A PERCEPTION-ACTION APPROACH TO RHYTHMIC MOVEMENT COORDINATION

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Abstract

Coordinated rhythmic movement is very specifically structured in humans. 0° mean relative phase (the two oscillating limbs doing the same thing at the same time) is easy and stable; 180° (the two limbs doing the opposite thing at the same time) is less stable; and no other relative phase is stable without training. The present study explored the identity and role of the perceptual information used in rhythmic movement coordination tasks in creating this pattern. 4 participants were trained to improve their perceptual resolution of 90° over a two week period. This training resulted in improved movement stability in a rhythmic movement coordination task, without additional practice of the task itself. Improved ability to detect the information at 90° allowed for improved performance in a movement task at 90°. In a second study, we systematically perturbed three aspects of the coordinated motion of two dots on a computer screen, and tested the effect of these perturbations on the same 4 participants. In line with predictions based on previous modeling results, perturbations that disrupted perceptual information about peak velocity and peak amplitude disrupted participants' ability to perform the task; this information allows rescaling of velocity information and is vital for stable perception of the underlying information (the relative direction of motion). Perturbations that increased the magnitude of the relative speed between the dots added noise to the task, again as predicted. Relative direction proved impossible to perturb, independently of mean relative phase, suggesting it has a vital role in the task. We conclude that the information used in rhythmic movement coordination tasks is both the phase (position within a cycle) and the relative phase, instantiated as the relative direction of motion. Movement stability is a function of perceptual stability, and improving the latter improves the former. The

results are explained within a perception-action framework, in which perceptual information is an integral part of the organization of a perception-action dynamical system.

General Introduction

The perception-action approach treats perception and action as fundamentally interconnected parts of the same system. It is inspired by Gibson's ecological approach to perception (e.g. Gibson, 1966. 1979; Turvey, Shaw, Reed & Mace 1981) and Bernstein's treatment of movement as a problem of coordination and control (Bernstein, 1967), and it integrates them by recognizing the role of perceptual information in the assembly and maintenance of coordinative action structures, as well as the role of action in creating part of that information.

The Bernstein approach is a solution to a fundamental problem in movement science, the 'degrees of freedom' problem. The human action system is a high-dimensional system, with many redundant degrees of freedom, any of which can become temporarily irrelevant given a current task. In addition, the same action can be achieved in a number of different ways (with different limbs, on different temporal and spatial scales, under different postural demands, etc). Finally, not every part of a movement is under direct neural control – gravity, for instance, is an important contributor to the form of movement. The problem for movement planning is to reduce those degrees of freedom to a manageable (i.e. controllable) number. The Bernstein solution is for the action system to form and exploit synergies, collections of action components assembled into a higher-order organization. The classic example is the organization of the muscles about the elbow into a mass-spring dynamical system, with the advantage that control of such a dynamic (in order to, for instance, perform a reach) is reduced to manipulating the stiffness and equilibrium point of the spring.

Gibson's ecological approach to perception is a solution to perception's version of the degrees of freedom problem; sensations, traditionally viewed as the basis for perception, are also not a one-to-one mapping of the world. A given pattern of sensations can arise from multiple states of the world. Gibson's solution was to realize that perception is also organized to take advantage of higher-order organizations, this time organization within energy arrays. These higher order variables can specify (map one-to-one onto) states of the world.

Bernstein's higher order action systems require assembly as well as online coordination and control. This is the role of perception, to provide information about the state of the system and the intended state of the system which then drives the dynamical behavior of the action system. Gibson's higher-order variables have the kind of stability and specificity required for the efficient and reliable control of action. This is the essence of the perception-action approach.

The current studies are an exploration of rhythmic movement coordination as just such a perception-action system. Rhythmic movement coordination is organized in a highly characteristic fashion; 0° and 180° mean relative phase are the only two stable modes, with 0° more stable than 180°. 90° is maximally unstable. The issue at hand is why this class of movement should be organized the way that it is.

Bingham (2001, 2004a, b) proposed a model, in which two oscillators are coordinated via a perceptual coupling function – each mass-spring is driven by the perceived phase of the other mass-spring. The model takes the form

$$\ddot{x}_1 + b\dot{x}_1 + k x_1 = c \sin(\phi_2)\, P_{ij}$$
$$\ddot{x}_2 + b\dot{x}_2 + k x_2 = c \sin(\phi_1)\, P_{ji} \qquad (1)$$

where Φ is perceived phase, and is equal to

$$\Phi = \arctan(V_n / x) \qquad (2)$$

and where P (rho) is perceived relative phase, and is equal to

$$P = \mathrm{sgn}(\sin(\phi_1)\sin(\phi_2) + \alpha(\dot{x}_i - \dot{x}_j)^3 N_t) \qquad (3)$$

V_n is the velocity normalized by the frequency, and x is position with reference to an origin (located at peak velocity). The coupling function drives each oscillator using the perceived phase of the other oscillator, modified by the perceived relative phase. Phase is predicted to be perceptually instantiated as a normalized velocity signal, and relative phase is predicted to be instantiated as the relative direction of motion, the detection of which is modified by the relative speed and a Gaussian noise term.

Perception-action systems are dynamical systems. They are described by the evolution over time of a set of state variables, which describe the components of the current system and their relation to one another. Dynamical systems are studied using perturbation methods – by perturbing a variable or parameter and measuring the consequences, we can discover both the make up and organization of the system being studied. A good example of this approach is found in Kay, Saltzman & Kelso (1991), who systematically perturbed the motion of a rhythmically moving limb and established that, in general, such a movement is organized as a non-linearly damped, autonomous mass spring system. Bingham's model was designed to reflect these constraints.

Up to this point, perturbation methods have focused on the action components of perception-action systems (perhaps partly due to the origins of these methods in the physical sciences). An equally crucial component of any perception-action system, however, is the perceptual information used for the online coordination and control of the rest of the coordinative structure. Uncovering the identity of this component and its relations to other parts of the system is a crucial step in fully describing the system at hand. Information is just another part of the system, not privileged over any other component. In order to investigate the identity of the information for a given task, as well as its relationship to the other components in the system, it is therefore still appropriate to employ perturbation methods.

Perturbations of various components of the movement (by spatial displacement of the limb (Kay et al, 1991), by changes in frequency (Kelso, 1984), or by learning (e.g. Zanone & Kelso, 1992) have been studied extensively. The measure, however, is always the effect of altering a movement characteristic on the movement itself, and these studies (of necessity) also perturb the information; Bingham proposed that the information required to maintain stable coordinated movements is, after all, information about the movement of the limbs (direction and speed). But the informational consequences of the movement perturbations have never been carefully controlled. The current study therefore manipulated the perceptual components of the rhythmic movement coordination perception-action system in two ways. First, four subjects were trained to improve their ability to visually discriminate 90° mean relative phase from neighboring phases – what effect does this improved perceptual discrimination have on the system's motor behavior at 90°? Second, we investigated what it was the subjects had learned to discriminate, i.e. the informational basis for the post-training changes we observed in their movement stability. We did this by systematically perturbing various candidate information variables – what effect do each of these perturbations have on subjects' discrimination performance? The answers to these questions will provide a more complete picture of the coordinated rhythmic movement perception-action system.

Introduction – Experiment 1

Bimanual rhythmic movement coordination is a paradigm case for the study of perception-action, because it is involves all the essential features of a perception/action system. These features include voluntary control of limb movements, coordination among multiple limbs or people, and online perceptual (informational) guidance and coupling of the voluntary movement. It is also an example of a pervasive behavior in people – rhythmic movements are found in walking, running, etc.

The variable of interest in studies of movement coordination is relative phase (ϕ). *Phase* is an angular measure of an oscillator's position within its cycle, and *relative phase* is simply the difference in phase between two oscillators. *0° Mean Relative Phase* (MRP) means that the two oscillators are at the same point in their cycle at the same time; 180° MRP means they are at opposite ends of their cycle at the same time; and 90° MRP is the point halfway in between these extremes.

Bimanual rhythmic movement coordination is very specifically structured in humans. The key phenomena are:

1. 0° and 180° are the only two stable coordinations that people can spontaneously produce. Other phase coordinations must be learned (previous studies have investigated learning of 90° (Zanone & Kelso, 1992a) and 135° (Zanone & Kelso, 1992b, 1997; also

0° and 180° +/- 30° and 60° - Wenderoth, Bock, & Krohn, 2002). Without training, 90° is maximally unstable.

2. 0° is more stable than 180°. Phase variability is higher at 180°, and lowest at 0°. In general, an increase in frequency leads to increased phase variability, especially at non-0° phase relations. This is followed (under a non-interference instruction) by a spontaneous transition to 0°. There is no tendency to transition from 0° to 180° or any other relative phase. This transition (from 180°) occurs around 3-4Hz.

This pattern is captured in the Haken-Kelso-Bunz (HKB) model by a potential function (Haken, Kelso & Bunz, 1985):

$$V = -a \cos\varphi - b \cos 2\varphi \qquad (4)$$

This function has two attractors, one centered at 0° and one centered at 180°. 90° is an unstable repellor point. Decreasing the ratio b/a simulates the effect of increasing frequency (the attractor at 180° is progressively annihilated, leaving 0° the only stable state). However, it is clear that this is an explicitly phenomenological model. The behavior simply arises from the superposition of two cosine functions, with no reference to the system instantiating the behavior. In addition, talk of attractors (while a convenient descriptive shorthand) is not explanatory. Haken et al provided no account of the origin of the potential function, nor did they have any intention of doing so. The question therefore remains – why is human movement coordination patterned this way?

Perceptual Coupling

The key fact about the coordinated rhythmic movement literature is that movements that are trivial when performed in isolation become difficult to maintain when performed simultaneously as a coordinated movement. This fact reflects that a constraint (or constraints) on task performance emerges from the coordination requirement.

Coordination entails a coupling of the things to be coordinated. The emergent constraint is a preference for symmetrical behavior, caused by some characteristic of the coupling mechanism. This preference manifests itself as stable in-phase behavior and unstable anti-phase behavior. What coupling mechanism accounts for this preference?

There is strong evidence that the coupling is in general informational, or perceptual. The basic movement phenomena persist when the oscillators belong to two different people (Schmidt, Carello & Turvey, 1990; Temprado, Swinnen, Carson, Tourment & Laurent, 2003) or when one of them is a simulated oscillator (Buekers, Bogaerts, Swinnen & Helsen, 2000; Wilson, Collins & Bingham, 2005a; Wimmers, Beek & van Wieringen, 1992). In these cases, the coupling was mediated completely visually.

Motivated by these findings, a series of perceptual studies had participants make judgments of phase variability in oscillators that were presented visually (Bingham, Schmidt & Zaal, 1999; Bingham, Zaal, Shull & Collins, 2000; Zaal, Bingham & Schmidt, 2000; Bingham 2004b) and proprioceptively (Wilson, Bingham & Craig, 2003). Levels of phase variability are best discriminated at 0°. 180° is judged to be more variable than 0°, even with no added variability, and when there are added levels of variability, these are not well discriminated. 90° is judged to be maximally variable (even in the absence of added variability) and the added levels of phase variability are not distinguished at all. As frequency was increased, 180° was judged to be increasingly variable and discrimination at 0° got worse. In other words, judgments of phase variability follow an inverted, asymmetric U-shaped function of mean relative phase, the same shape as the HKB potential function.

The next step in the research program was to explicitly manipulate the perceptual information used to perform the task. Changing the information changes the stability of that movement. Bogaerts, Buekers, Zaal, & Swinnen (2003) transformed the visual feedback from a movement task (so that 180° movement produced 0° on a screen, or so that orthogonal movements produced parallel motion on a screen). They found that if the visual signal was at 0°, non-0° movements were stabilized, and orthogonal movements were stabilized by parallel feedback. Wilson, Collins & Bingham (2005a) replicated this phenomena using a different paradigm. Participants tracked a computer controlled moving dot on a screen with a joystick controlling a second dot. In one condition, participants were told to move so as to produce 0°, 90° or 180° between the two dots. Movement stability was an HKB shaped function of mean relative phase. In a second condition, the mapping between the joystick and the dot was altered, such that in order to produce 0° between the two dots, participants had to move at 90° or 180°. In these cases movement stability increased and did not show the HKB shape.

These studies demonstrate that non-0° movements are not intrinsically unstable. If the participant can readily discriminate the information used to perform the task, then this stable perception allows for stable movement. Non-0° movements are unstable under normal conditions because the conditions do not allow the participant to clearly discriminate the information. Movement stability is a function of perceptual stability.

The evidence for perception is compelling. However, there are two other common places to look for a symmetry preference that should be noted. These are the central nervous system and muscle homology.

At least two separate attempts to model the phenomena have placed the coupling in the nervous system. Cattaert, Semjen & Summers (1999) modeled data from a bimanual circular drawing task, using a model whose central feature was neural cross talk. Cross talk entails mirror-image motor commands being sent by the motor system controlling one hand to the other hand. This has the effect of destabilizing non-0° movements. Beek, Peper & Daffertshofer (2002) modeled movement coordination as two neurally implemented non-linear oscillators, coupled to each other and driving a linearly damped end-effector. Both of these approaches, however, fail to explain how the phenomena are preserved when the coupling is between people, or between a person and a computer display. In these cases, neural coupling is simply eliminated. Additionally, it is not clear that modeling the end-effector with linear damping is appropriate, given the dynamic characteristics of a rhythmically moving limb[1] (Kay, Kelso, Saltzman, & Schöner, 1987; Kay et al 1991).

The other place to look is in the muscles implementing the movements. Kelso's original (1984) paper specifically describes in-phase movement as entailing the coactivation of homologous muscle groups – simultaneous flexion and extension. Swinnen and colleagues (e.g. Swinnen, Jardin, Meulenbroek, Dounskaia, & Hofkens-Van Den Brandt, 1997) refer to this as the egocentric constraint, because symmetry is defined with respect to the midline of the body. Making two functionally identical muscle groups act the same way at the same time is easier than making them act differently – the lower stability of non-0° phase relations reflects a bottleneck, this time in our ability to activate coalitions of muscles. While it is empirically the case that such movements are more stable, the precise mechanism that leads to such a symmetry preference is not yet elaborated. Again, this fails to account for the phenomena persisting between people and for the persistence of the phenomena when using non-homologous muscle groupings (e.g. coordinating a leg and an arm; e.g. Baldissera, Cavallari & Civaschi, 1982; Kelso & Jeka, 1992; Swinnen, Dounskaia, Verschueren, Serrien & Daelman, 1995).

There is therefore a clear motivation to explore the nature of the perceptual coupling in these tasks. While the data does support a role for (at least) muscle homology, the alternate explanations fails to account for many of the basic phenomena, and any effect of muscle homology is almost certainly underwritten by proprioception.

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[1] These characteristics, for example phase resetting and an inverse frequency-amplitude relation, require the limb to be treated as an autonomously driven, non-linear oscillator. If a neural driver is required to provide the observed non-linearities, it is difficult to maintain the required autonomy.

Learning New Coordinations

It is possible to learn to move at phases other than 0° and 180°. The first learning studies in this field (Zanone & Kelso, 1992a, 1992b, 1997; Kelso & Zanone, 2002) have trained participants to move at 90° or 135°, and investigated how this training generalizes to other relative phases and effectors. Learning 90° was described as a qualitative change in the shape of the potential function. Specifically, learning 90° created a new attractor in the HKB potential function that maps the relative performance levels. This new attractor only generalizes to the symmetry partner[2] of 90°, namely 270°. Participants who already exhibited this tri-stability (i.e. attractors at 0°, 90° and 180°) have been trained to perform 135°. In this case, learning does not involve the creation of a new attractor - instead, the 90° attractor is moved to centre on 135°. Again, however, this new skill only generalizes to the symmetry partner of 135°, namely 225°. In both cases, there is a temporary loss of the (less stable) 180° attractor during training. It is regained as performance around the new mean relative phase stabilizes. Kelso & Zanone (2002) found a similar pattern of results, but this time also showed that training a new coordination in one set of effectors (e.g. the arms) transferred to a different set of effectors (the legs). Kelso and Zanone interpreted their results as showing that what is learned is a high-level, abstract (but neurally implemented) dynamic representation of the action.

Another set of learning studies focused in more detail on how learning varied across different parameters that characterize performance (Wenderoth & Bock, 2001) or across

[2] A symmetry partner is a coordination that is identical except for which oscillator is ahead and which is behind; in other words, movement stability is independent of which limb leads and which follows.

different locations in HKB potential function space (Wenderoth et al, 2002). Wenderoth & Bock (2001) showed that learning to perform 90° seemed to occur over three separable processes, each occurring on their own time scale. The fastest improvement was in mean performance (being able to maintain an average of 90° mean relative phase); next fastest was mean accuracy (lowering the variability of performance); and slowest was improvements in switching time (with practice, participants took less and less time to intentionally switch from 90° to 0° or 180° and back again). They equated these parameters with attractor location (mean performance), attractor depth (variability) and the steepness of the attractor (switching time; see Scholz & Kelso, 1990). This time scale ordering seems quite sensible; achieving the target phase-to-be-learned on average means that performance has been constrained to a smaller region of the potential function space. This then allows for a period of consolidation in which variability is reduced, which in turn allows for the new pattern to become well learned (more stable).

Wenderoth et al (2002) trained participants to produce coordinations that were either 36°, 60° or 90° away from 0° or 180°. Participants were able to learn these coordinations with extensive training; interestingly, however, they were not learned in the same way, nor to the same extent. Zanone & Kelso (1994) had predicted that learning rate should vary inversely with the stability of the closest attractor, because competition between learning requirements and intrinsic coordination dynamics would become smaller with greater distance. Wenderoth et al found, however, that patterns close to 0° were stabilized faster than patterns closer to 180°. This replicated the empirical findings of Fontaine, Lee & Swinnen (1997). Given their results, Wenderoth et al (2002) hypothesized that perception of the movements may be playing a key role, rather than competition between attractors. Specifically, they suggested that because visually presented phase relations close to 0° are more easily discriminated than those close to 180° (Zaal et al, 2000), learning 36° is easier than learning 144° because the former can be easily discriminated from 0°, while the latter is not easily discriminated from 180°. If a person cannot discriminate between two different movements, they will be unaware that they are moving incorrectly and hence be unable to improve.

Wenderoth et al (2002) also classified their novel coordinations in terms of a ratio which describes how many equal sized periods of time (epochs) within a half cycle were spent moving in the same or opposite directions. For instance, 90° is 1/1, because one half cycle consists of one same direction epoch and one opposite direction epoch, both of equal length. 60° is 2/1, because there are two equal time epochs spent moving in the same direction and one spent moving in opposite direction (see Figure 1, Wenderoth et al, 2002). Dividing the coordination-to-be-learned in this way is one possible strategy for learning the task. If this *rhythm setting* underlies performance, they predicted that tasks with more subdivisions would be harder than tasks with fewer; more complex timing ratios are generally harder to learn (Walter, Corcos & Swinnen, 1998). However, this was not the case – in general, performance was better for coordinations with more time spent moving in the same direction (so 4/1 (36°) was performed more accurately than 2/1 (60°)).

