrewDWilson@gmail.com

Web: https://cognitioninaction.wordpress.com/

Twitter: @PsychScientists

All data and a preprint available at https://osf.io/z7c9q/

Abstract

The stability of coordinated rhythmic movement is primarily affected by the required mean relative phase. In general, symmetrical coordination is more stable than asymmetrical coordination; however, there are two ways to define relative phase and the associated symmetries. The first is in an *egocentric* frame of reference, with symmetry defined relative to the sagittal plane down the midline of the body. The second is in an *allocentric* frame of reference, with symmetry defined in terms of the relative direction of motion. Experiments designed to separate these constraints have shown that both egocentric and allocentric constraints contribute to overall coordination stability, with the former typically showing larger effects. However, separating these constraints has meant comparing movements made either in different planes of motion, or by limbs in different postures. In addition, allocentric information about the coordination is either in the form of the actual limb motion, or a transformed, Lissajous feedback display. These factors limit both the comparisons that can be made and the interpretations of these comparisons. The current study examined the effects of egocentric relative phase, allocentric relative phase, and allocentric feedback format on coordination stability in a single task. We found that while all three independently contributed to stability, the egocentric constraint dominated. This supports previous work. We examine the evidence underpinning theoretical explanations for the egocentric constraint, and describe how it may reflect the haptic perception of relative phase.

Introduction

Coordinated rhythmic movement is a well-established laboratory task used to study the composition and organisation of perceptually controlled action. It requires the online (perceptual) coordination and control of multiple limbs. The structure of the behaviour is surprisingly rich, and it is simple enough to model in great detail (e.g. Beek, Peper & Daffertshofer, 2002; Bingham, 2001, 2004a, b; Cattaert, Semjen & Summers, 1999; Daffertshofer, Peper, & Beek, 2005; Haken, Kelso, Bunz, 1985; Peper, Ridderikhoff, Daffertshofer & Beek, 2004; Snapp-Childs, Wilson & Bingham, 2011). In addition, there are some coordinations that are difficult to produce without practice, allowing us to study the acquisition of these actions (e.g. Zanone & Kelso, 1992a, b, 1997; Wilson, Snapp-Childs, Coats & Bingham, 2010).

The current study directly compares the effects of three factors on coordination stability; egocentrically defined relative phase, allocentrically defined relative phase, and the format of the allocentric feedback.

Relative Phase

The primary factor that affects coordination stability is the target relative phase. When two oscillating limbs are at the same point in their cycle (phase) at the same time, this is 0° mean relative phase, or in-phase, and it is the most stable state. If the two limbs are at opposite points in their cycle at the same time, this is 180° mean relative phase, or anti-phase. This is also a stable state, although it is less stable than 0°/in-phase (e.g. if the frequency is steadily increased, phase variability increases and there is a tendency to transition from 180° to 0°; Kelso, 1984). These are typically the only two coordinations people can produce stably without practice; other relative phases are easily perturbed by small errors leading to a transition to one of the stable states. This basic pattern was captured in the original Haken-Kelso-Bunz (HKB) model (Haken et al, 1985), which describes 0° and 180° as the only attractors in a potential function spanning the space of possible relative phases (see

Golonka & Wilson, 2012 and Kelso, 1995 for overviews, and Park & Turvey, 2008 for a detailed analysis of the nature of the HKB modelling approach).

In human movement coordination, relative phase can be defined in two different frames of reference: an egocentric, body relative frame of reference; and an allocentric, external frame of reference.

The Egocentric Frame of Reference

The egocentric frame of reference is body centred about the sagittal midline. In this frame, a coordinated rhythmic movement that entails mirror symmetrical movements (i.e. in-out/in-out movements) about the midline is referred to as *in-phase* coordination. Side-to-side movements (e.g. in-out/out-in) are referred to as *anti-phase* coordination. In-phase movements are more stable than anti-phase movements. The HKB model (Haken et al, 1985) defines relative phase in an egocentric frame of reference.

This *egocentric constraint* (Swinnen, 2002) on coordination stability is attributed to muscle homology. Homologous muscles are the functionally equivalent muscles in matching limbs; for example, the biceps of the two arms are homologous, as are the triceps. Thus, under normal postural conditions, in-phase coordinations require the simultaneous use of homologous muscles, and anti-phase coordinations require the simultaneous use of non-homologous muscles.

One proposed mechanism for how muscle homology might affect coordination stability is neural crosstalk (e.g. Marteniuk, MacKenzie & Baba, 1984; Swinnen, Young, Walter & Serrien, 1991). Specifically, when non-homologous muscles must be activated simultaneously, the relevant motor commands interact with and inhibit one another at various stages of planning and implementing the movement. This has been formalised in several models (e.g. Beek et al, 2002; Cattaert et al, 1999; Daffertshofer et al, 2005).