All the learning studies cited above trained people to move at a novel coordination by having them move at that coordination, paced by some external stimulus (such as a visual metronome). But the characteristics of learning all suggest that it's not the movement, per se, that's being learned. First, learning a novel coordination allows you to move at the symmetry partner of that coordination for free; this suggests that the specific action being implemented during training (a particular limb leading or lagging) is not what's being acquired. Second, learning is not specific to the limbs instantiating the movement; for instance, learning to move at 90° generalizes from arms to legs (Kelso & Zanone, 2002). Kelso and Zanone discuss learning in terms of acquiring an abstract dynamical coordinative structure that defines how the limbs are to be controlled, but this, like the HKB model, is just a redescription of the phenomena. So what is it that changes over the course of learning?

From an ecological perspective (Gibson, 1966, 1979; Turvey et al, 1981) perception and action are based in information that lawfully specifies the events and objects of the world. Perceptual learning, from the ecological perspective (Gibson, 1969; Gibson & Pick, 2000) entails differentiation of the information required for the task from the relevant ambient energy array, followed by progressive attunement. Perception, however, does not exist in a vacuum – it is inextricably related to action. The coordination and control of action requires detection of the requisite information, information that is generated by the action itself.

The judgment and movement studies cited above clearly implicate a vital role for perception in determining movement stability (see also Mechsner, Kerzel, Knoblich & Prinz, 2001, and Mechsner & Knoblich, 2004). The results of Bogaerts et al (2003) and Wilson et al (2005a), in which non-0° movements are stabilized by transformed feedback, suggest that movement stability is a function of perceptual stability. The reason 0° is easy while other phases are hard is that the requisite information is detected most stably at 0° and less so elsewhere. Improved stability of movement in the various learning studies therefore implies improved stability of perception; what has changed is the participants' ability to detect the requisite information at the novel coordination. The current study is therefore designed to test an informational hypothesis about the stability of rhythmic movement coordination.

The first experiment asks whether improving perceptual discrimination of the space around 90° lead to improvements in movement stability at 90°? Participants were trained to be able to discriminate 90° from neighboring phases. It was predicted that improved resolution would translate to an improved ability to maintain a movement at 90° in the absence of practice at the actual movement.

Methods - Experiment 1

The first experiment was a learning study. 4 participants were trained to visually discriminate a display of two dots moving at 90° relative phase from displays showing nearby phases by performing a 2 alternative forced choice (2AFC) judgment task.

Previous learning studies have had people improve movement stability by practicing the movement itself. The current hypothesis is that movement stability is a function of perceptual stability. It predicts that if you improve the latter, you will also improve the former, even if you have not practiced the movement. There were therefore three parts to this first experiment. First, we established a baseline level of performance in the visual judgment task, as well as in a movement coordination task. This tested movement and perceptual stability prior to training. Second, participants performed multiple training sessions, in which they performed progressively harder perceptual discriminations around 90° with feedback. There was no practice at the movement task. Third, two post training sessions repeated the baseline measures (visual discrimination and movement) to test whether changes in performance in the perception task translated to changes in performance in the movement task.

Participants: There were 4 participants (3 female, 1 male, average age 28 years). They were paid $10 for each hour long session.

Baseline - Judgments

Procedure: Participants performed a series of 2AFC judgments on successively presented stimuli. There were two tasks – Choose 90° and Choose 180°. Each trial consisted of a pair of successively presented stimuli (two dots moving harmonically on the screen at some mean relative phase, for 4s at 1.5Hz). Within the Choose 90° task, one of each pair showed two dots moving at 90°, and the other was either the same or different. The 'same' trials were catch trials and were there to provide a measure of response bias. The 'different' stimuli were 45°, 54°, 63° 72°, 81°, 99°, 108°, 117°, 126° and 135°. 90° was either the first or second display – there were therefore 21 different trial types (10 different locations x 2 orders, plus the catch trial). Participants were presented with 5 blocks. Each block contained one of each trial type, with display order randomized within block. Their task was to identify which display in the pair was 90° (they responded 'first' by pressing the 'A' key, 'second' by pressing 'L'). This design was repeated for the Choose 180° task, with the 'different' stimuli being 135°, 144°, 153°, 162°, 171°, 189°, 198°, 207°, 216° and 225°. Participants identified which display was 180°. There was no feedback given during these trials; there was, however, a brief practice session that gave examples of 0°, 90° and 180° as well as four practice trials of the 2AFC task, with feedback.

Data Analysis: Data from this task was the frequency with which participants responded "90° First" or "180° First". 90° (or 180°) was shown first on half the trials, second on the other half.

For the Baseline and Post-Training sessions this frequency data was first analyzed with each trial being described by the magnitude of the phase difference. This places data from '45-90' trials and '135-90' at the same point on the axis, specifically -45. This data will be referred to as 'compiled', and was analyzed both as a single data set (all four subjects) and for each individual subject.

Bingham (2001, 2004a, 2004b) hypothesized that the information underlying performance in this task is the relative direction of motion, with the resolution of this variable affected by the relative speed. Relative direction behaves differently on different sides of 90° - as the relative phase decreases (towards 0°) the proportion of time spent moving in the same direction increases towards 1; similarly, as the relative phase moves from 90° to 180°, the proportion of time spent moving in the same direction decreases towards 0. Relative direction is symmetrical about 180°, however. A similar story is true for relative speed, which is zero at 0°, ranges from zero to maximum at 180, and is highly variable at 90°. Changes in relative speed are also symmetric about 180°. If relative direction (modulated by relative speed) constitutes the information, there should be different behavior above and below 90° but not above and below 180°. The data was therefore sorted by trial type into two sets for each subject, which were analyzed separately – data for discriminations of 90° from lower mean relative phases (e.g. '45-90' and '90-45') and data for discriminations of 90° from higher mean relative phases (e.g. '135-90' and '90-135'). The analogous sorting was also done for the Choose 180° data. This data will be referred to as 'uncompiled'. This format allowed us to look for asymmetries in judgment behavior above and below 90° and 180°. This data was also analyzed both as a single data set (all four subjects) and for each individual subject.

A nominal logistic regression model was fit separately to each data set. The model fitting procedure estimates two parameters, intercept and slope, as well as confidence intervals for each parameter. A mean regression curve was fit using the parameter estimates. The analysis also provides an analogue to R^2 called the uncertainty coefficient U, which measures whether the model containing the experimental terms is better than the null model (rather than expressing 'percentage of variance explained' as in linear regression). U ranges from 0 (no improvement) to 1 (a perfect fit/maximum improvement).

The absolute value of the mean relative phase difference at which the probability of responding '90° First' was 25% and 75% was computed from each regression line, and averaged. This provides a measure of the threshold, expressed as the magnitude of the phase difference required before participants were above chance in their discriminations. This threshold should approach 0° in the limit as learning occurs.

Methods - Movement

Procedure: Refer to Figure 1. Participants sat in front of a Dell Optiplex GX110 PC, which was connected to a Microsoft joystick. The joystick sat in a box with the open side facing the participant, who sat so that they could comfortably use the joystick but not see it. The computer presented a display of two dots, white on a black background, one above

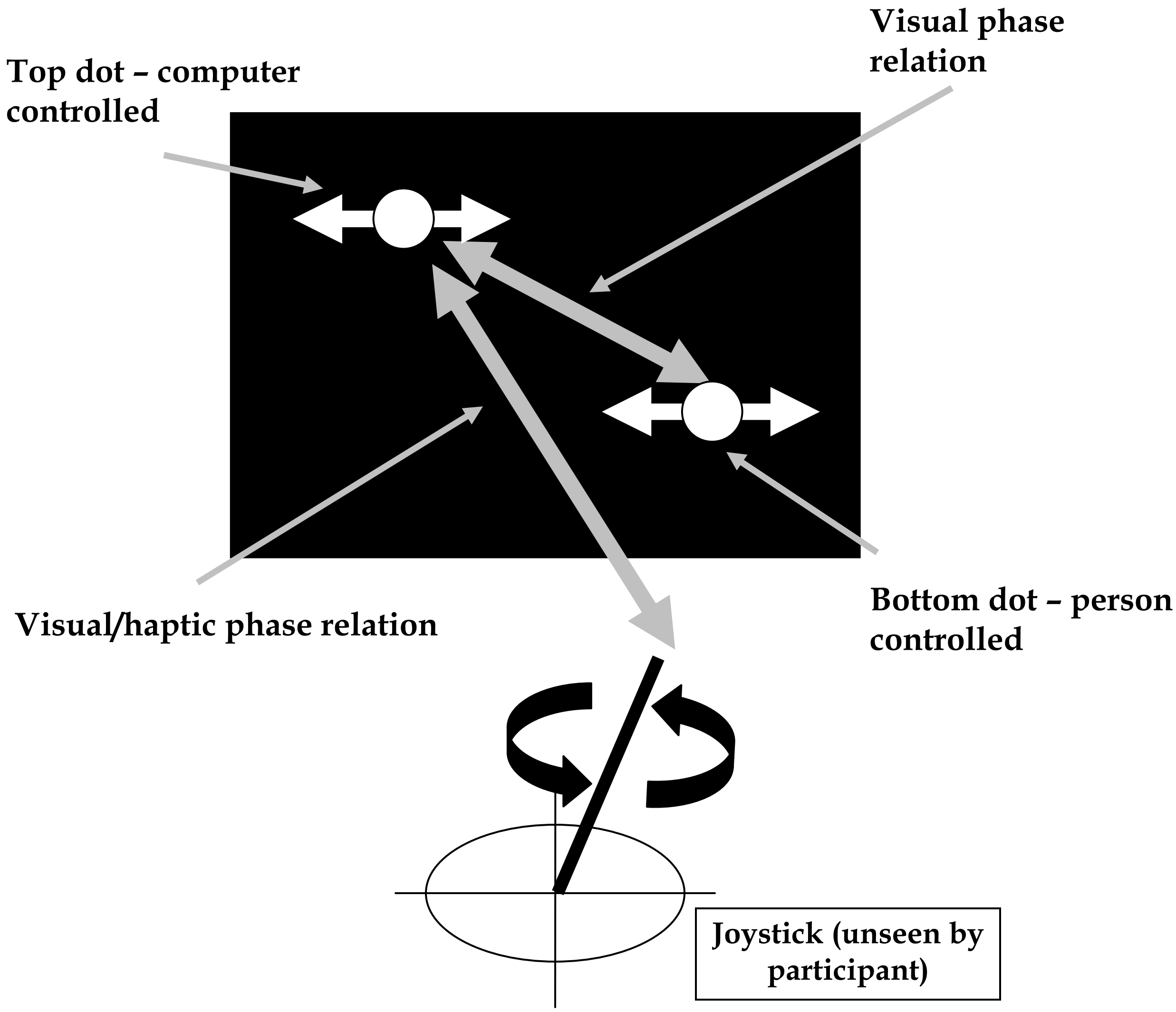


Figure 1. Schematic diagram of the movement task set up.

the other. The screen refresh rate was 85Hz, and each trial was 60s long. The top dot was under the control of the computer, and it oscillated from side to side at 1.5Hz. The bottom dot was controlled by the participant, using the joystick. This dot was made to move from side to side by moving the joystick in a smooth, circular movement. (This movement could be either clockwise or counter-clockwise, but participants were instructed to choose one direction and stick with it within a trial.) The computer recorded the x and y coordinates of the joystick and computed its phase (the measure of an oscillator's location within a cycle; $\tan^{-1}(y/x)$ at each time step. This phase was used to specify the location of the bottom dot within its side-to-side cycle. This procedure is identical to that used in Wilson et al (2005a, b) – the circular movement allows for phase to be manipulated directly, and does not alter the fundamental nature of the task (see Wilson et al 2005b for discussion of this point).

There were 15 Baseline Movement trials. Participants were instructed to move so as to produce a mean relative phase of 0°, 180°, or 90° between the dots on the screen. There were 5 trials at each phase, blocked by phase and presented in the noted order. The first trial of each block was a practice trial, and the data from this trial were not analyzed. Participants viewed demonstrations of dots moving at these relative phases prior to beginning the experiment.

<u>Data Analysis:</u> The data for this task is the relative phase between the two dots, which was computed at each screen refresh. Relative phase is a circular variable, i.e. its distribution of possible values lies on a circle. This creates a problem for calculating

basic descriptive variables. For instance, taking the “normal” mean of 1° and 359° yields 180°, which is a vector pointing in the opposite direction of what the mean direction actually is, namely 0° (or 360°). Also, any two angles separated by 360° are the same position on that circle, and they hence indicate the same relative phase.

Batschelet (1981), Fisher (1993), Mardia (1972) and Jammalamadaka and SenGupta (2001) provide trigonometric methods for computing circular equivalents of the mean and standard deviation, as well as for performing basic statistical tests. Two measures were taken – first, the mean vector θ is the direction of the resultant vector obtained by summing the relative phase vectors from each time step. Second, the normalized length of this vector (mean vector length; MVL) is the measure of within trial stability. The MVL statistic (Eq, 1.3.8; Batschelet, 1981) ranges from 0 (indicating minimum stability, i.e. a uniform circular distribution) to 1 (indicating maximum stability, i.e. no variability). If MVL is not significantly different from 0 (using the Rayleigh test for randomness; Batschelet, 1981) the mean vector for that data set is uninterpretable.

Results - Baseline

Judgments

Overall: We first looked at all the data from all four subjects together. Refer to the dark lines in Figure 2. The top row depicts the compiled data, and the bottom row of Figure 2 depicts the uncompiled data for all four subjects. Subjects were worse at the Choose 90° task than the Choose 180° task overall (see Table 1 for thresholds and U’s), although as

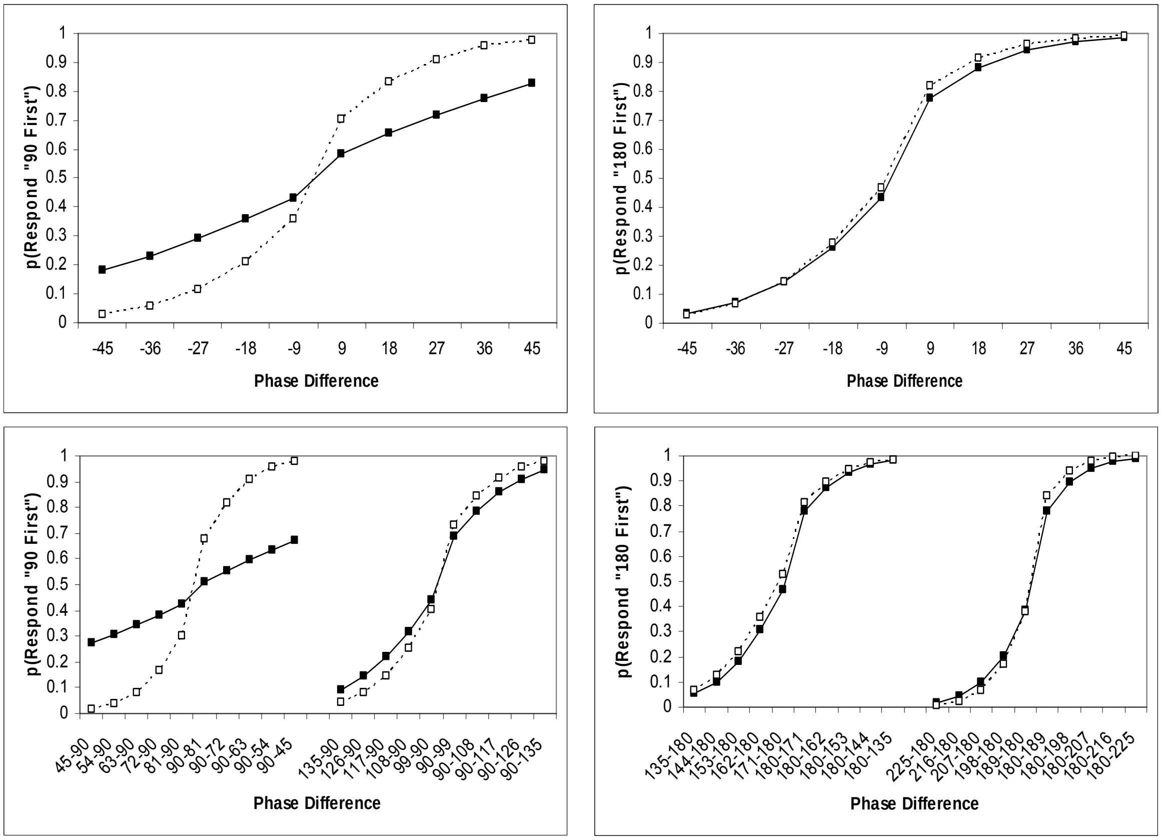


Figure 2. Logistic regression model fits for Baseline (filled squares) and Post Training 1 (open squares) judgment data from all subjects.

Top – Compiled 90° (left) and 180° (right)

Bottom – Uncompiled 90° (left) and 180° (right)

Session	Threshold	Uncertainty Coefficient (U)
Baseline 90°	31.95	0.1568
Post Training 1 90°	13.52	0.4925
Post Training 2 90°	15.28	0.4325
Post Training 3 90°	13.89	0.4790
Baseline 180°	12.87	0.5105
Post Training 1 180°	11.92	0.5412

Table 1. Thresholds (in degrees) and uncertainty coefficients (U) for the compiled data from all four subjects combined.

Session	Threshold (°)	Uncertainty Coefficient U
Baseline <90	56.37	0.0571
Baseline >90	19.37	0.3281
Post <90 (1)	12.56	0.5270
Post >90 (1)	14.31	0.4642
Post <90(2)	10.51	0.6055
Post >90(2)	20.20	0.3083
Post <90(3)	11.93	0.5395
Post >90(3)	14.94	0.4457
Baseline <180	14.34	0.4585
Baseline >180	11.34	0.5706
Post <180(1)	14.33	0.4519
Post >180(1)	9.19	0.6576

Table 2. Thresholds (in degrees) and uncertainty coefficients for uncompiled data for all four subjects combined.

Session	Subject 1	Subject 2	Subject 3	Subject 4	Average
Baseline 90°	22.84	23.11	121.61*	24.78	23.58*
Post Training 1 90°	10.50	11.16	12.68	16.79	12.78
Post Training 2 90°	11.73	11.06	26.26	12.05	15.26
Post Training 3 90°	7.87	12.00	19.93	13.56	13.09
Baseline 180°	15.08	9.51	16.38	12.91	13.47
Post Training 180°	8.66	8.30	15.86	16.55	12.34

Table 3. Thresholds (in degrees) for the compiled data for each individual subject.

*As the slope of the regression line was nearly 0, this threshold is unstable and is not included in the average.