The Allocentric Frame of Reference

Coordinated rhythmic movements must be parallel to each other to produce the HKB stability differences, because relative phase is only uniquely defined under these conditions. When two coordinated movements are orthogonal to each other, the asymmetries between in-out/in-out motions and in-in/out-out motions disappear (e.g. Bogaerts, Buekers, Zaal, & Swinnen, 2003; Wimmers & Beek, 1992).

This means that there is a second human-relevant way to define relative phase, and that is in an allocentric frame of reference. In this frame, when the two oscillators in a coordinated rhythmic movement move in the same direction throughout the cycle, they are at *0°* mean relative phase. When they move in the opposite direction throughout the cycle, they are at *180°* mean relative phase. 0° movements are more stable than 180° movements. The Bingham model (Bingham, 2001, 2004a, b; Snapp-Childs et al, 2011) defines relative phase in an allocentric frame of reference.

This *allocentric constraint* (Swinnen, 2002) on coordination stability is attributed to the relative direction of motion of the two oscillators. 0° coordinations are more stable than 180° because relative direction is more stable (and because the relative speeds are lower; Snapp-Childs et al, 2011). Intermediate relative phases are specified by varying proportions of the same/different direction of motion and cannot be stably produced without training.

There are two strands of research that have revealed the effects of the allocentric constraint on coordination stability. The first strand investigated coordination of non-homologous limbs (e.g. Serrien & Swinnen, 1997; Swinnen, Dounskaia, Verschueren, Serrien & Daelman, 1995). In these tasks, muscle homology is not definable and coordination stability was strongly governed by the relative direction of motion (with isodirectional, 0° coordination more stable than non-isodirectional, 180° coordination).

The second strand considers the perception of relative phase. The first clue that internal, neural constraints may not be the sole player came from Schmidt, Carello & Turvey (1990), who showed that the HKB stability pattern persisted when two people coordinated with each other, coupled only by vision. Bingham then embarked on a research program to investigate the informational basis for the perception of relative phase. He and colleagues have shown the HKB pattern in judgments of relative phase and phase variability, both visually (Bingham, Schmidt & Zaal, 1999; Bingham, Zaal, Shull & Collins, 2000; Zaal, Bingham & Schmidt, 2000; Bingham 2004b) and haptically (Wilson, Bingham & Craig, 2003). Unstable coordinated actions (such as 90°) can also be stably produced without training if the visual feedback is altered to be more readily detected. This can be done by mapping a non-isodirectional coordination movement into an isodirectional feedback display (Wilson, Collins & Bingham, 2005a), or by removing the relative direction component entirely with Lissajous feedback (Kovacs, Buchanan & Shea, 2009a, b; Kovacs & Shea, 2011). Perceptual stability leads to action stability, independently of how the limbs are being used.

This research has been formalised into a perception-action model of coordinated rhythmic movement (Bingham, 2001, 2004a, b; Snapp-Childs, Wilson & Bingham, 2011; see Golonka & Wilson, 2012 for an overview). This model couples two phase-driven damped mass-spring oscillators via perceived relative phase. The information for relative phase is the relative direction of motion, with the detection of this variable modified by the relative speed. The key predictions of the model have all been successfully tested (Wilson & Bingham, 2008; Wilson, Snapp-Childs & Bingham, 2010; Snapp-Childs et al, 2011); however it does not yet address the egocentric constraint.

Egocentric vs Allocentric Constraints

Homologous muscle use produces isodirectional limb movement if the motion is in the sagittal plane, parallel to the body's midline. The two frames of reference for measuring relative phase are therefore often confounded. However, it is possible to separate these frames, either by altering the plane of the motion (e.g. into the transverse plane orthogonal to the body's midline) or altering the posture of the limbs (e.g. one prone, one supine). In each case, egocentric in-phase movements produce allocentric 180°, while anti-phase produces 0°.

The general result from studies using these manipulations is that while both factors contribute to coordination stability (e.g. Amazeen, DaSilva, & Amazeen, 2008; Meesen, Wenderoth, Temprado, Summers, & Swinnen, 2006; Salesse, Temprado, & Swinnen, 2005; Wilson, Collins, & Bingham, 2005a, 2005b), homology tends to show larger effect sizes and can often dominate (e.g. Kagerer, Summers, & Semjen, 2003; Li, Levin, Forner-Cordero, Ronsse & Swinnen, 2008; Peper, de Boer, de Poel, & Beek, 2008; Temprado, Swinnen, Carson, Tourment & Laurent, 2003; although see Meschner, Kerzel, Knoblich & Prinz, 2001, and Brandes, Rezvani, & Heed, 2017, for examples of allocentric dominance).