Session	Subject 1	Subject 2	Subject 3	Subject 4
Baseline <90	21.695	42.895	24.885	17.02
Baseline >90	23.755	11.47	11.9	34.8
Post <90 (1)	8.9	9.39	10.84	21.54
Post >90 (1)	14.945	12.63	13.89	12.365
Post <90(2)	6.115	9.51	15.095	10.075
Post >90(2)	16.375	12.365	51.31	13.19
Post <90(3)	9.27	11.765	18.2	12.99
Post >90(3)	10.555	11.237	20.97	13.805
Baseline <180	20.165	13.245	15.085	13.89
Baseline >180	10.15	7.93	17.67	11.91
Post <180(1)	11.735	8.71	22.205	25.62
Post >180(1)	8.71	10.83	11.22	8.235

Table 4. Thresholds (in degrees) for uncompiled data for each subject.

the bottom row reveals most of that difference is in the below 90° data. Performance above 90° was actually quite good, with the threshold at 19.37°, but it was not quite as good as at 180° (see Table 2 for thresholds and U's for all conditions). The good performance above 90° was not predicted – the hypothesis that relative direction of motion is the information predicts that performance should be better below 90°. However, that same hypothesis predicts no asymmetry about 180°, which was the case for the combined data set.

Individual subjects: We next looked at the compiled data for each subject individually. Refer to the dark lines in Figure 3 (left hand column). Subjects 1, 2 & 4 are all very similar in their overall ability to discriminate 90° from other phases, and the combined data in Figure 2 is representative of these three subjects. Subject 3 is effectively at chance (although this is primarily due to the compiling of the data – when separated out into below 90° and above 90°, Subject 3 was equivalent to the others above, but was reversed below – see the text below & Figure 4).

Refer to Table 3 for the individual subject thresholds. Note that Subject 2's threshold is extra-ordinarily high, due to the slope of the compiled regression line being effectively 0. The average threshold (excluding Subject 3) was 23.58°.

Refer to Figure 3 (right hand column). All participants were better at discriminating 180° from other phases than they were at 90°, and are well represented by the combined data

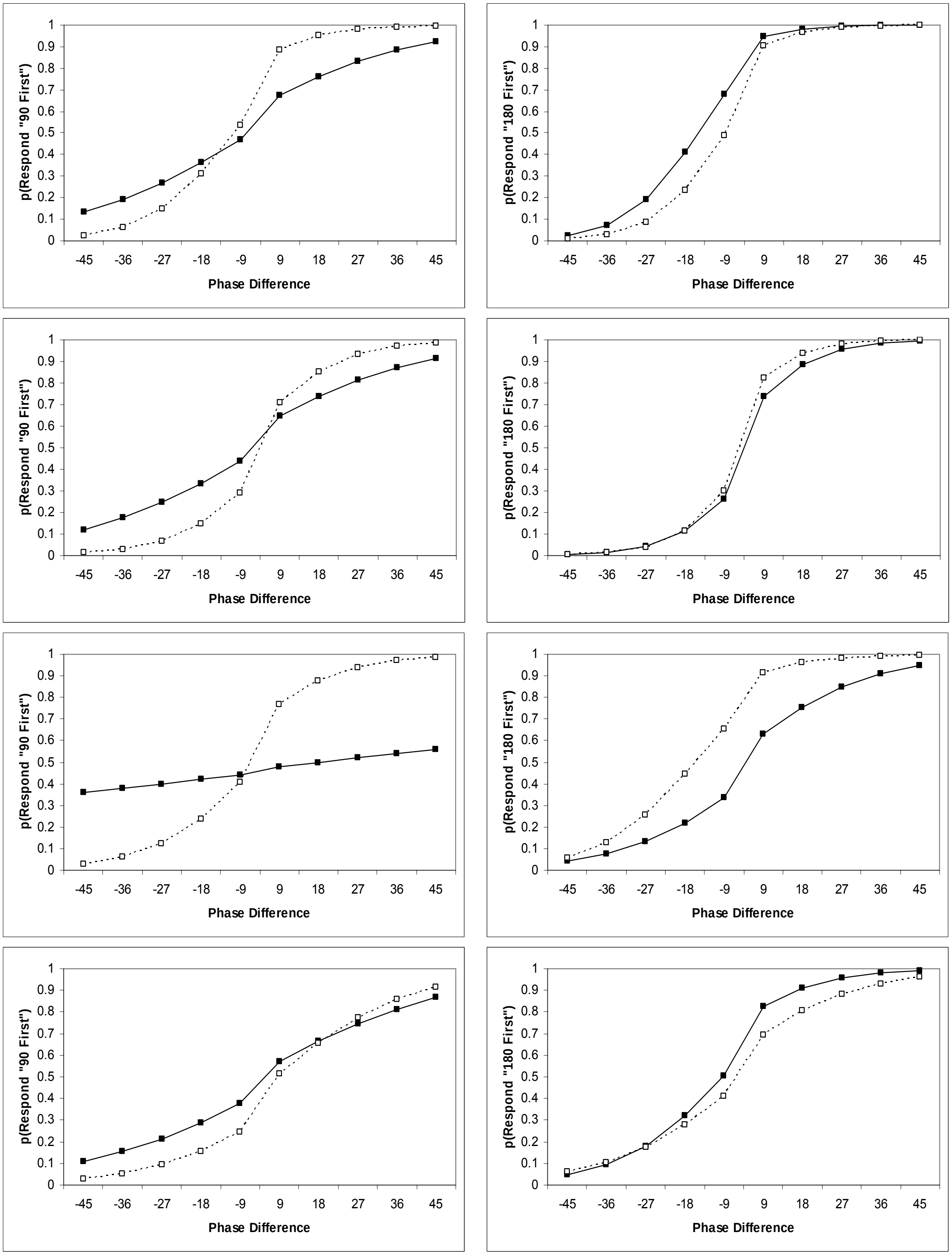


Figure 3. Logistic regression model fits for the compiled data from each individual subject, comparing performance in the Baseline (filled squares) and Post-Training 1 (open square) judgment tasks.

Left hand column – Choose 90°; right hand column – Choose 180°

Row 1 – Subject 1; Row 2 – Subject 2; Row 3 – Subject 3; Row 4 – Subject 4

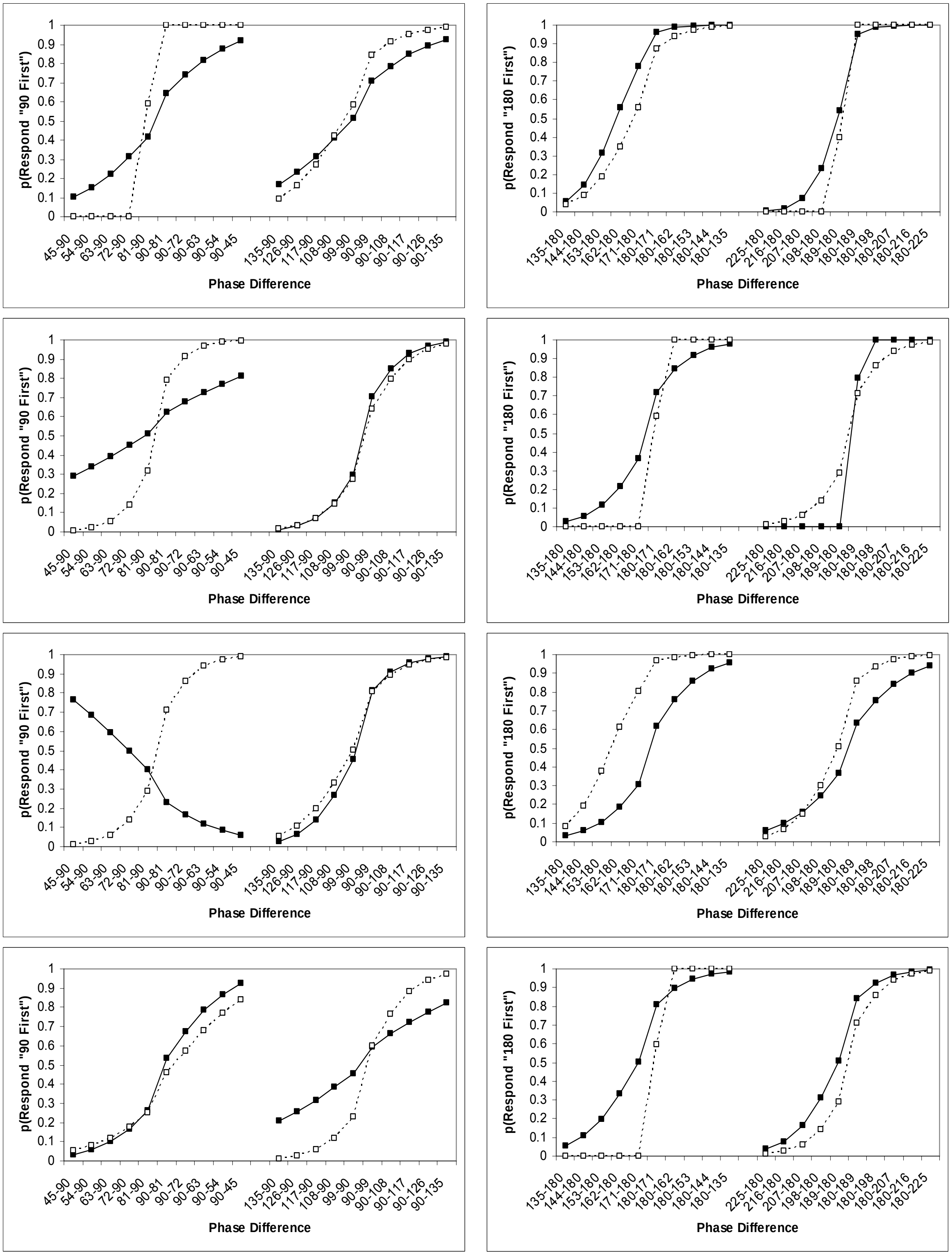


Figure 4. Logistic regression model fits for the uncompiled data from each individual subject, comparing performance in the Baseline (filled squares) and Post-Training (open square) judgment tasks.

Left hand column – Choose 90°; right hand column – Choose 180°

Row 1 – Subject 1; Row 2 – Subject 2; Row 3 – Subject 3; Row 4 – Subject 4 set in Figure 2. Refer to Table 3 for the individual subject thresholds. The average threshold for all four subjects was 13.47°.

We next looked at the uncompiled data for the individual subjects. Refer to the dark lines on the left hand column of Figure 4, which compares Baseline performance above and below 90°. Subjects 2 & 3 are worse below 90° than above it, while Subject 4 is slightly better and Subject 1 shows only a small difference.

Refer to the right hand column of Figure 4, which shows the comparable graphs for discriminations above and below 180°. Subjects 3 & 4 show identical behavior above and below 180°. Subjects 1 & 2 are slightly worse below 180°, but the difference is quite small. Overall there is no clear difference between discriminations made above or below 180°, and the behavior is highly consistent across subjects.

Movement - Baseline

Refer to Figure 5a. There is no repeated measures ANOVA for circular data, and hence the mean performance could not be analyzed in detail. Mean performance for all subjects at all phases was good, with the exception of Subject 1 at 180°. Good mean performance, even at 90°, is typical for this paradigm. A low mean suggested the subject spent time during each trial at or near 0° and transitioning between 0° and 180° in an attempt to

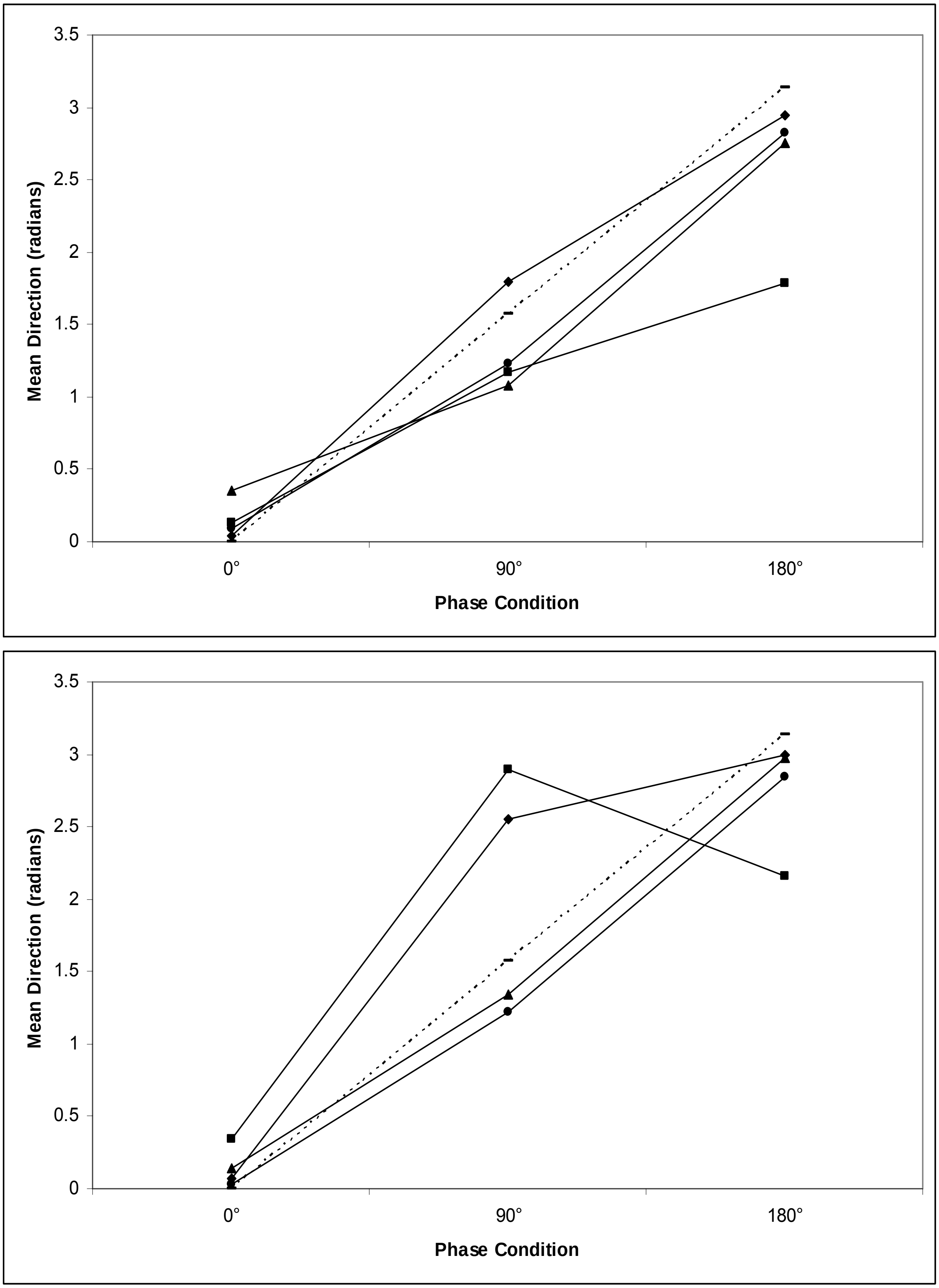


Figure 5. Mean performance in the movement task. Subject 1 (square); Subject 2 (diamond); Subject 3 (triangle); Subject 4 (circle); Target phase (dotted line).

Top – Baseline

Bottom – Post Training 1

correct the movement. If this was true, Subject 1 will show low within trial stability (see below).

The real information about movement stability lies in the mean vector length, which is not itself a circular variable and hence can be analyzed normally. We compiled the mean vector lengths for all subjects and performed a repeated measures ANOVA. Refer to the top graph on Figure 6. There was a main effect of phase ($F_{(2,30)}=7.1$, $p<.01$). Post hoc pairwise comparisons revealed 0° was more stable than both 90° and 180°, which were not different from each other. This is also not an uncommon result for this paradigm (see Wilson et al, 2005a).

We also analyzed the data for each subject separately, to see whether any changes had occurred that may have been averaged out by combining the data. The dark lines in the bottom four graphs in Figure 6 show the mean vector lengths for the Baseline condition. Subjects 2-4 showed only a main effect of Phase Condition ($p<.05$), with 0° significantly more stable than either 90° or 180°. 180° was only significantly higher than 90° for Subject 4 (with the lack of difference mostly due to the high standard deviations at 90°). Subject 1 also showed a main effect of phase ($p<.01$), but in this case her performance at 180° was lower than either 0° or 90°. The low within trial stability of Subject 1 confirms the explanation for her low mean performance at 180°.

Summary – Baseline

Subjects were less able to discriminate phase relations around 90° compared to those around 180°; thresholds at 90° were twice as large on average as those at 180°, and the uncertainty coefficients (representing the model fits) were correspondingly lower. There was also a high degree of variability between subjects in the 'Choose 90°' task, while performance was overall more consistent at 180°. This variability indexes the fact that there is nothing biasing behavior in one direction or another at 90° (i.e. nothing that can be described as an attractor), while there is more structure at 180°. The baseline pattern in the judgment data qualitatively replicates the findings of the various judgment studies (e.g. Bingham et al, 2000; Wilson et al, 2003). The movement data was also consistent with previous findings using this task (Wilson et al, 2005a, 2005b).

Method - Visual Discrimination Training

Procedure – In each of nine subsequent sessions, participants performed 12 blocks of the Choose 90° task, but this time they received feedback. The participants compared 90° to four other phases, two less than 90° and two greater then 90°[3]. Location 2 was set halfway between Location 1 and 90°, and Location 3 was set halfway between Location 4 and 90° (refer to Table 5 for the exact phases displayed). The 'different' relative phases changed over the course of training – as each participant improved, the discrimination task was made harder. The outermost locations (1 & 4) were reduced by 10° between

[3] As noted earlier, the hypothesis that relative direction and relative speed constitutes the relevant information (Bingham, 2001, 2004a, 2004b) predicts an asymmetry in sensitivity on either side of 90° - 81° may be easier than 99°, for instance, because more of the time is spent moving in the same direction and the relative speed becomes lower and less variable as you move from 90° to 0°.

each set, and the innermost locations (2 & 3) were reduced by 5°. Refer to Table 6 for details of subject's progression through the training sets. Each of the 12 blocks had one repetition of each trial type, with the order of presentation randomized within block. Participants were told whether their response was correct or incorrect, and if incorrect, they were shown an example of 90°.

At the end of each session, there were 5 blocks of Choose 90° trials and 5 blocks of Choose 180° trials, with no feedback. These 'scanning sets' measured the current state of the subjects' discrimination abilities. The 'Choose 90°' scanning set was the same level of difficulty as the training set had been; the difficulty of the 'Choose 180°' scanning set progressed as a function of the subjects' performance in the previous session (see Table 6).

Performance in the 'Choose 90°' scanning set determined whether the subject progressed to the next hardest training set in the following session. If the participant was making no more than 1 error at each location then they progressed to the next training set for the next session. If the scanning set of a session showed too many errors, they repeated the current training set in the following session; if the scanning set revealed too many errors two sessions in a row, they were stepped down one training set. This was designed to mimic an adaptive psychophysical procedure (Treutwein, 1995) which would allow subjects to settle at their own learning limit.

Scan Set	Task	Location 1	Location 2	Location 3	Location 4
1	**90° vs**	40	65	115	140
2	**90° vs**	50	70	110	130
3	**90° vs**	60	75	105	120
4	**90° vs**	70	80	100	110
5	**90° vs**	80	85	95	100
1	**180° vs**	130	155	205	230
2	**180° vs**	140	160	200	220
3	**180° vs**	150	165	195	210
4	**180° vs**	160	170	190	200
5	**180° vs**	170	175	185	190

Table 5. Phases (in degrees) of the four 'different' locations comprising each training set for the training sessions.