For example, Temprado et al (2003) used both kinds of manipulations across two experiments. First, they compared coordination stability of movements in the transverse and sagittal planes (Experiment 2). Muscle homology dominated; coordinations that required homologous muscle activations were nearly always more stable[1]. They then compared coordination stability of movements about the wrist in the sagittal plane, with hands either both prone, both supine, or one prone and the other supine (Experiment 3). Here they again found a large effect of homology, but also a smaller, reliable effect of direction.

Despite the evidence for substantive contributions to coordination stability from both egocentric and allocentric constraints, the two fields have progressed very separately. Thus, currently, no model adequately addresses both egocentric and allocentric constraints. Our goal in the present paper is to begin to explore how to expand Bingham's perception-action model to account for the egocentric constraint.

Feedback Displays

Coordination stability is also affected by the form of the allocentric feedback provided. A common method for continuous online feedback is the *Lissajous display* (Lee, Swinnen & Verschueren, 1995). In this display, the relative motions of the two oscillators are integrated and drive the motion of a

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[1] 180° motion did destabilise anti-phase movements in one condition.

single target in two dimensions. One oscillator defines the *x* coordinate, the other defines the *y* coordinate. At 0°, this yields a line of slope 1; at 180°, a line of slope -1. Intermediate relative phases produce ellipses of varying eccentricity, with 90° producing a circle. This feedback is now well known to support the production of any mean relative phase very easily, and to stabilise movements that vary in amplitude or frequency (Kennedy, Wang, Panzer & Shea, 2016; Kovacs et al, 2009a, b; Kovacs & Shea, 2010; Kovacs, Buchanan & Shea, 2010a, b). If the limbs are concealed from view, there is no allocentric relative direction information available from them to affect coordination stability, and the egocentric effects, while present, are often mitigated by the easily detected feedback about performance.

It is interesting that altering the perceived outcome of an action can affect how well it can be performed (e.g. Wilson et al, 2005a, b) but in the context of studying coordination there are two downsides. Firstly, there is the issue of feedback dependence. People trained on a novel coordination using Lissajous feedback cannot maintain their improved performance when the feedback is removed (although fading the use of the feedback does help; Kovacs et al, 2011; Maslovat et al, 2009). Secondly, and more importantly, Lissajous feedback removes relative direction information and so its contribution to coordination stability cannot be assessed or controlled.

To address these issues, Wilson, Coats, Snapp-Childs & Bingham (2010) developed *Coordination displays* and *Coordination feedback*. Coordination displays present a simple point-light display of two dots (one per oscillator) on a screen. The dots can be controlled by a computer (for judgment studies; e.g. Wilson & Bingham, 2008), by a person using joysticks (for bimanual coordination experiments), or by both (for unimanual coordination experiments in which a person coordinates with a computer-controlled dot; see Snapp-Childs, Wilson & Bingham, 2015 for a comparison of the two action methods). The mapping between the joysticks and the dots can also be altered to map any coordinated movement onto any visual outcome (as in Wilson et al, 2005a, b). Coordination feedback can then be added to drive learning. This feedback simply changes the colour of the dots from white to green when the person is moving at a target relative phase, +/- an error bandwidth. Thus, these displays are 'full cue' with regards to information about allocentric constraints, and the feedback simply augments, and does not transform, the display in any way. With this display, therefore, movement production can be both egocentrically and allocentrically constrained, these can be combined in many ways, and the feedback drives learning without creating dependence on the colour change signal (Wilson et al, 2010).

The Current Experiment

As noted, previous work comparing egocentric and allocentric constraints on coordination stability has separated the two by changing the movements being produced across conditions. This makes it difficult in principle to compare the various tasks, and it has led to a variety of results in the literature. Temprado et al (2003) manipulated both the plane of the movements (from frontoparallel to sagittal) and the hand posture (from both limbs prone or supine to one prone, one supine). The first manipulation mostly produced an egocentric dominance across conditions. The second condition again produced egocentric dominance, but there was also a smaller, but detectable contribution from the allocentric constraint. Conversely, Meschner et al (2001) used the hand posture manipulation and found allocentric dominance. They then used a finger tapping task in which the *fingers* being coordinated were homologous or not; again, regardless of limb homology, they again found allocentric dominance. Finally, they had people perform unseen circular movements to control the linear motion of two flags, and found allocentric dominance once more. Perhaps these mixed results are a consequence of separating the frames of reference with postural/planar manipulations.

The other issue is the presence or absence of allocentric, relative direction information about relative phase. When it is present, it is typically through vision of the limbs, and one way it can be absent is through using Lissajous feedback. The former forces the use of the postural/planar manipulations to separate the constraints, while the latter is actually an additional constraint on coordination stability, one that works to remove the differences between productions of various relative phases (e.g. Kovacs et al, 2009).

The current experiment therefore tested the contributions of the egocentric and allocentric constraints on coordination stability while addressing these issues. Participants produced bimanual coordinated rhythmic movements in the fronto-parallel plane only, and these were either in-phase or anti-phase (Egocentric Relative Phase). These movements either produced 0° or 180 mean relative phase on the screen (Allocentric Relative Phase), and the display was either in Coordination or Lissajous (Feedback Format). These three factors were fully crossed within-subject. Therefore, we were able to separate egocentric and allocentric constraints without changing the action requirements, while also investigating the consequences of the feedback display format.

Method

Participants

Thirty-two students and staff (12 male, 20 female, M_{age} = 29.81, SD_{age} = 6.85, age range = 20-47) from Leeds Beckett University participated. All participants had unrestricted movement and self-reported normal/corrected to normal vision. Ethical permission was granted from the Leeds Beckett Psychology Research Ethics Committee.

Design

The study was a 2x2x2 repeated measures design. There were three independent variables: Egocentric Relative Phase (2 levels: In-Phase, Anti-Phase), Allocentric Relative Phase (2 levels: 0°, 180°), and Feedback Display (2 levels: Coordination, Lissajous). Each participant took part in all 8 conditions with their hands concealed under a box, in a partially counterbalanced order (see Table 1). In addition, at the end of the session there was a No Vision control condition in which participants produced coordinated movements using either In-Phase or Anti-Phase movements. In these trials, the feedback display was turned off entirely and the hands remained concealed under the box.

We analysed two dependent variables: Coordination Stability (assessed as the proportion time-on-target, +/-20°; **PTT20**), and Coordination Consistency (assessed as **SDΨ** = (-2*lnU)^1/2, where U is the uniformity measure, here the mean vector length; Batschelet, 1981). While PTT20 is a better measure of coordination performance (Snapp-Childs et al, 2011, 2015), we also analysed SDΨ to allow more direct comparisons to previous work using this and related variability measures.

Apparatus and Stimuli

Refer throughout this section to Figure 1. Participants sat at a desk on a height adjustable chair, approximately 75cm from a Dell monitor (resolution 1920x1080, refresh rate 60Hz) placed with eye level aligned with the top of the monitor. Two Logitech 3D pro joysticks were connected via USB 2.0 to a Dell PC (3.2GHz, NVIDIA graphics, Windows 7). Joysticks were fixed firmly to the desk with minimal distance between them. The rumble feature was disabled and the plastic cladding had been removed to provide unrestricted movement. A modified cardboard box concealed the joysticks to ensure participants received visual feedback from the display only.

The displays, data recording, and calculation of dependent variables was handled by a custom MATLAB toolbox written by ADW incorporating the Psychtoolbox (Brainard, 1997; Kleiner et al. 2007; http://psychtoolbox.org).

Egocentric Relative Phase

In the *In-Phase* conditions, in-out/in-out movements were required to produce the target Allocentric Relative Phase. In the *Anti-Phase* conditions, side to side, parallel movements were required. The mapping of joystick motion to display motion was altered in software so that all four combinations of egocentric and allocentric relative phase could be produced for each feedback display.

Allocentric Relative Phase and Feedback Format

Coordination displays (Wilson et al, 2010) consisted of two white dots displayed centrally on a black background, one above the other. The left joystick controlled the upper dot and the right joystick controlled the lower dot. A target Allocentric Relative Phase of 0° required participants to keep both dots aligned, moving from left to right (and back again), and a target Allocentric Relative Phase of 180° required participants to move both dots in opposite directions (and back again), crossing in the middle.

Lissajous displays (Lee et al, 1995) consisted of a single white dot and a single white line, displayed centrally on a black background. The left joystick controlled the dot's horizontal movement, and the right joystick controlled vertical movement. 0° was depicted by a line of slope +1, and 180° was depicted by a line of slope -1. Both required participants to track the line with the dot.

In the *No Vision* condition, the screen displayed the black background only.

Procedure

Each condition was presented as a block of trials. The first trial was a demonstration of the target Allocentric Relative Phase at 1Hz in the relevant Display mode, accompanied by verbal instructions on how to produce it ("in and out" or "side to side"). This was followed by a 20s practice trial of the movements required for this block (data not recorded). Participants were not paced (metronomes have been shown to act as distractors; Kovacs et al, 2009a) but were asked to maintain the 1Hz frequency shown in the demo trial. Instructions and practice were repeated if participants misunderstood. Participants then proceeded to 5 recorded 20s trials.

Refer to Table 1. Conditions were blocked by Display type. The first two sets of blocks were either Coordination or Lissajous feedback, with the subsequent sets testing the alternative feedback condition. Within each set, the first block target Allocentric Relative Phase was always 0°, and the second block target always 180°. Between sets, we alternated between In-Phase and Anti-Phase movements. The final set of two blocks were always the No Vision condition, with a block of 5 Anti-Phase trials followed by 5 In-Phase trials.