	Subject 1			**Subject 2**			**Subject 3**			**Subject 4**		
Session	**Learn 90**	**Scan 90**	**Scan 180**	**Learn 90**	**Scan 90**	**Scan 180**	**Learn 90**	**Scan 90**	**Scan 180**	**Learn 90**	**Scan 90**	**Scan 180**
1	1	1	1	1	1	1	1	1	1	1	1	1
2	2	2	2	2	2	2	2	2	2	2	2	2
3	3	3	3	3	3	3	3	3	2	3	3	3
4	4	3	3	3	3	3	3	3	2	3	3	3
5	4	4	4	4	4	4	4	4	3	4	4	4
6	4	4	4	4	4	4	4	4	4	4	4	4
7	5	5	5	3	3	3	3	3	3	4	4	4
8	5	5	5	3	3	4	3	3	3	3	3	3
9	4	4	4	4	4	5	3	3	3	4	4	4

Table 6. Individual subject progressions through the training sets. 'Learn 90' are the feedback trials; 'Scan 90' and 'Scan 180' are the no-feedback trials.

It is important to note that the training did not involve any additional practice at the movement task, nor was any feedback ever given to the 180° discriminations.

Results - Visual Discrimination Training

As Table 6 shows, subjects readily progressed through the first 2 training sets, at which point the task became noticeably harder. Subject 1 progressed to Set 5, although her performance there was consistently poor and her final session saw her move down one set. Subjects 2-4 all spent two sessions on Set 3 before their performance warranted moving up to Set 4. It was around this point that the subjects began to separate out in their performance. Subjects 2 and 4 peaked at Set 4, after being stepped back down to Set 3. Being stepped down generally improved performance once they were stepped back up – for instance, Subject 4's performance on Set 4 in Session 9 was better than her performance on Set 4 in Session 7, even though the intervening training session was one set easier. The same was true for Subject 2. Subject 3 spent two sessions on Set 4 but never improved past chance. She was stepped down to Set 3, and although she improved over the last three sessions, her performance was never good enough to progress back to Set 4.

Scanning sets centered on 180° showed that subjects reached good performance quite quickly and remained at their personal peak quite consistently once there. We performed scans around 180° because Zanone & Kelso reported movement stability being lost at 180° during training. We had hypothesized, based on this result and on the proposed role for perceptual stability in creating movement stability, that something similar would show up during the perceptual training. However, we found no evidence that 180° became less stable during training at 90°.

Summary – Training

All 4 subjects improved in their ability to discriminate the region around 90°, but idiosyncratically. 180° showed no decrement, as may have been predicted based on previous movement learning studies. There are several possible reasons why we failed to see a decrement at 180°. First, there may have been no decrement to detect. While the decrement is quite a robust finding in Zanone & Kelso's work, our tasks are quite different and it's still unclear what the mechanism underlying the phenomena is in their studies. Second, there may have been one but early on in training, and the early scanning sets may have been too easy to be sensitive to a decrement. While we cannot rule either of these out based on the current data, the former hypothesis seems more likely. Given that improved performance in the current task entails improved ability to discriminate the information underlying the task, it seem implausible to claim that this improved discrimination would cause problems elsewhere in the space. For this to happen, subjects would need to be learning a different variable for use at 90°, one that actively interferes with the one they are using at 180°. Its unclear what such a variable would be like for this task.

The next step was to quantify the improvement and test whether it had any effect on movement stability. In two separate sessions, participants repeated the Baseline session tasks (both judgment and movement). These will be referred to as Post Training 1 & 2.

Results – Post Training 1

Judgments

Overall: We first looked at the compiled data from all four subjects together, in which discriminations of 90° from locations above and below 90° are combined. Refer to the dotted lines in Figure 2, and compare them to the dark lines (from the Baseline). The top row depicts the compiled data, and the bottom row of Figure 2 depicts the uncompiled data for all four subjects. Overall, the subjects showed a drastic improvement in their ability to discriminate 90° from neighboring phases. The compiled threshold went from 31.95° in the Baseline to 13.52°. There was no change, however, in subjects' performance at 180° (the threshold only decreased by approximately 1°).

We next looked at the uncompiled data for all subjects (refer to Figure 2 again). There was only a small improvement above 90° (the threshold decreased by approximately 5°). Most of the improvement happened for discriminations below 90°, where the threshold went from 56.37° to 12.56°. There was no change either above or below 180°, consistent with the predictions of no asymmetries in that task.

Compiled: We next looked at the compiled data for each individual subject in the Choose 90° task. Refer to the dotted lines in Figure 3 (left hand column), and compare these to the Baseline data (the dark lines). Subjects 1-3 dramatically improved their ability to discriminate the area around 90°, with thresholds dropping to an average of 11.44°. Subject 4 showed only a slight improvement (her threshold went down by 8° and remained 4-6° higher than the new thresholds for the other subjects) Refer to Table 3 for all thresholds.

Refer to the right hand column of Figure 3, which shows the compiled data for judgments in the 'Choose 180°' task. Again, the dotted lines show the post training data. There was very little change in discriminations around 180°. Subject 1 got a little better and Subject 3 got a little worse, but on average the threshold only went down by 1.13°.

Uncompiled: Refer to the dotted lines in the left hand column of Figure 4, which depicts the post-training model fits for the 'Choose 90°' task. Compare these model fits to the dark lines (the Baseline models).

As already noted in the Overall data, there was very little change in performance above 90° (which was already quite good). All of the improvement for Subject's 1-3 occurred in the below 90° judgments (except for Subject 4, who's small improvement all occurred above 90° where she had initially been poorer). Overall, performance has become much more structured and consistent across subjects (i.e. there is now something like an attractor which is structuring behavior at 90°).

Refer to the dotted lines in the right hand column of Figure 4, which depicts the post-training model fits for the ‘Choose 180°’ task. Compare these model fits to the dark lines (the Baseline models).

There are some asymmetries in the individual post-training data above and below 180°. The nature of the asymmetry is not consistent across subjects, however. Subject 1 improves above 180° (and hence improves somewhat in the compiled analysis); Subject 2 improves below but gets worse above 180° (and hence shows no difference in the compiled analysis); Subjects 3 gets worse below 180° and stay about the same above (and hence shows a slight decrement in the compiled analysis); and Subject 4 gets slightly better above and slightly worse below 180° (again, leading to no overall change in the compiled analysis). The lack of consistency and the lack of overall improvement all suggest that whatever is being learned about 90°, it is not transferring to 180° (either positively or negatively).

<u>Movement</u>

Refer to Figure 5b. Mean performance was again good for Subjects 3 & 4 at all phases, but Subjects 1 & 2 both got significantly worse at 90°, both showing elevated means (suggesting time spent at or around 180°).

Refer to Figure 6, with the dotted lines showing the post-training mean vector length (stability) data. The overall Post Training 1 data (top graph) again showed a main effect of phase ($F(2, 30) = 14.4$, $p<.01$), with pairwise comparisons showing that 0° was more stable than both 90° and 180° ($p<.01$), with the latter two not different from each other ($p=.126$).

We performed a repeated measures ANOVA to compare the Baseline movement stability data to the Post Training movement stability data. We predicted one of two things would happen – either movement stability would improve only at 90°, or at both 90° and 180° (depending on what it was that was being learned during training). Either way, we predicted a Training x Phase condition interaction (because 0° was unlikely to change after training). However, there was only a main effect of Phase ($F(2,30) = 18.1$, $p<.01$). There was no effect of Training ($p=.73$) nor an interaction ($p=.51$). Overall, there was no improvement in movement stability at 90°, nor any other phase.

We also analyzed the data for each subject separately. The dotted lines in the bottom four graphs in Figure 6 show the mean vector lengths for the Post-Training condition. Subjects 2-4 all showed only a main effect of Phase Condition ($p<.05$), with no interaction between Phase Condition and Training. Subject 4's main effect of phase was due to stability at 0° being higher than at 180°, which in turn was higher than at 90°. The other subjects showed no difference between 90° and 180°. Subject 1 showed a main effect of Phase Condition, Training and an interaction, but in the wrong direction – she had started out performing well at 90° and poorly at 180°; post-training, she got significantly worse at both, with the most dramatic drop being at 90°.

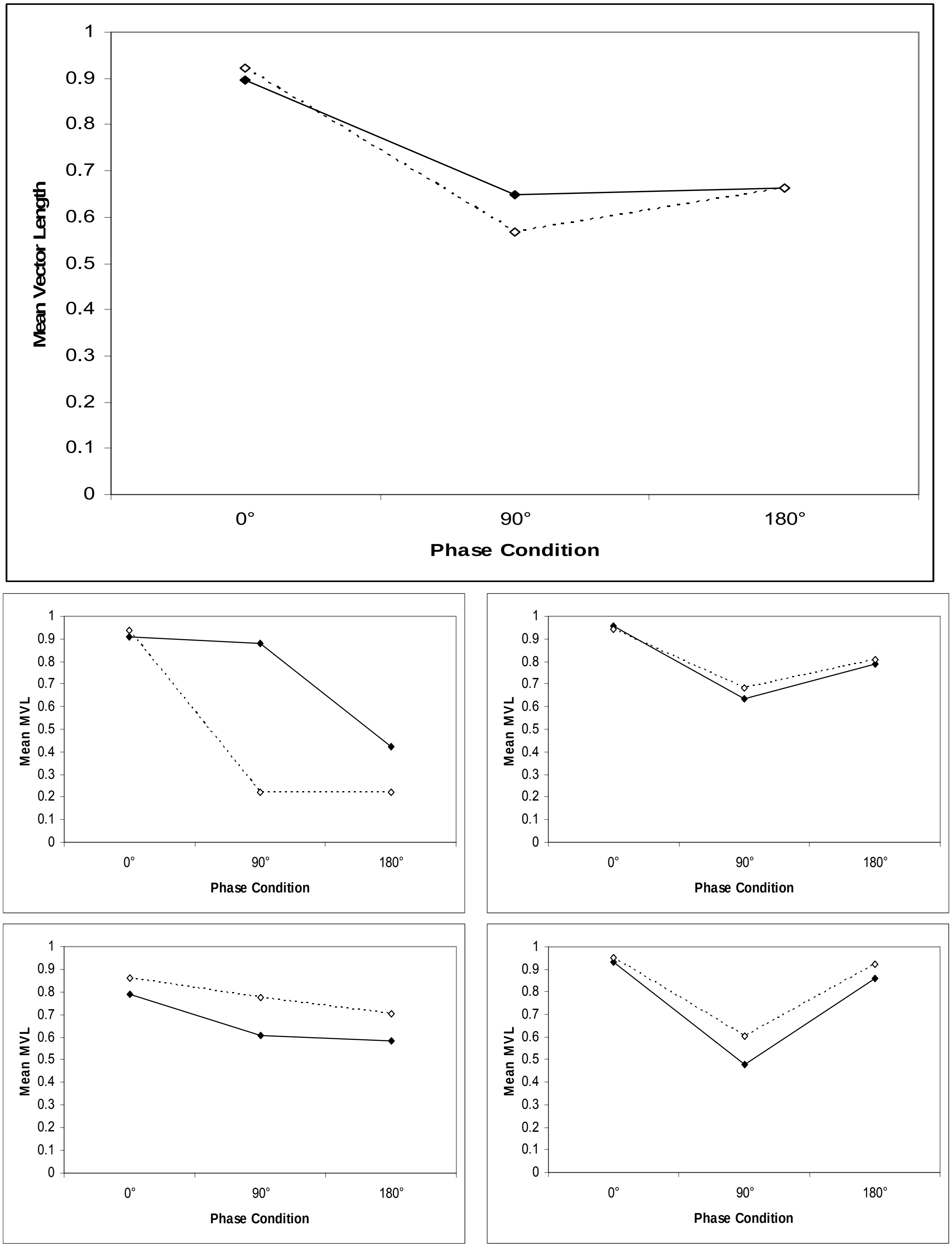


Figure 6. Mean within trial movement stability for Baseline (solid lines) and Post Training 1 (dotted lines)
Top – Overall data (all subjects)
Middle – Subjects 1 and 2
Bottom – Subjects 3 and 4

Summary – Post Training 1

Subjects significantly improved their ability to discriminate 90° from neighboring phases, but this new discrimination skill did not lead, in the initial post training session, to any improvement in movement stability at 90° (and one subject got significantly worse at 90°). There was no consistent change in discrimination around 180°.

Methods and Results – Post Training 2

The fact that an improvement in perceptual discrimination performance at 90° had not translated to an improvement in movement stability was, obviously, surprising given the hypotheses and their motivation from previous literature. We therefore decided to retest the subjects to see whether the null result was robust.

The four subjects were brought in 3-4 weeks after they performed the first Post Training session. They were about to perform the tasks that will be reported in Experiment 2, and we needed to re-measure their current ability to perform the 'Choose 90°' task because of how much time had passed. This gave us an opportunity to re-measure their movement performance as well. Subjects performed a version of the Baseline session. First, we measured their movement stability at 0°, 90° and 180°. They then completed the 'Choose 90°' task (identical in format to the Baseline session described above). We did not collect any more Choose 180° data.

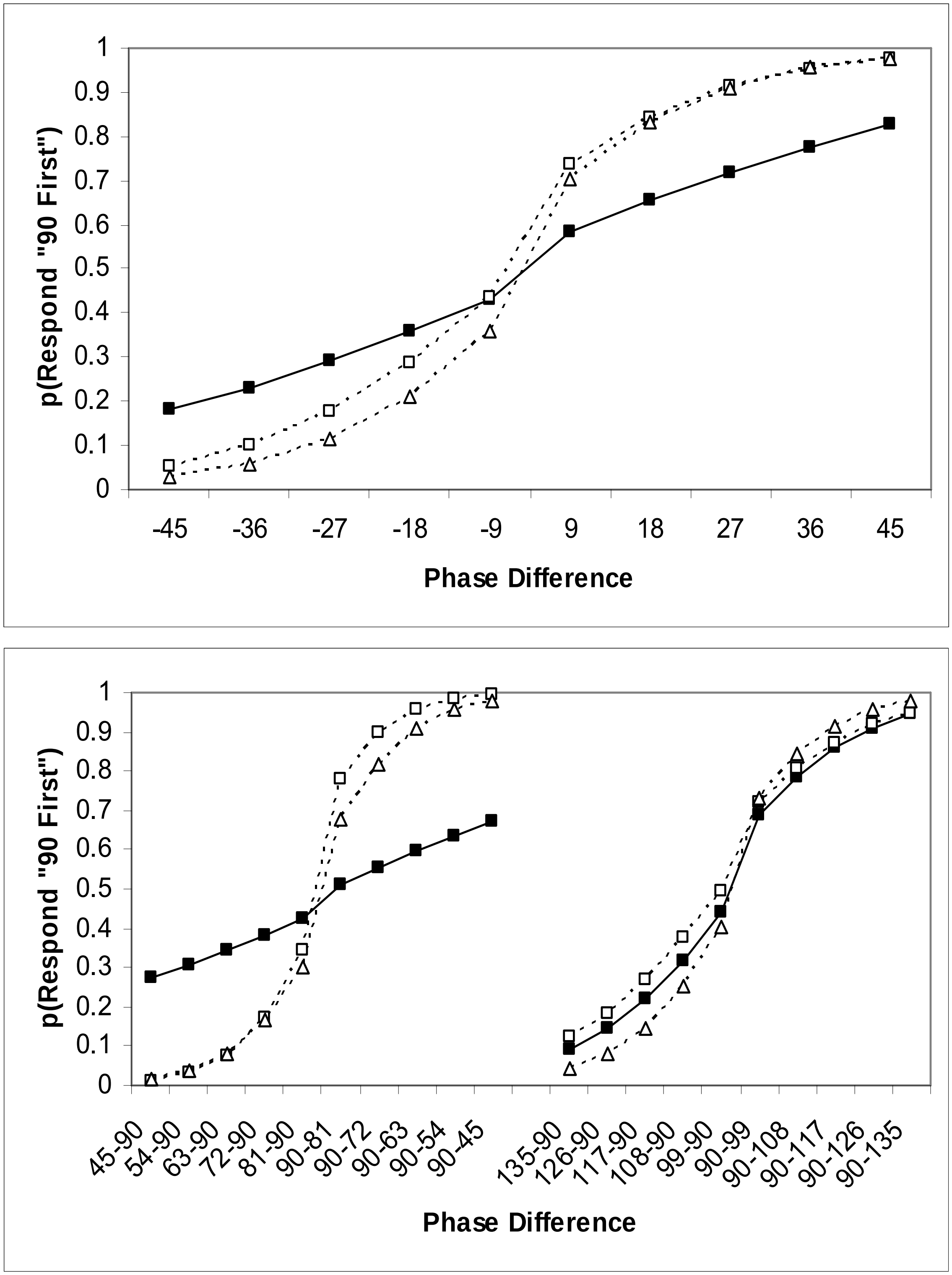


Figure 7. Logistic regression model fits for Baseline (filled squares) and Post Training 2 (open squares) judgment data from all subjects. The model fit for Post Training 1 (open triangles) is included for comparison.

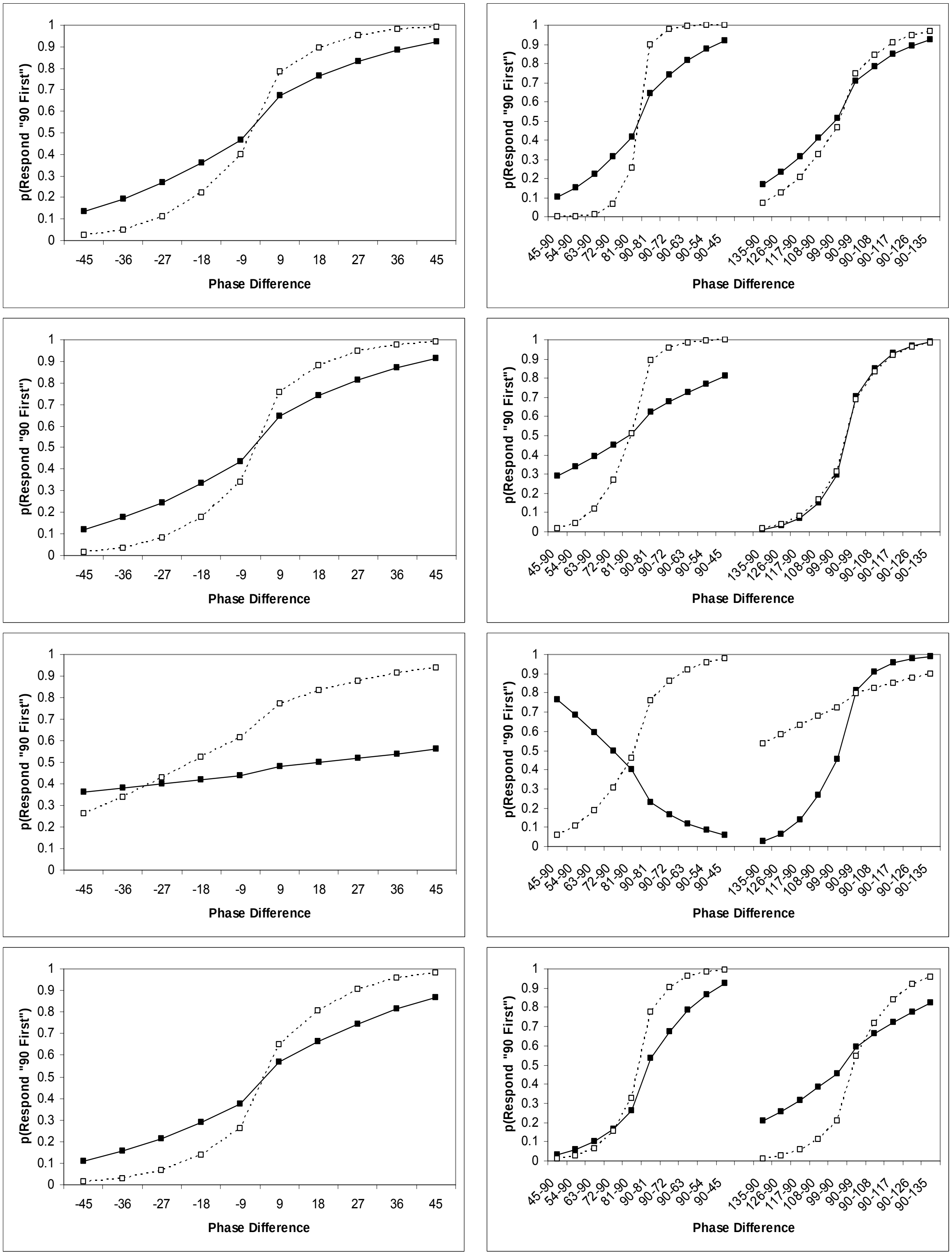


Figure 8. Logistic regression model fits for the compiled (left hand column) and uncompiled (right hand column) for each individual subject, comparing performance in the Baseline (filled squares) and Post-Training 2 (open square) judgment tasks.