Analysis

The position time series from each joystick was recorded at 60Hz throughout each trial and filtered using a Butterworth low-pass filter with cut-off frequency 10Hz. This filtered signal was differentiated to yield velocity, and continuous relative phase calculated as $\tan^{-1}(V/X)$ at each sample. Coordination stability (PTT20°) was calculated as the proportion of time the joysticks were within 20° of the target Allocentric Relative Phase. Coordination consistency (SDΨ) was calculated from a log transformation of circular uniformity as per Snapp-Childs et al (2011). These calculations were performed in MATLAB 2014.

Fourteen trials were excluded in which the joysticks became loose, the monitor lost power, or the participant did not follow instructions. Participants' mean PTT20 and SDΨ was calculated from all valid trials for each condition.

Data from each of the eight Egocentric Relative Phase * Allocentric Relative Phase * Display conditions were analysed in JASP v0.8.5.1 (2018) using a separate repeated measures ANOVA for each dependant variable. The data from the No Vision condition were analysed in JASP with a paired-sample one-way Student t-test for each DV, testing the prediction that In-Phase movements would be 1) more stable and 2) more consistent than Anti-Phase movement.

Results

Coordination Stability (PTT20°)

Refer to Figure 2. A three-way repeated measures ANOVA on PTT20 revealed significant main effects of Egocentric Relative Phase ($F(1, 31) = 85.8$, $p < .01$, $\eta p^2 = .74$), Allocentric Relative Phase ($F(1, 31) = 8.17$, $p < .01$, $\eta p^2 = .21$), and Feedback Display ($F(1, 31) = 7.53$, $p < .05$, $\eta p^2 = .20$). Participants were able to produce the target relative phase more stably with In-Phase movements ($M = .83$, $SD = .07$) than with Anti-Phase Movements ($M = .77$, $SD = .06$); with Allocentric Relative Phase at 0° ($M = .80$, $SD = .07$) than with it at 180° ($M = .79$, $SD = .07$); and with Coordination feedback ($M = .81$, $SD = .07$) than with Lissajous feedback ($M = .79$, $SD = .08$). No interactions were significant (all $ps > .197$).

A one-way paired samples Student's t-test on PTT20 revealed a significant difference between Egocentric Relative Phase conditions in the No Vision control ($t(31) = 3.78$, $p < .01$). As predicted, In-Phase movements ($M = .82$, $SD = .08$) were more stable than Anti-Phase movements ($M = .77$, $SD = .06$).

Coordination Consistency (SDΨ)

Refer to Figure 3. A three-way repeated measures ANOVA on SDΨ revealed significant main effects of Egocentric Relative Phase ($F(1, 31) = 73.7$, $p < .001$, $\eta p^2 = .70$); and Allocentric Relative Phase ($F(1, 31) = 4.33$, $p = .046$, $\eta p^2 = .12$). Participants were able to move more consistently using In-Phase movements ($M = .27$, $SD = .07$) that with Anti-Phase movements ($M = .35$, $SD = .07$) and with Allocentric Relative Phase at 0° ($M = .31$, $SD = .08$) than at 180° ($M = .32$, $SD = .08$). The main effect of Feedback Display was only close to significance ($F(1, 31) = 4.00$, $p = .054$). No interactions were significant (all ps > .164).

A directional paired samples Student's t-test on SDΨ revealed a significant difference between Egocentric Relative Phase conditions in the No Vision control ($t(31) = 3.37$, $p <.01$). As predicted, In-Phase movements ($M = .29$, $SD = .08$) were more consistent than Anti-Phase movements ($M = .31$, $SD = .06$).

Discussion

This experiment evaluated the contributions of egocentric relative phase, allocentric relative phase and allocentric display format on coordination stability and consistency. To improve and build upon previous work, we separated the egocentric and allocentric constraints without confounding the required actions by altering the plane of the movements or posture of the hands across conditions. In-phase movements were more stable than anti-phase movements, 0° was produced more stably than 180°, and Coordination feedback led to more stable performance than Lissajous feedback. The egocentric effect was by far the largest. This pattern is consistent with previous studies and expands the result to demonstrate how the format of the visual feedback also affects stability.

On one hand, our data seems to support models of coordinated rhythmic movement in which the egocentric constraint (modelled as muscle homology and neural crosstalk) is the primary factor in coordination stability (e.g. Beek et al, 2002; Cattaert et al, 1999; Daffertshofer et al, 2005) over perception-action models that currently emphasise the allocentric constraint (e.g. Bingham, 2001, 2004a, b; Snapp-Childs et al, 2011). In order to develop the Bingham model to account for the egocentric constraint, we need to consider the evidence about the source of the egocentric constraint, and that evidence does not entirely favour a neural crosstalk explanation.

What Is the Source of the Egocentric Constraint?