Judgments

Overall: Refer to Figure 7, which shows the combined judgment data for the Baseline (dark lines) and Post Training 2 sessions (dotted lines). The data for Post Training 1 (open triangles) is included for comparison.

Subjects' performance in the Choose 90° remained high, even after a 3-4 week delay. The overall threshold remained low (15.28°). In the uncompiled data, the threshold for the below 90° data actually decreased again (to 10.51°) while the threshold for the above 90° data increased slightly. Overall, the effect of learning persisted over the delay.

Figure 8 compares the Baseline data to the Post Training 2 data; the left hand column shows the compiled data for each subject, while the right shows the uncompiled data. Performance in Post Training 2 was again a significant improvement over the Baseline. There were, in general, no differences from performance in Post Training 1. The two exceptions were Subject 3, who's performance above 90° deteriorated relative to both the Baseline and Post Training 1, and Subject 4, who's performance below 90° improved relative to both the Baseline and Post Training 1. Otherwise, the learning observed in Post Training 1 persisted over nearly a month without any further training or exposure to the task.

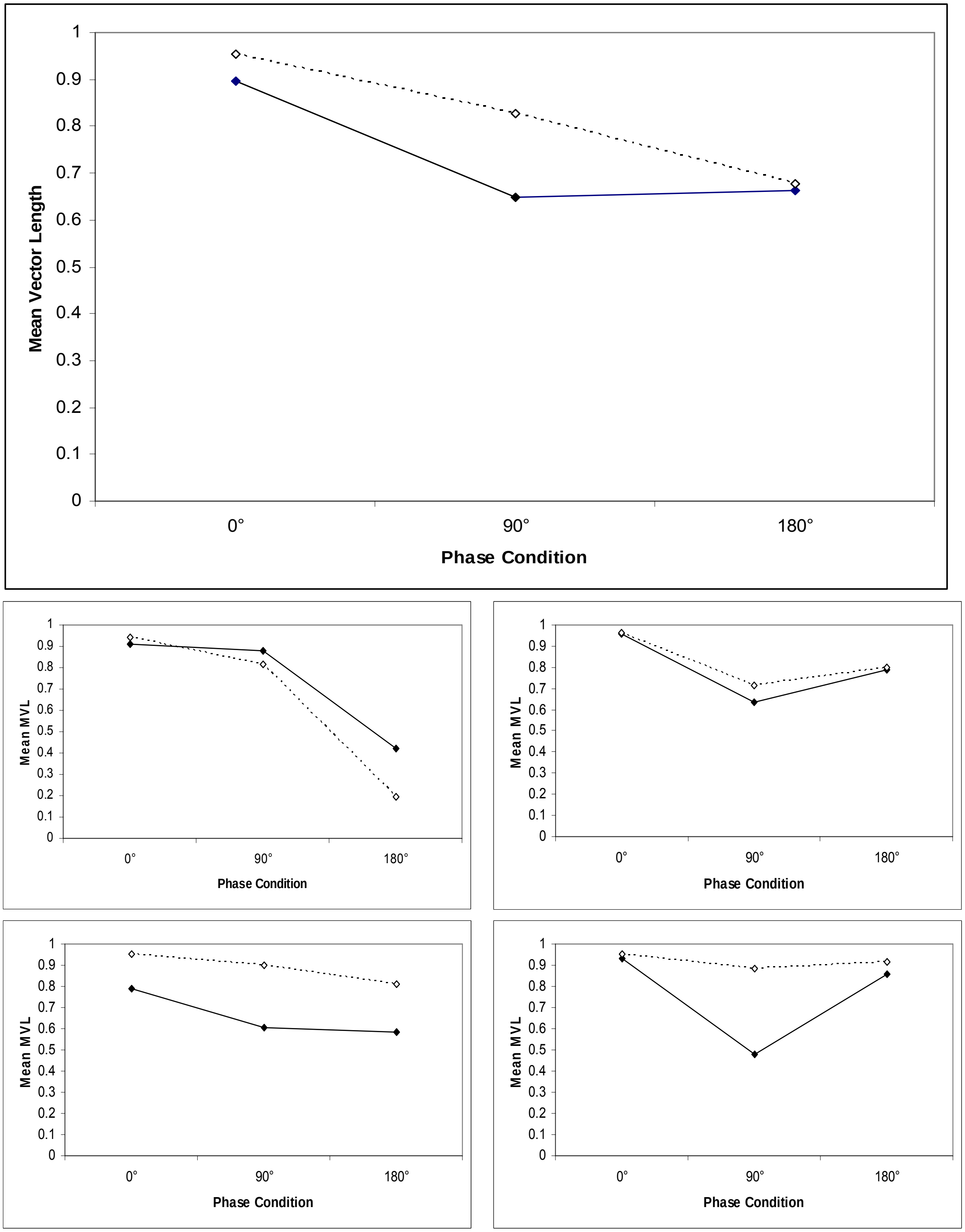


Figure 9. Mean within trial movement stability for Baseline (solid lines) and Post Training 2 (dotted lines)

Top – Overall data (all subjects)

Middle – Subjects 1 and 2

Bottom – Subjects 3 and 4

Movement

Refer to Figure 9. The top figure shows the data for all subjects. We ran a repeated measures ANOVA to compare the Baseline to the Post Training 2 data (as Post Training 1 was not different from Baseline, this is analogous to comparing the two post-training sessions). The ANOVA revealed a nearly significant main effect of Training ($p=.053$), a significant main effect of Phase ($p<.01$) and a significant Training x Phase interaction ($p<.05$). Movement stability at 90° rose significantly between the Baseline and the second Post Training at both 0° and 90°, but not at 180°. Pairwise comparisons revealed that Post Training 2 90° was more stable than Baseline 90° and 180° ($p<.05$), but less stable than Post Training 2 0° and the same as Post Training 2 180°. Interestingly, Post Training 2 90° was not different from Baseline 0° ($p>.05$).

The bottom four graphs in Figure 8 show the individual data. Each of the four subjects each showed a slightly different pattern. Subject 1's performance at 90° returned to Baseline levels (which were high), but her performance at 180° decreased slightly again. Subject 2 showed only a main effect of Phase ($p<.05$) – 90° did not improve significantly. Subject 3 showed a main effect of both Phase and Training (both $p<.05$), but no interaction – her performance improved in the second Post-Training, but across the board. Pairwise comparisons showed her final movement stability at 90° was the same as Baseline 0° performance ($p>.05$) but slightly lower than Post Training 2 0° ($p<.05$). It was higher than Baseline 180°, but not different from Post Training 2 180° due to a significant increase in movement stability at 180°. Finally, Subject 4 showed the overall pattern, with a main effect of Phase and a significant interaction between Phase and

Training (both p<.05). Her performance improved only at 90°, and her Post Training 2 level of movement stability at 90° was not significantly different from the Post Training 2 levels at either 0° or 180°.

<u>Summary: Post Training 2:</u> Performance in the judgment task remained stable and good compared to the Baseline. The predicted improvement in movement stability occurred in this second, retention session. Overall, only movement stability at 90° improved over the Baseline.

Discussion – Experiment 1

The goal of Experiment 1 was to explicitly demonstrate the role of perception in the emergence of the characteristics of rhythmic movement coordination. Four subjects were trained to improve their perceptual resolution of the space around 90°, and we measured the effect on their movement stability at 90° and 180°. Overall, the subjects improved in the perception task, and this translated (in a retention session) to improved movement stability at 90° but not at 180° without practice of the movement task.

Initial performance in the Choose 90° task was poor (with high thresholds) and erratic (poor model fits, high between subject variability both qualitatively and quantitatively). This erratic initial performance was not entirely unexpected – recall from the previous judgment studies (e.g. Wilson et al, 2003; Zaal et al, 2000) that discrimination of the region around 90° is poor, which causes the variability of the judgments of both the mean and the variability to be at ceiling. In other words, not only do people not know where

90° is (variability in the judgments of the mean phase) but they do not know that they do not know (variability in the judgments of variability).

The HKB model describes this in terms of attractors. The purpose of an attractor in a model is to account for a particular structure to behavior in that region of the state space. But attractors are not explanatory, they are descriptive. 0° is not stable because there is an attractor there – there is an attractor there because 0° is stable. The question always remains, what is causing there to be an attractor here, rather than there?

The perceptual judgment data suggests the reason why there is an attractor at 0° and 180°, but not at 90°; people have poor access to the requisite information at 90°, better access at 180° and best access at 0°. Improving access to the information at a location should allow behavior to be structured at that location (i.e. an attractor). The advantage in moving to this account is that we can now experimentally investigate the information in a way you cannot investigate an attractor. We demonstrated this here with the post training Choose 90° performance – not only did thresholds come down, but model fits improved and performance became more consistent across subjects. Performance in the Choose 180° task was already more stable within and between subjects, reflecting the fact that 180° is already a stable location in the state space. Interestingly, performance in the Choose 180° task did not improve in either post-training session. Movement stability at 180° also did not change, which tells us two things. First, it contributes another piece of evidence for the role of perception – no improvement in perception, no improvement in movement. Second, learning to discriminate 90° from neighboring phases did not transfer to 180°, suggesting that what was learned during training is not available or is irrelevant at 180°.

The results demonstrate that learning to move entails learning to perceive. But what does the data suggest is being learned, and how? Gibson (1969; Gibson & Pick, 2000) describes perceptual learning as a process of differentiation of and attunement to an information variable. Over time and activity, energy arrays such as the optic array transform, or flow. Within this transforming flow field, certain aspects of the flow field will remain invariant. That which remains invariant can convey information about the world to the extent that it is specific to some part of the world, and it can serve as a target for perceptual learning by virtue of being invariant over the transformations (and therefore persistent over time). The first part of Gibson's account, differentiation, is the initial process of distinguishing an invariant component of an energy flow field from the transforming background. Once it has been differentiated, the learner progressively attunes to it, steadily improving their ability to detect the invariant when it is present; the 'education of attention'. A good example of this process is Wenderoth & Bock (2001), who characterized learning as taking place over three distinct timescales. The first time scale (improvement in mean performance) reflects the initial period of differentiation; the next two time scales (lowering of variability and decrease in switching time) reflects the consolidation phase of learning.

The current results provide us with some clues as to what it is that is being learned. Previous learning work (e.g. Wenderoth et al, 2002; Zanone & Kelso, 1992a, 1992b,

1997) trained subjects to improve movement stability by having them perform the movements to be stabilized. But 90° is not a stable pattern – in order to have people move at 90° and hence be learning to move at 90°, both Wenderoth et al and Zanone & Kelso were forced to have people perform a tracking task that had the consequence of making people move at the required phase. Wenderoth et al had subjects control the vertical and horizontal components of a circle being drawn on a screen by moving two parallel sliders; the task is set up so that moving the sliders at 90° draws a circle, which becomes more elliptical as you deviate from 90°. Zanone & Kelso had people track two visual metronomes, one for each finger, which was similar to the haptic tracking task in Wilson et al (2003). The latter showed that subjects were able to track a manipulandum moving at 90° quite well, even though their judgments about the variability of that movement replicated the HKB pattern found in visual judgments. This distinction implied that the two tasks (tracking and coordination) are informationally distinct, i.e. the information used to perform the tracking task is different from the information used to perform the coordination task. Wilson et al's data clearly showed, however, that movements produced in a tracking task could be evaluated in terms of their coordination by the participants. Information about the coordination was available by virtue of the fact that the limbs were, in fact, moving at some phase. It remained unclear in the previous learning studies, however, whether the participants were learning about what was required for a tracking task, or for a coordination task. To address this, the current study explicitly trained subjects in the discrimination of the information for a coordination task at 90°, and showed effects of that training in the form of much improved movement stability at 90°.

This is a clear demonstration of the role perception plays in movement stability – movement stability *is* a function of perceptual stability.

Learning was asymmetrical around 90° - performance improved markedly for discriminations between 90° and relative phases below 90°, but did not change for relative phases above 90°. Again, this is informative about what is being learned. Bingham (2001, 2004a, b) proposed that the information underlying performance in these coordination tasks is the relative direction of motion, the detection of which is a function of the relative speed. As noted earlier, relative direction and relative speed are asymmetric about 90° - as you move towards 0°, the proportion of time spent moving in the same direction increases towards 1, with a related drop in both magnitude and variability of relative speed. As you move towards 180° from 90°, the proportion of time spent moving in the same direction decreases towards 0, and the magnitude of the relative speed difference increases towards its maximum. Bingham proposed that it is this pattern in the information that accounts for the movement phenomena.

Assuming this account is correct, we would expect clear differences in behavior above and below 90°. The ecological approach to perceptual learning predicts that factors which should affect the rate and ease of learning include the persistence of the invariant and its strength relative to the transforming background (i.e. the signal-to-noise ratio). With respect to the latter factor, Bingham's description of the informational state space clearly predicts the asymmetry above and below 90° observed in the judgment data. The noise component (relative speed) is lower in magnitude and variability below 90°, and hence the information variable (relative direction) is more readily differentiated. This asymmetry was clear in the overall data, and three of the four subjects clearly showed this pattern. What is not clear by this account is why (overall) performance above 90° was better to begin with.

Another aspect of the learning process was that subjects benefited from being stepped down one training set and then stepped back up. This demonstrates that whatever is being learned, it was not limited to the specific phase being displayed – something about the motion is being learned. This also relates to the signal-to-noise ratio aspect of Gibson (1969). Stepping down to an easier discrimination still provides the information that is the target of learning, but provides it in a display from which it is more readily detected. The easier training set therefore provided an additional opportunity to consolidate learning, which in turn gave the subject a foothold on the harder discrimination, which then enabled the entire process of differentiation and attunement to continue.

One curious result was the lack of improvement in movement stability in the first post-training session, especially in light of the size of the eventual improvement in the second, retention session. By hypothesis, being able to detect when you are not moving at the target relative phase is part of being able to maintain movement at that phase – errors can only be corrected if they are detected. It was surprising, therefore that subjects were unable to correct their movements, given their improved discrimination performance. There was not even any evidence of improvement over the course of the four 90° trials in Post Training 1 (mean vector lengths remained low and constant across trials).

This may be an example of perceptual or motor consolidation (an analogue to memory consolidation for skilled movement acquisition which has been reported in several studies). Perceptually, Karni & Sagi (1993) showed continued improvement in a visual discrimination task, but only between sessions, which implicated a consolidation process rather than an effect of the current training. In the motor training literature, Brashers-Krug, Shadmehr & Bizzi (1996) demonstrated that learning of a novel motor task continues over a 24 hour period (by showing continued improvement in a second testing session). The improvement can be disrupted by learning an interfering task, but only if that second task is learned less than 4 hours after the first task is learned. They proposed that consolidation has a neural basis – it takes time to form robust neural control structures. Other examples include Karni et al (1998), who reported continued improvement in a tapping task after the end of the training, while Faugloie, Bardy & Stoffregen (2005) reported continued improvement in a postural sway learning task.

In light of these findings, there are two potential explanations for the current puzzle. First, the time between the first and second post-training sessions may have been more than sufficient for consolidation to occur, while the time between the final training session and the first post-training session was not sufficient. However, each subject had at least 24 hours between the final training session and the first post training, not to mention the fact that the training itself occurred over a two week period. So it seems unlikely that it was simply a matter of insufficient time for the perceptual learning to settle in.

There is, however, more to this task than perceptual discrimination of mean relative phase. This discrimination ability has to be used to coordinate and control an action. More likely, then, is the second possibility - the first post-training session may have constituted a practice session, in which subjects initiated a perception-action learning process that required a period of consolidation. There were fifteen movement trials in Post Training 1. No feedback was given, but it seems plausible that subjects may have been able to provide their own feedback. Even though they were unable to move stably at 90°, their perceptual training should have enabled them to detect the consequences of this failure more reliably than before. They were unable to use this to produce an actual movement within Post Training 1, but this may have been due to the fact they had never been asked to use their new discrimination abilities in service of this particular action. The 15 movement trials in Post Training 1 set in motion a perception-action learning and consolidation process, which, three weeks later, resulted in improved performance. With the current data, this hypothesis is only an inference; however, future studies with this paradigm could explicitly manipulate the amount of time and post training exposure to the task to look for more explicit evidence of consolidation. If this account is true, it is likely that much less time than three weeks is required; the key is likely to be exposure to the movement task under conditions where the room for improvement can be detected.

In summary: the first experiment clearly showed that perceptual learning has profound consequences for movement. It also provided several hints as to exactly what was learned during training; learning was best below 90°, and it did not generalize to 180°. The second series of experiments was designed to explore the informational basis for the task in more detail.

Introduction – Experiment 2

Experiment 1 established the importance of learning the perceptual information underlying a movement coordination task. The question remains, however, as to the exact form of the information.

Bingham and Collins (submitted) reported a series of studies designed to identify characteristics of the information. First, they had participants judge phase variability at five mean relative phases, each with four levels of phase variability (from 0° to 15°), at three frequencies. They replicated the results from Bingham et al (2001). Phase variability was only clearly discriminated at 0°; what resolution there was at 180° disappeared with an increase in frequency; and non-0° relative phases were judged to be intrinsically variable, 90° maximally so.