As described in the Introduction, the current candidate explanation for the egocentric constraint on coordination stability involves neural crosstalk and interference. The basic idea is that neural commands sent to the two limbs interfere with one another when non-homologous muscles are required, and that this interference occurs in the brain.

However, Swinnen, Dounskaia & Duysens (2002) tested this hypothesis by manipulating where in the workspace the coordinated movements were happening, while Swinnen, Dounskaia, Levin, & Duysens (2001) spring loaded the arms producing the movements to affect patterns of muscle activation. The evidence from these studies clearly showed that while relative phase *was* defined in an egocentric frame of reference, this frame was *not* being defined with respect to patterns of muscle activation. Swinnen et al (2002) concluded that because the egocentric frame of reference was abstracted away from the details of the limbs, it was the result of how the brain encodes direction information.

To align this result with the ecological approach underpinning the Bingham model (Golonka & Wilson, 2012), we would like to reframe this conclusion in terms of perception. From an ecological point of view, the first place to look for an explanation for structure in behaviour is in the structure of the perceptual information used to coordinate and control the behaviour. In the case of coordinated rhythmic movement, one source of information is the relative direction of motion of local regions of optic flow. The medium of the optic array in which this flow occurs shares the allocentric frame of reference of the things moving in the world. This is why the allocentric constraint is a factor in coordination stability and why it is implemented the way that it is in the perception-action Bingham model (Bingham, 2001, 2004a, b; Snapp-Childs et al, 2011).

Unlike the optic array, the medium of haptic perception is literally composed of body tissue (Turvey & Fonseca, 2014) and so the frame of reference is often egocentric (Kappers & Bergmann Tiest, 2015). We therefore propose that the source of the egocentric constraints on coordination stability is not the brain, but *the haptic perception of relative phase*. We also propose that the haptic information will also be relative direction of motion (as in vision), just measured in an egocentric frame of reference.

There is some supporting evidence for this perceptual (vs neural) analysis, although none comes from work explicitly designed to test the hypothesis. Wilson, Bingham & Craig (2003) tested the haptic perception of relative phase variability, and showed that the information here was the relative direction of motion. The coordinated movements to be judged were tracked, not generated by the participants, and so neural crosstalk is unlikely to have played a role. However, the movements were made in the sagittal plane where egocentric and allocentric measurements of relative direction produce the same answer; future work should test haptic judgments in the fronto-parallel plane or with different limb postures. More recently, Zhu, Mirich, Huang, Snapp-Childs & Bingham (2017) showed that people could learn a novel 90° coordination with either visual or haptic feedback, but that this training did not transfer across modalities. This would be expected if the frames of reference are incompatible (although it is not the only explanation). Finally, the work by Swinnen et al (2001, 2002) suggests that it is the frame of reference in which direction information is treated that matters most, and ecologically that frame is best analysed in terms of perception, rather than at the level of neural encoding.

The perceptual hypothesis remains speculative, however, and it needs data from a programme of research matching the investigation of the visual perception of relative phase (see Wilson, Huang, Bingham & Zhu, 2018 for an initial, exploratory analysis). The resulting understanding of the haptic perception of relative phase could then be implemented in an extended version of the Bingham model, and the competing hypotheses about the origins of the egocentric constraint tested explicitly.

Summary

The current experiment examined the effects of egocentric relative phase, allocentric relative phase and feedback format on coordination stability and showed that while all three factors matter, egocentric relative phase has the largest effect. In order to move towards expanding Bingham's perception-action model to include the egocentric constraint, we considered the existing evidence for what, in the human body, seems to be implementing that constraint. Although the effects have been discussed for many years in terms of muscle homology and neural cross-talk, recent evidence favours direction information being either neurally encoded (Swinnen, 2001, 2002) or, as we suggest here, ecologically perceived in an egocentric frame of reference that is not defined by patterns of muscle activation.

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Tables

A

	Sets				
	1	**2**	**3**	**4**	**5**
Block 1 (5x 20s trials)	Coordination Allocentric 0° Egocentric In-Phase	Coordination Allocentric 0° Egocentric Anti-Phase	Lissajous Allocentric 0° Egocentric In-Phase	Lissajous Allocentric 0° Egocentric Anti-Phase	No Vision Egocentric Anti-Phase
Block 2 (5x 20s trials)	Coordination Allocentric 180° Egocentric Anti-Phase	Coordination Allocentric 180° Egocentric In-Phase	Lissajous Allocentric 180° Egocentric Anti-Phase	Lissajous Allocentric 180° Egocentric In-Phase	No Vision Egocentric In-Phase

B

Set Order 1	1	2	3	4	5
Set Order 2	1	2	4	3	5
Set Order 3	2	1	3	4	5
Set Order 4	2	1	4	3	5
Set Order 5	3	4	1	2	5
Set Order 6	3	4	2	1	5
Set Order 7	4	3	1	2	5
Set Order 8	4	3	2	1	5

Table 1.