A second experiment in the series placed the variability at various points in the trajectory (aligned with peak velocity, peak amplitude, both peak velocity and peak amplitude, or all throughout the trajectory). Two mean phases (0° and 180°) with 4 levels of phase variability were presented to subjects, who were asked to judge the amount of variability. At 0°, variability was detected identically at all points in the trajectory; at 180°, variability was detected at all points in the trajectory but not equally. It was still detected at peak velocity, but not as clearly as at peak amplitude (i.e. when relative speed was close to or at zero). Bingham and Collins concluded that relative speed functioned as a noise term, affecting the subject's ability to resolve the underlying information. They also concluded that the information itself was present to be detected at all points in the trajectory; phase perception is continuous.

Based on these results, Bingham (2001, 2004a, 2004b) described a model, which predicts that the information is <u>detected relative direction of movement,</u> with the ability to resolve the relative direction affected by the <u>relative speeds</u>. 0° and 180° are distinctive points on the circle, by this account, because they are the mean relative phases at which the relative directions are always the same (0°) or always different (180°). 90° and 270° are the points at which the direction is the same half the time, and different the other half of the time, i.e. relative direction is maximally variable. 0° is easy because the relative speed is zero, and the relative directions (which are consistent, and consistently the same) are therefore easily resolved; 180° is hard because the relative speed ranges from zero to maximally different, and the relative directions (which are still consistent but now consistently different) are therefore more difficult to discriminate (because of the non-zero relative speeds). Relative direction is hardest to detect at 90° because it is maximally variable, and also because relative speed is not only non-zero, but highly variable as well.

A role for relative direction in coordination tasks has been implicit in other research for some time. Wimmers et al (1992) showed that when the movements to be coordinated were orthogonal to each other, performance was uniformly less stable but with no tendency to transition from 180° to 0°. They tested both possible mappings (the top of a vertically moving signal corresponded on different trials to either the left or the right of a horizontal limb movement), and found no difference, nor any preference for in-phase (e.g. top/left or top/right) movement. It is technically possible to talk about a relative phase between two orthogonally moving oscillators, but this result shows that the mapping is arbitrary - left can equally map to top or bottom. Relative phase is only unambiguously defined when the oscillators are moving in parallel to one another (or with significant parallel components of motion). This, by hypothesis, is because relative direction is only defined in these cases. Wimmers et al concluded that there was no informational advantage for in-phase defined across orthogonal motions, and hence no drive to transition. This result clearly implicates a key role for relative direction in the perception of relative phase.

More direct evidence of a role for relative direction comes from Bogaerts, Buekers, Zaal & Swinnen (2003). They had people performing cyclical drawing movements with both hands, and the movements were either parallel or orthogonal to each other. Orthogonal movements were less stable than parallel movements. When visual feedback of the task was altered so that the orthogonal movements produced parallel motion on a monitor, the orthogonal movements were stabilized. The biggest improvement was seen while moving orthogonally/anti-phase (defined as up/down vs. left/right) and viewing transformed feedback depicting parallel anti-phase motion (up/down vs. down/up). The authors cite this as demonstrating how important the parallel component of motion is to forming a clearly perceived (perceptually coherent) form, which can then be used to produce stable coordinated movements. The fact that parallel motion was more important than iso-directional motion in stabilizing movement suggests that parallel motion is a prerequisite for movement coordination – relative direction must be definable for the perception-action system to begin coordination.

Finally, recent work (Wilson et al, 2005b) found that adding an orthogonal component to the motion being coordinated had no phase specific effects on movement stability. Across mean relative phases, tracking a linear motion with a circular action was qualitatively the same as tracking it with a linear action. Relative speed is still defined across orthogonal motions; the additional component therefore added noise to the task, but uniformly at all mean relative phases.

The hypothesis that relative direction is the information used to detect relative phase has the added benefit of predicting the various characteristics of rhythmic movement coordination that need to be explained. It is a variable that both vision and proprioception can detect, which accounts for the replication of the judgment results in these two modalities (e.g. Zaal et al, 2000, and Wilson et al, 2003). It also predicts the transfer of learning seen in Zanone & Kelso (1992a, 1992b, 1997). 90° and 270° are symmetry partners because relative direction is the same half the time and different half the time in both cases. Similarly, 135° and 225° are symmetry partners because relative direction behaves identically at both mean relative phases (ignoring which oscillator leads and which follows). Learning does not transfer per se from 90° to 270°, or from 135° to 225°; rather, from the perspective of relative direction, the symmetry partners are identical coordinations. Relative direction also accounts for the fact that learning generalizes across limbs (Kelso & Zanone, 2002) - it has nothing to do with the oscillator per se but only with the motion of the oscillator. Finally, relative direction unifies the results from Wenderoth et al (2002) with the rest of the learning literature. Their hypothesis, that coordinations near 0° were learned more easily than those near 180° for perceptual resolution reasons, is correct; perception of relative direction, conditioned on relative speed, predicts that the region around 0° should be very clearly and finely resolved. 30° will, perceptually, be much more distinct from 0° than 150° is from 180°, making it easier to learn. Also, learning rate varied inversely with proportion of time the oscillators spent moving in the same direction – as in Experiment 1, where the bulk of the learning of 90° occurred below 90°, the better you can detect the information the easier it is to learn it.

A common way to explore what dynamical or informational components are being used in a task is the perturbation experiment. These are premised on the idea that a given perception-action task uses specific informational and motor components, and explicitly does not use others. Formation of a stable perception-action system requires that the required components become temporarily functionally 'walled off' from other components, especially components that they may interact with in other perception-action systems. This softly-assembled task specific device (Bingham, 1988) becomes relatively impervious to irrelevant distractions, allowing the behavior in question to be accomplished stably and reliably for the duration of the task. It follows that perturbing an information variable that the system is currently ignoring will have no effect on the behavior, while perturbing a variable required for the task will interfere with the performance of the task.

A good example of the former is found in Mechsner & Knoblich (2004). They made the fingers being coordinated more visually salient by adding colored cuffs to the fingers, but this manipulation had no effect whatsoever on movement stability. Color is an example of an information source to which the coordinated rhythmic movement task specific device is insensitive – it is functionally irrelevant to the task and hence performance was impervious to the manipulation.

The evidence for the role of relative direction is quite clear, but still inferential. In principle, there are three candidate variables that people could be using to perceive relative phase – relative position, relative speed and relative direction. We therefore selectively perturbed several candidate variables in a series of experiments.

First, it is quite plausible that relative phase perception entails perception of the phases of each individual oscillator and a computation of the difference between them. Phase is a measure of the position of an oscillator within its cycle, and relative phase is therefore a measure of the relative position of two oscillators within their cycles. In Bingham's model, phase is instantiated as a normalized velocity signal (see Eq. 2). The model predicts that the perception of phase entails that velocity is scaled by the frequency, and position is measured with reference to an origin, which is the point at which peak velocity occurs.

During a coordinated rhythmic movement, the model assumes that each oscillator is being driven by the perceived phase of the other oscillator. When modeling perceptual judgments, however, Bingham did not use phase, but instead integrated the relative phase term P (Eq. 3). In other words, the model assumes that judgments about relative phase do not require information about phase, per se.

To test this assumption, we perturbed the perception of phase by perturbing subjects' ability to perform the required normalization. This was done independently of relative direction, and therefore the model predicts that this perturbation should have no effect on the perception of relative phase. Trajectories are normalized by using the frequency, yielding a circular trajectory on the phase plane with an origin at zero position and peak velocity. First, we perturbed the reference frame for position by randomly altering amplitude on each half cycle of motion (Perturb Position). The amplitude on one half-cycle was no longer informative about the amplitude of the next cycle, and the origin of the position axis was therefore not specified ahead of time. Second, we perturbed frequency by systematically varying it over the course of a trial (Perturb Speed, v2).

Relative speed is the second candidate. Different mean relative phases do indeed show different relative speed profiles, which may be enough to specify the phase. This is only true for a given pair of amplitudes, however - if the two dots in the display are moving at different amplitudes, then the relative speed profile 0° could now be identical to that of movement at 180° with equal amplitudes. It seems unlikely, however, that a subject would rate 0° motion to be 180° motion under such circumstances. Bingham's model predicts that the speed difference is only a noise term (see Eq. 3 in the General Introduction). This predicts that when the absolute value of the speed difference is increased it should interfere with subjects' ability to detect the underlying information but not disrupt performance entirely, as it would if it were the perceptual instantiation of relative phase. We tested this by increasing the amplitude of one of the dot's motion, thereby increasing the magnitude of the relative speed difference (Perturb Speed, v1).

Finally, the proposed information variable specifying relative phase is the relative direction of motion. Bingham's model proposes that the relative direction term P is integrated over time to generate judgments about relative phase. Relative phase is therefore specified by the proportion of time the oscillators spend moving in the same or opposite directions. We attempted to perturb this relative direction behavior (independently of mean relative phase) in two different ways (the Perturb Direction experiment).

While the evidence clearly implicates relative direction (with relative speed serving as a noise component), the results thus far have all been inferential, and no direct test of the hypothesis has been made. Experiment 2 was designed to systematically test three candidate variables. As the evidence at this point is overwhelming that the information underlying the judgment and movement tasks is identical, Experiment 2 systematically perturbed each of the components described above in versions of the 'Choose 90°' judgment task.

Methods – Experiment 2

The same four subjects returned approximately 3-4 weeks after Post Training 1 to participate in the perturbation experiments. They were again paid $10 per hour long session. They first participated in Post Training 2 to test whether their learning had persisted in the interim. The results of that session are reported above, and confirmed that performance in the Choose 90° remained at initial post-training levels.

Procedure: Perturb Position

It is, as noted in the Introduction, quite plausible that perception of relative phase depends on the perception of phases of the two oscillators, i.e. relative phase is simply perceived as the relative position of the two oscillators within their respective cycles. Bingham's model predicts that the information for phase is a normalized velocity signal. Normalization is vital for the computation of phase (Eq. 2), because it assumes a circular trajectory on the phase portrait. Any deviation from circularity makes the computation of phase inaccurate.

Normalization is performed with respect to the origin of the phase portrait, which in the current displays is the mid-point of the harmonic oscillatory movement of the dots. Without a constant amplitude, the origin keeps changing location. An observer should be unable to perform the normalization and hence be unable to successfully perform the coordination task. Normalization was therefore perturbed by randomly changing the

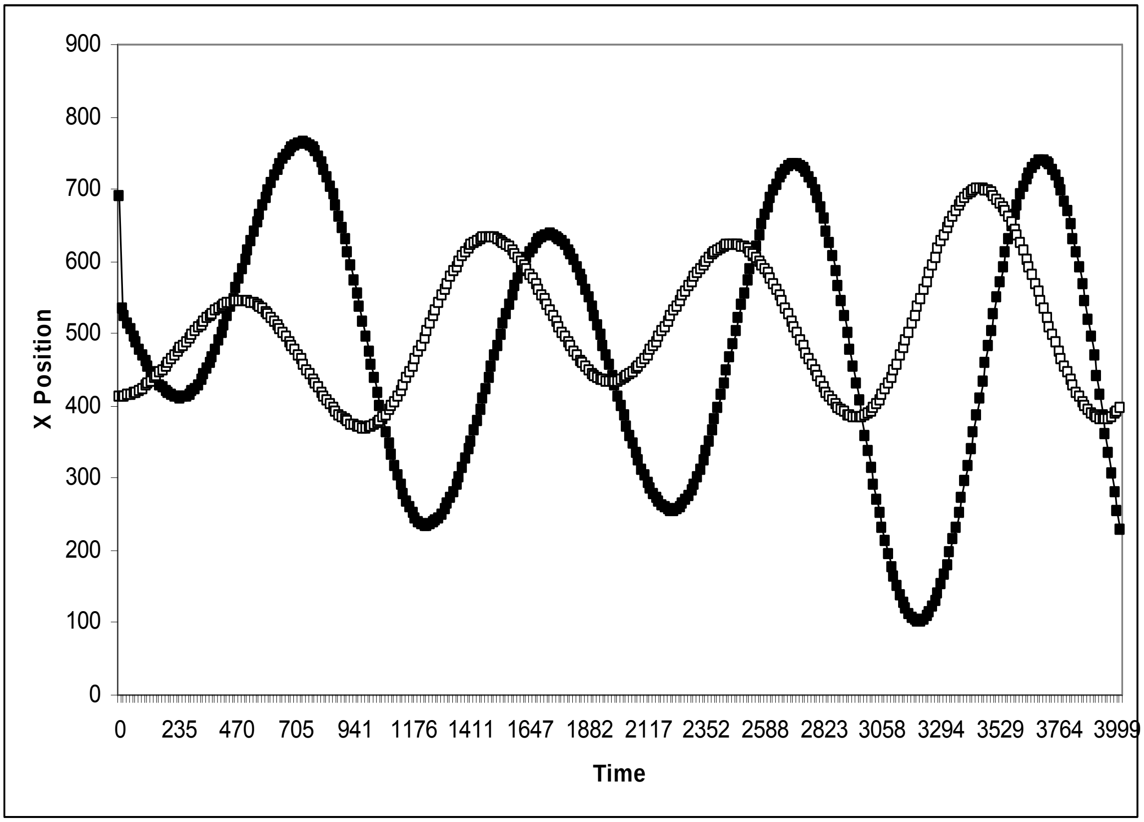


Figure 10. Time series for the Perturb Position display with a mean relative phase of 90° between the top dot (dark line) and the bottom dot (white line).

amplitude of the dots from half-cycle to half cycle (where a half-cycle is defined as the dot moving from one side of the screen to the other).

If the amplitudes of the two dots remain identical (i.e. if they change by the same amount each half-cycle) they remain moving in lockstep. The position of the mid-point is successfully perturbed, but at non-0° relative phases there would be two opportunities to detect it, one for each dot. The amplitude of the bottom dot was therefore set to be half the amplitude of the top dot, which meant that the position of the mid-point was always different for the two dots. See Figure 10 for a position time series of the two dots during a display of a mean relative phase of 90°.

The task was Choose 90°, and involved discriminations between 90° and 60°, 75°, 105° and 120° (i.e. Set 3 from the training sessions). This set was chosen to be hard but not at the limit of post-training performance. The model predicts that because this perturbation does nothing to relative direction, there should be no effects of the perturbation on judgments about relative phase. There was a brief practice session prior to the main experiment, with examples of perturbed displays showing 0°, 90° and 180°. There were also several easy discrimination trials, with feedback. No feedback was provided during the experimental trials. There were 5 blocks, with each block containing one of each trial type presented in random order.

Session	Threshold (°)	Uncertainty Coefficient (U)
Perturb Position		
Full	53.3	0.0331
<90	117	0.0071
>90	33.12	0.0802
Perturb Speed (version 1)		
Full	14.47	0.2968
<90	16.93	0.2389
>90	12.24	0.3645
Perturb Speed (version 2)		
Full	23.92	0.1424
<90	21.89	0.1645
>90	25.58	0.1266

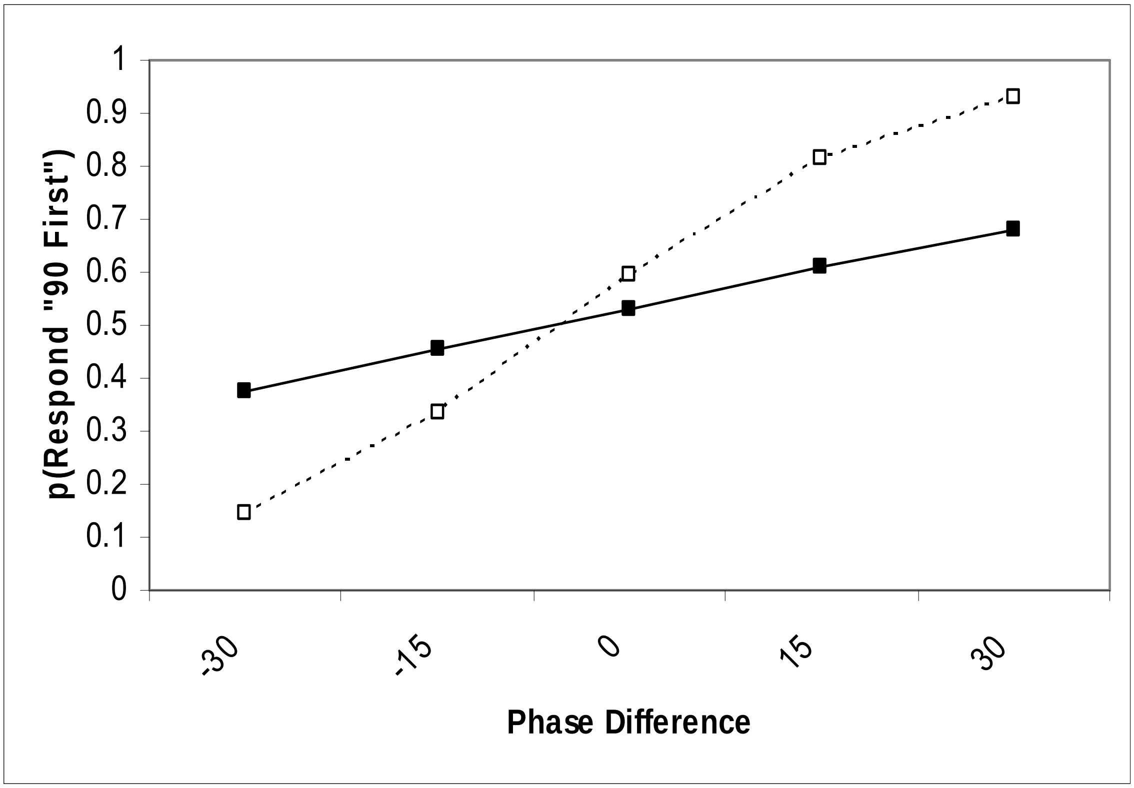
Table 7. Thresholds (in degrees) and uncertainty coefficients (U) for the compiled Perturbation data from all four subjects combined.

Results & Discussion – Perturb Position

Refer to Figure 11, which shows the compiled and uncompiled data from all subjects. The dark lines are the model fits for the perturbation condition; the dotted lines show the model fit from Post Training 2 as a reference. Table 7 contains the threshold and uncertainty coefficient data. The overall threshold in the perturbation condition was 53.3° (compared to 15.28° in Post Training 2 and 32° in the Baseline). Clearly, this perturbation dramatically interfered with the subjects' ability to discriminate 90°, indicating that the reference fram required to normalize the velocity signal (amplitude) is indeed crucial to performance in this task.

Refer to the uncompiled data – below 90° was hit much harder (threshold was 117°) by the perturbation than above 90° (threshold was 33.12°). The perturbation was still having a significant effect above 90°; this threshold was significantly worse than even the comparable Baseline threshold. The reason for the poorer overall performance below 90° can be found in the individual data (Figure 12) – Subjects 2 and 4 showed negative slopes below 90°, which, when combined with the low but positive slopes of Subjects 1 and 3 produce the observed overall flat line. This still leaves the difference in the individual data to be explained.