A) We created 5 different sets of trials. Participants either did all the Coordination conditions first, or all the Lissajous conditions first, then switched. The No Vision set was always done last. Within a set, Allocentric 0° was always the first block of trials, and Allocentric 180° the second. We then alternated the actions required (Egocentric In-Phase or Egocentric Anti-Phase) to achieve each target Allocentric Relative Phase so that a different movement was required to produce each display behaviour. This set-up allowed some counterbalancing of conditions while not overloading the participant with constantly changing task demands.

B) The 8 partially counterbalanced orders. 4 participants did each order for a total N of 32.

Figures

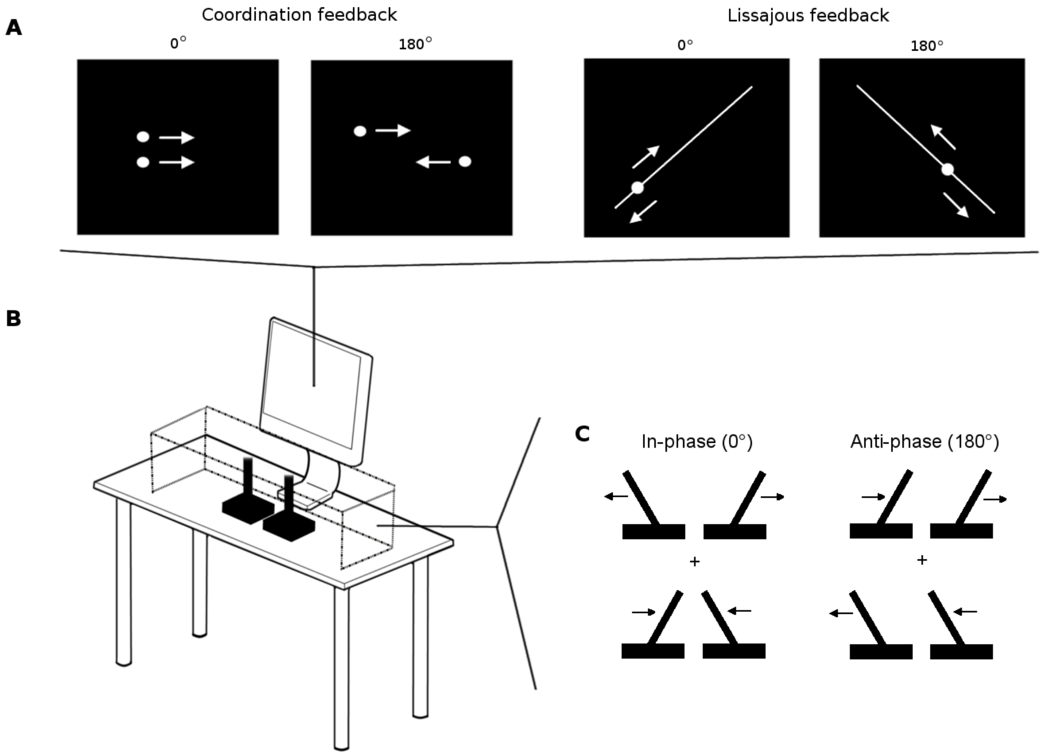

Figure 1.

Schematic of the experimental apparatus and conditions. A) Coordination feedback and Lissajous feedback depicted with Allocentric Relative Phases of 0° and 180°. B) Apparatus. Dotted line denotes the solid box concealing joysticks. C) Egocentric conditions: In-Phase movements required "out and in" movements, Anti-Phase movements required "side to side" movements.