Three of the subjects were affected by this perturbation, which could not happen if the information for relative phase is just relative direction. The data clearly suggests that perceived phase matters to the perception of relative phase. There is information about



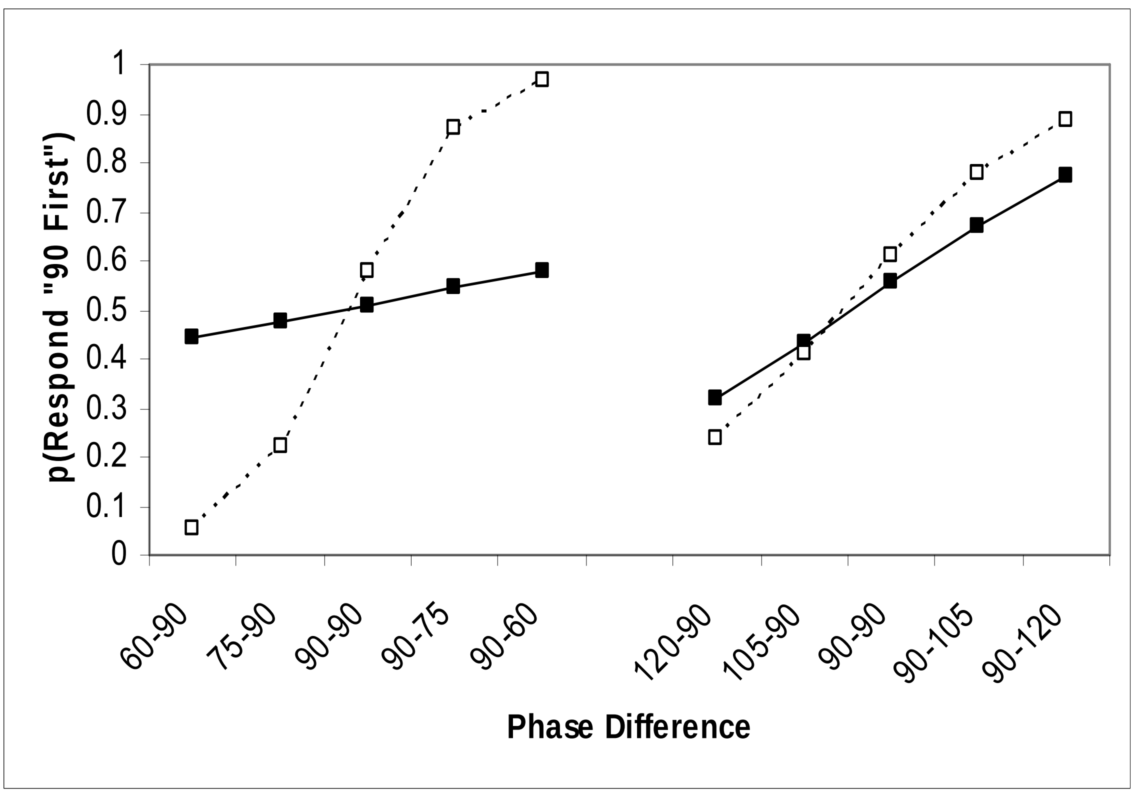


Figure 11. Logistic regression model fits for Perturb Position (filled squares) and Post Training 2 (open squares) judgment data from all subjects.

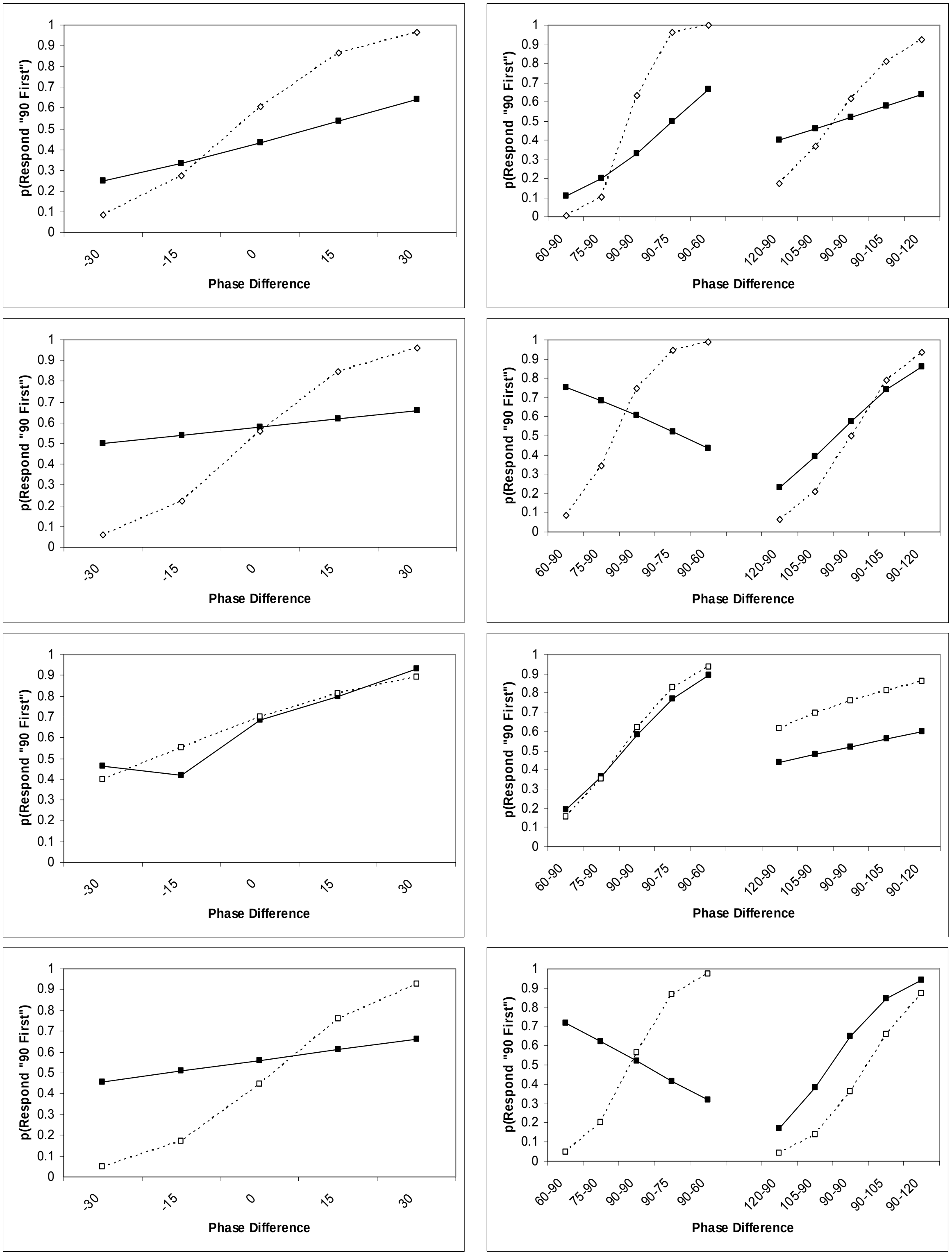


Figure 12. Logistic regression model fits for the compiled (left hand column) and uncompiled (right hand column) for each individual subject, comparing performance in the Perturb Position (filled square) and Post-Training 2 (open square) judgment tasks.

phase in these displays; however, with normalization impossible this information is unstable and therefore unreliable. The question remains, however – why the asymmetry about 90°? We analyzed the data in the uncompiled format because the hypothesis that the information is relative direction predicts asymmetric behavior above and below 90°. However, the current results now suggest that phase, not relative direction, is the information being used by these three subjects, and this does not predict an asymmetry about 90°. The source of the individual subject variability is therefore unclear, and remains a topic for future research.

Subject 3 was almost entirely unaffected by the perturbation, relative to her performance in Post Training 2. Her performance below 90° was identical to that in Post Training 2 (her thresholds were 15.1° for Post Training 2 and 18.7° for the perturbation). Her performance above 90° is perturbed, but this may have something to do with the fact that her performance above 90° in Post Training 2 was unstable to begin with (Post Training 2 threshold was 51.3°, which is very poor performance in the context of this study). It seems that Subject 3 has learned to use only relative direction as the information for relative phase, and because this was unperturbed in these displays, she was unaffected.

<u>Summary – Perturb Position</u>: The effect of the perturbation was to perturb the reference frame of the motion and hence make it impossible to normalize the velocity information. This normalization is essential to the production of rhythmic movement coordination in Bingham's model, but not to judgments about such coordinations, because the detection of relative direction does not require normalization. The model therefore predicted that

this perturbation would not affect performance in a judgment task. However, three of the four subjects were unable to perform the Choose 90° task under these conditions, suggesting that phase is perceived and used to make judgments about relative phase. The remaining subject was hardly affected at all by the perturbation, which implied she used only relative direction to perceive relative phase.

<u>Procedure - Perturb Speed (version 1)</u>

Relative speed is simply the magnitude of the speed difference between, in the present case, two moving dots. Harmonic motion at different mean relative phases show different relative speed profiles, and these could therefore be used to perceive relative phase. If the two dots are at 0° mean relative phase (with identical frequency and amplitude), the relative speed is always zero. At 180°, relative speed varies from zero (at the end points) to a maximum (at the mid point, where the two dots are both at peak velocity but heading in opposite directions). The story is slightly more complicated for harmonic motion at 90°; the peak magnitude (for a given frequency and amplitude) is never as high as at 180°, but it is also never zero. The relative speed profile over the course of an oscillation is also more variable, with one dot reaching peak speed while the other is at an end point, and the dots crossing twice halfway between the midpoint and each end.

Bingham's model predicts that the speed difference is effectively a noise term that acts on the detection of relative direction (Eq. 3). Recall that when Bingham and Collins placed variability was placed at peak velocity, it was easily detected at 0° mean relative phase

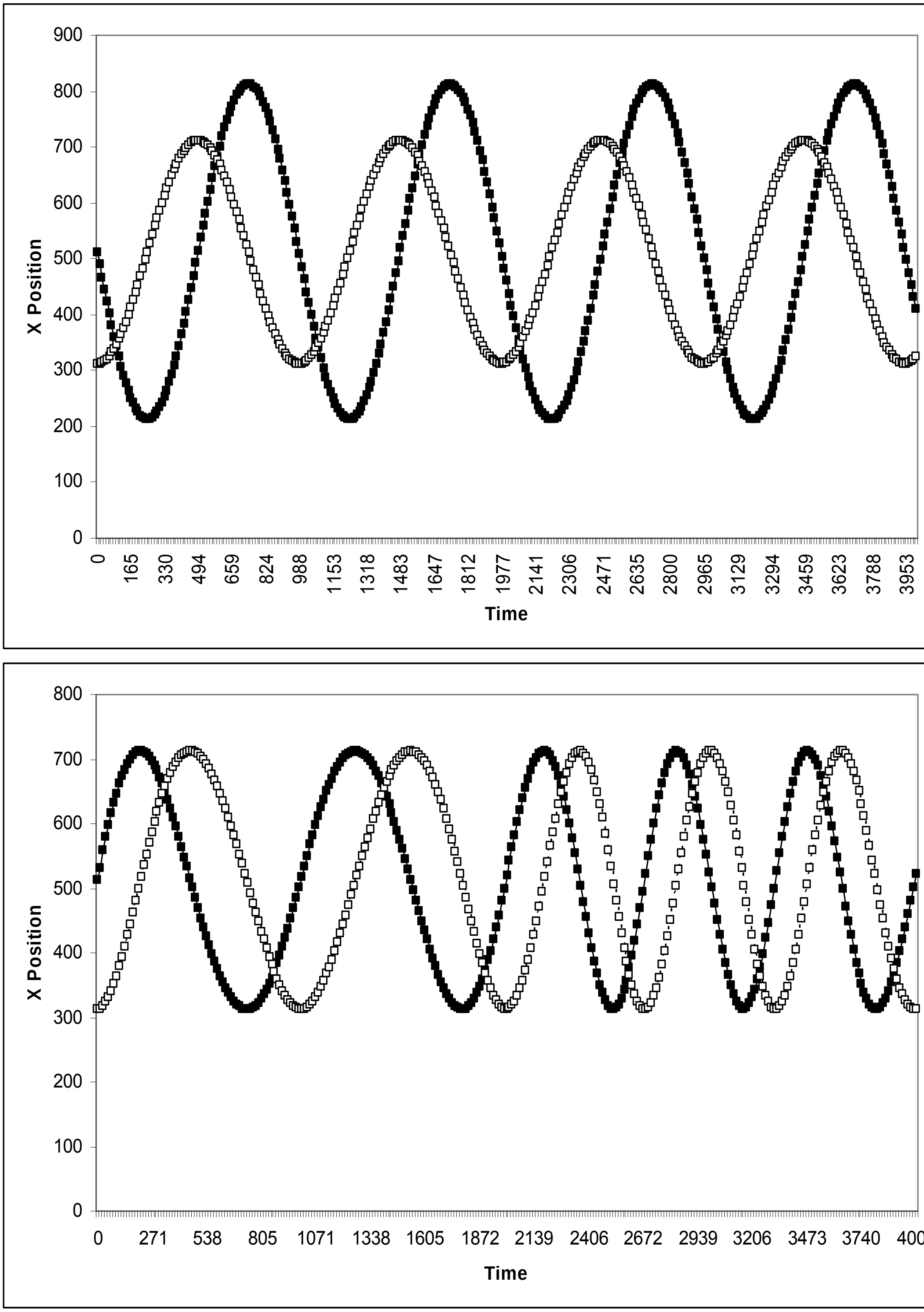


Figure 13. Time series for the Perturb Speed displays with a mean relative phase of 90° between the top dot (dark line) and the bottom dot (white line).

and detected but not as easily at 180° mean relative phase. Variability placed at peak amplitude was readily detected at both mean relative phases. When relative speed is zero (at 0°, or at the endpoints of a 180° motion) the noise is zero and relative direction is easily detected. When it is non-zero, it affects the resolution of relative direction.

Relative speed was perturbed by an amplitude manipulation. One oscillator (the top dot) moved at 1.5 times the amplitude of the bottom dot, the amplitude of which was identical to the unperturbed displays. These amplitudes were constant within and between trials. To preserve a global mean relative phase, the oscillator with the larger amplitude has to move faster. The magnitude of the speed difference was therefore higher than in the unperturbed displays, all the way through the trajectory, increasing the amount of noise but uniformly for all mean relative phases. See Figure 13a for a time series for a perturbed display showing a mean relative phase of 90°.

The task was again Choose 90°, and involved discriminations between 90° and 60°, 75°, 105° and 120° (i.e. Set 3 from the training sessions). Bingham's model predicts that the increased magnitude of the speed difference will make detection of the information harder, and that therefore performance in this task will decrease relative to Post Training 2. There was a brief practice session prior to the main experiment, with examples of perturbed displays showing 0°, 90° and 180°. There were also several easy discrimination trials, with feedback. The experimental trials did not give any feedback. There were 5 blocks, with each block containing one of each trial type presented in random order.

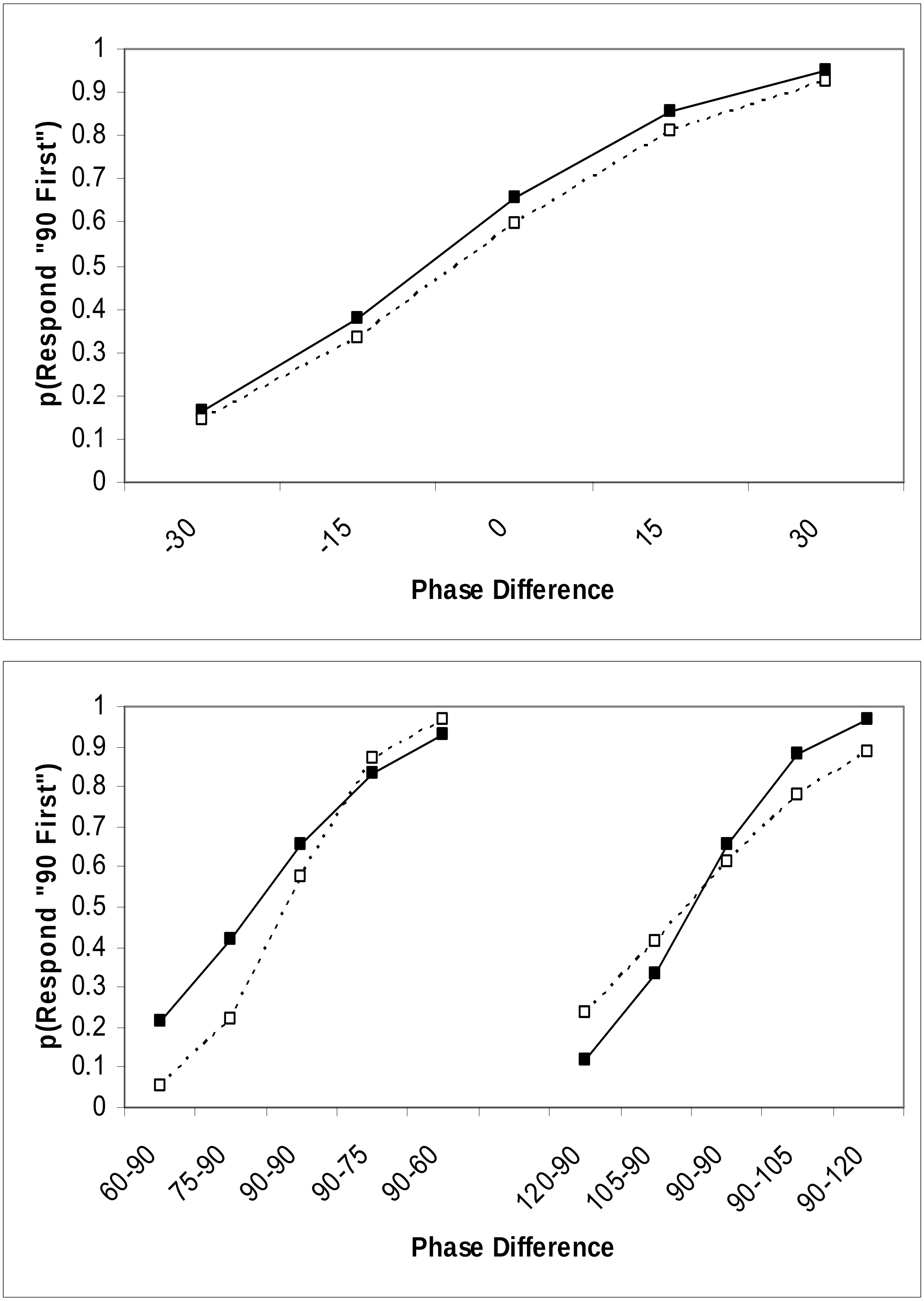


Figure 14. Logistic regression model fits for Perturb Speed v1 (filled squares) and Post Training 2 (open squares) judgment data from all subjects.