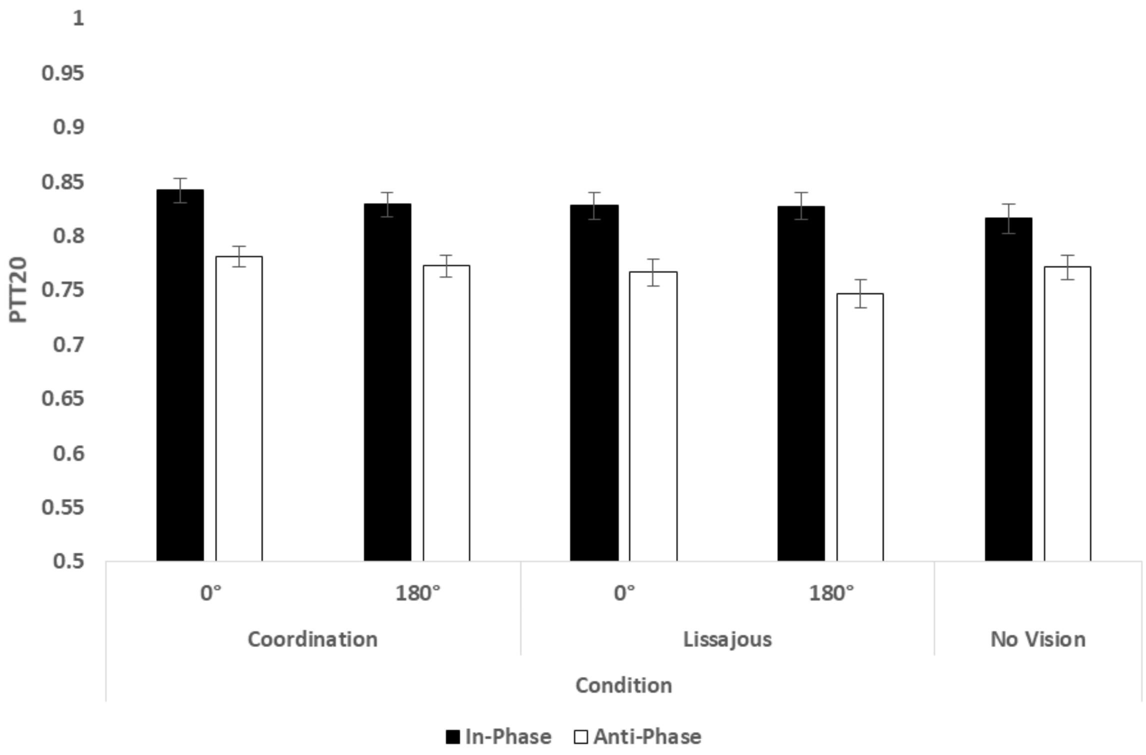

Figure 2.

Proportion time-on-target (PTT20) across all conditions. All three main effects were significant, and the two No Vision conditions were also different in the predicted direction.

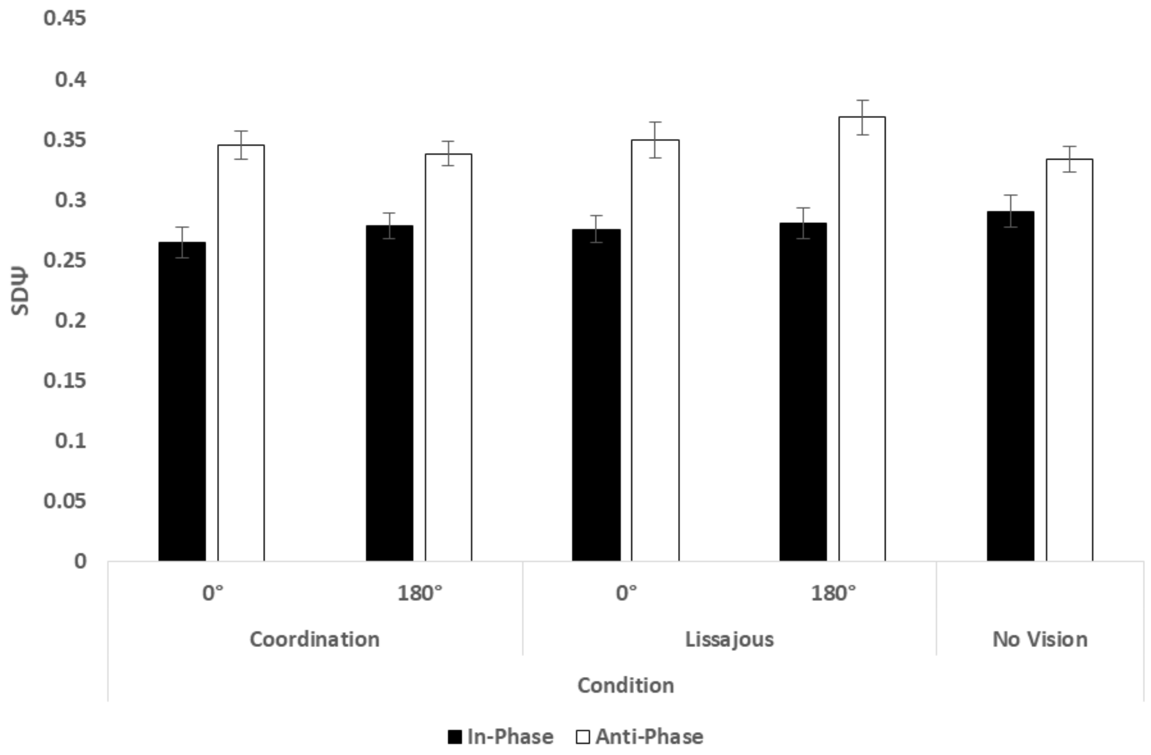

Figure 3.

Coordination consistency (SDΨ) across all conditions. The main effects of Egocentric and Allocentric Relative Phase were significant, and the two No Vision conditions were also different in the predicted direction.