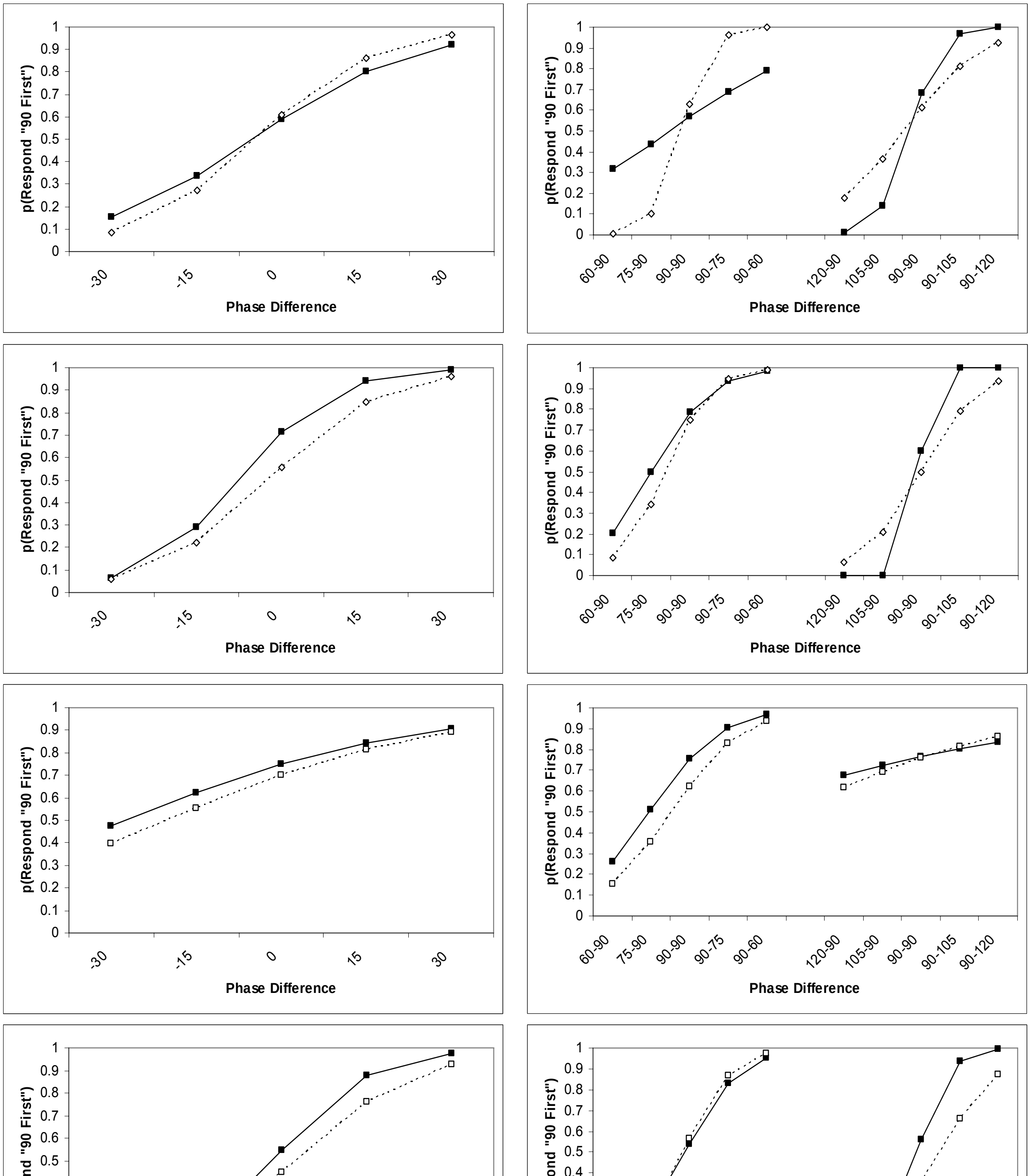


Figure 15. Logistic regression model fits for the compiled (left hand column) and uncompiled (right hand column) for each individual subject, comparing performance in the Perturb Speed v1 (filled square) and Post-Training 2 (open square) judgment tasks.

Results and Discussion – Perturb Speed (version 1)

Refer to Figure 14, which shows the compiled and uncompiled data from all subjects. The dark lines are the model fits for the perturbation condition; the dotted lines show the model fit from Post Training 2 as a reference. Table 7 contains the threshold and uncertainty coefficient data. The overall threshold in the perturbation condition was 14.47° (compared to 15.28° in Post Training 2 and 32° in the Baseline). Overall, there was no effect of the perturbation. It seems that the perturbation may have been too small to have caused an effect. Performance was slightly worse below 90° (overall threshold was 16.9) than it was above 90° (overall threshold was 12.24°), suggesting that the perturbation was having a small effect but that effect was only detectable below 90°. This result supports the hypothesis that the region below 90° is more clearly discriminated, and that when detectable, an increase in relative speed adds a relatively constant level of noise to the judgments.

The individual data (Figure 15) essentially replicates the overall results. Subject 1 was affected quite profoundly below 90° (her threshold went from 6.1° to 31.4°). This is consistent with the idea that a perturbation must be detected to be effective – Subject 1's Post Training 2 threshold below 90° was by far the lowest of all four subjects either above or below 90°, indicating excellent resolution of that region. She was therefore most able to detect (and be affected by) the perturbation. Subject 3's performance above 90° was very poor, but almost identical to her performance there in Post Training 2, suggesting that it was not the perturbation causing the decrement.

Summary – Perturb Speed (version 1): The speed perturbation had almost no effect on performance in the judgment task, except in one case where the perturbation was being clearly detected and hence was able to have an effect. The magnitude of the perturbation (limited by the size of the computer monitor) is a problem for drawing strong conclusions; however, it seems safe to conclude that the absolute speed difference, per se, is not the information underlying the task.

Post Training 3 and Perturb Speed (version 2)

After we analyzed the Perturb Position data, we realized that we had a potential confound in interpreting the data. By having the amplitudes of the two dots be different, we succeeded in perturbing the information required to normalize the velocity information. The position perturbation also resulted in a highly variable relative speed profile, which is one of the aspects of 90° that potentially makes the information difficult to detect. We therefore designed a perturbation to make frequency (and hence the relative speed profile) variable, while keeping amplitude constant.

First, however, we needed to check the state of the four subjects performance in the Choose 90° task for a final time – this perturbation study took place some 6 weeks after Post Training 2 and the other perturbation studies.

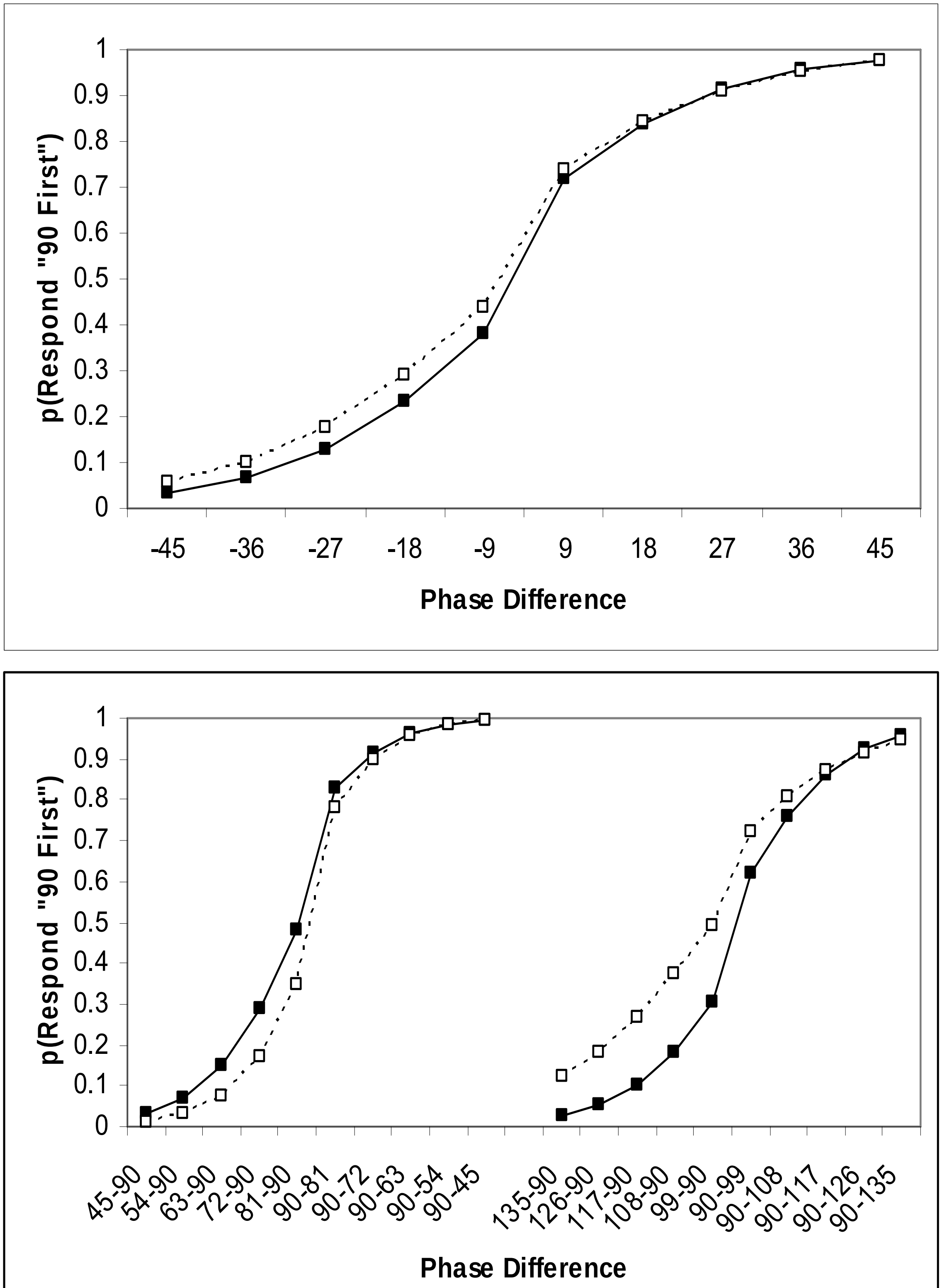


Figure 16. Logistic regression model fits for Post Training 3 (filled squares). The model fit for Post Training 2 (open squares) is included for comparison.

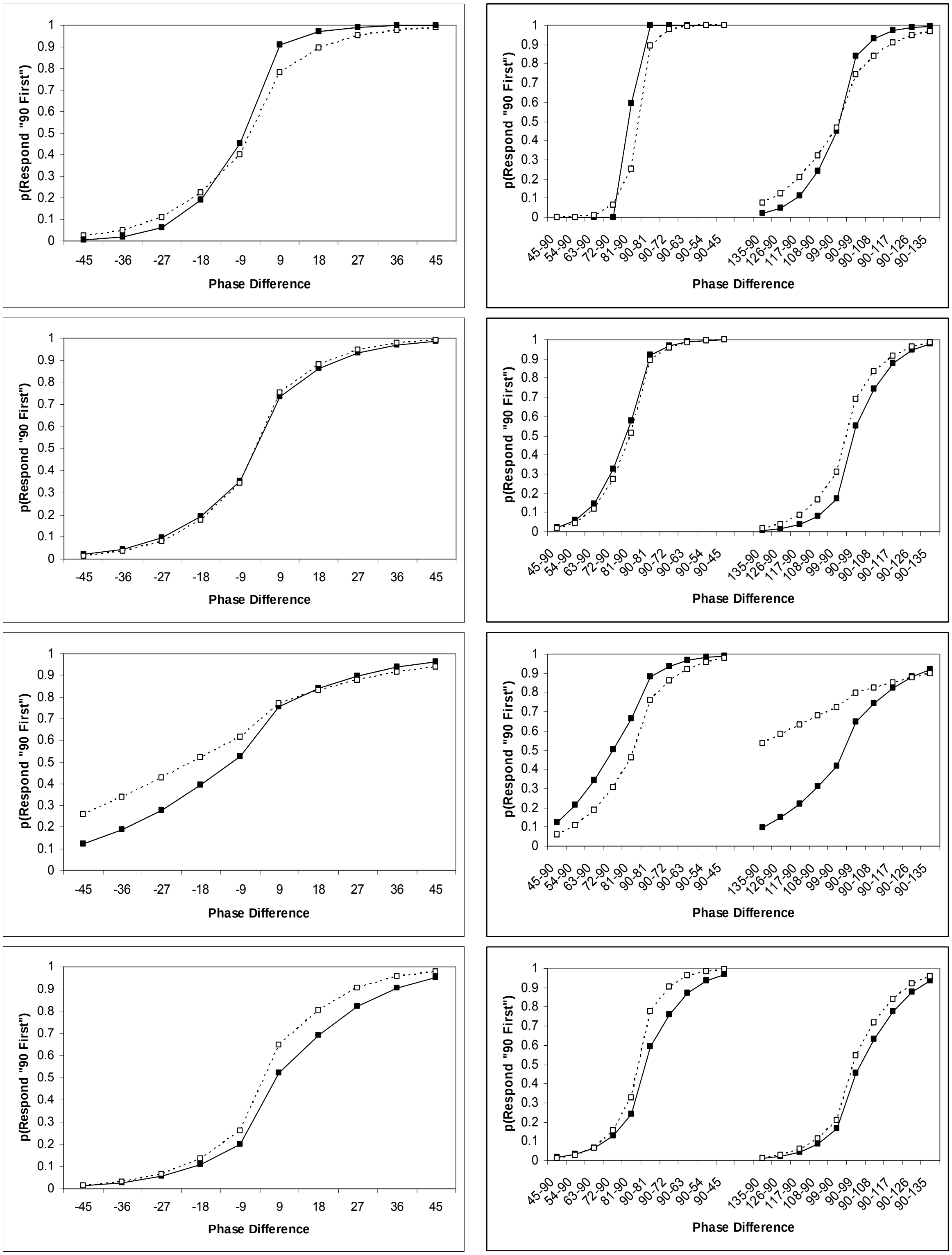


Figure 17. Logistic regression model fits for the compiled (left hand column) and uncompiled (right hand column) for each individual subject, comparing performance in the Post Training 3 (filled squares) and Post-Training 2 (open square) Choose 90 task.

Procedure: Post Training 3

Because of the delay between the second round of perturbation experiments and Post Training 2, we tested the four subjects on the Baseline Choose 90° task, to make sure that their learning had persisted.

Results – Post Training 3 Judgments

Refer to Figures 16 (all subject data) and 17 (individual subject data). Tables 1 & 2 show the thresholds and uncertainty coefficients for the overall data, while Tables 3 & 4 show the individual data. Overall, performance in the Choose 90° task remained good. Any changes that did occur were mostly for the better; performance improved slightly for all subjects above 90° (in fact, the change was not so slight for Subject 3). The process of consolidation appears to be continuing, and performance in the harder part of the space is finally starting to benefit. This data confirmed that the subject's learning had persisted, in the absence of specific practice. The fact that performance in the above 90° trials improved last over the course of the post-training probes supports the hypothesis that these trials are, indeed, more difficult, a result which adds another piece of inferential support to the relative direction hypothesis.

Procedure – Perturb Speed (version 2) – Frequency was varied over the course of each trial according to the function

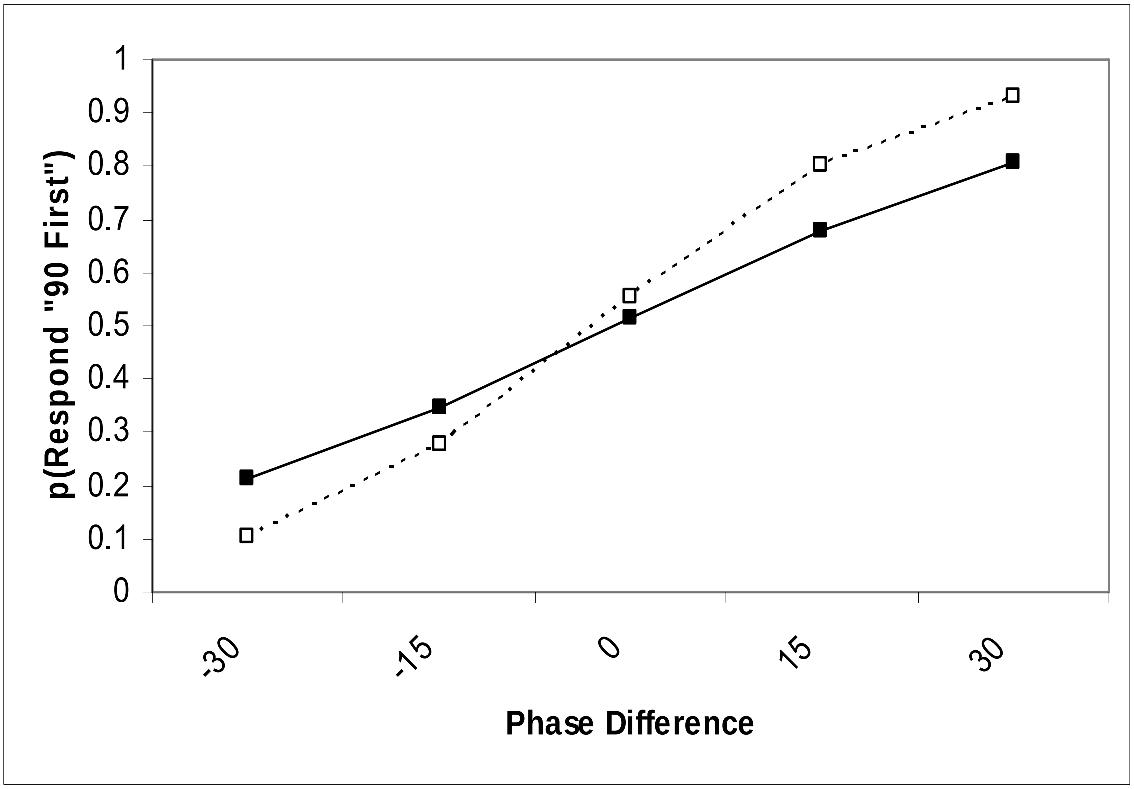
$$F = (1.25 + 0.25 * \sin(time / 4000) * (2 * PI); \qquad (2)$$

This equation was evaluated at each time step, and the new value for frequency was used in computing the positions. Frequency therefore began at 1.25Hz and smoothly varied sinusoidally from a minimum of 1.0Hz to a maximum of 1.5Hz. In half the trials the frequency first decreased, then increased (the negative frequency function; see Figure 13b for a time series), while in the other half this was reversed (the positive frequency function; effectively running the time series in Figure 13b in reverse).

The task was again Choose 90°, and involved discriminations between 90° and 60°, 75°, 105° and 120° (i.e. Set 3 from the training sessions). There was a brief practice session prior to the main experiment, with examples of perturbed displays showing 0°, 90° and 180°. There were also several easy discrimination trials, with feedback. No feedback was given during the experimental trials. There were 5 blocks, with each block containing one of each trial type presented in random order.

Results & Discussion – Perturb Speed (version 2)

There were no differences in performance for the positive versus the negative frequency functions, so all analyses combined this data. Refer to Figure 18, which shows the compiled and uncompiled data from all subjects. The dark lines are the model fits for the perturbation condition; the dotted lines show the model fit from Post Training 3 as a reference. Table 7 contains the threshold and uncertainty coefficient data. The overall threshold in the perturbation condition was 23.9° (compared to 13.9° in Post Training 3 and 32° in the Baseline). Overall, there was an effect of making frequency variable. The



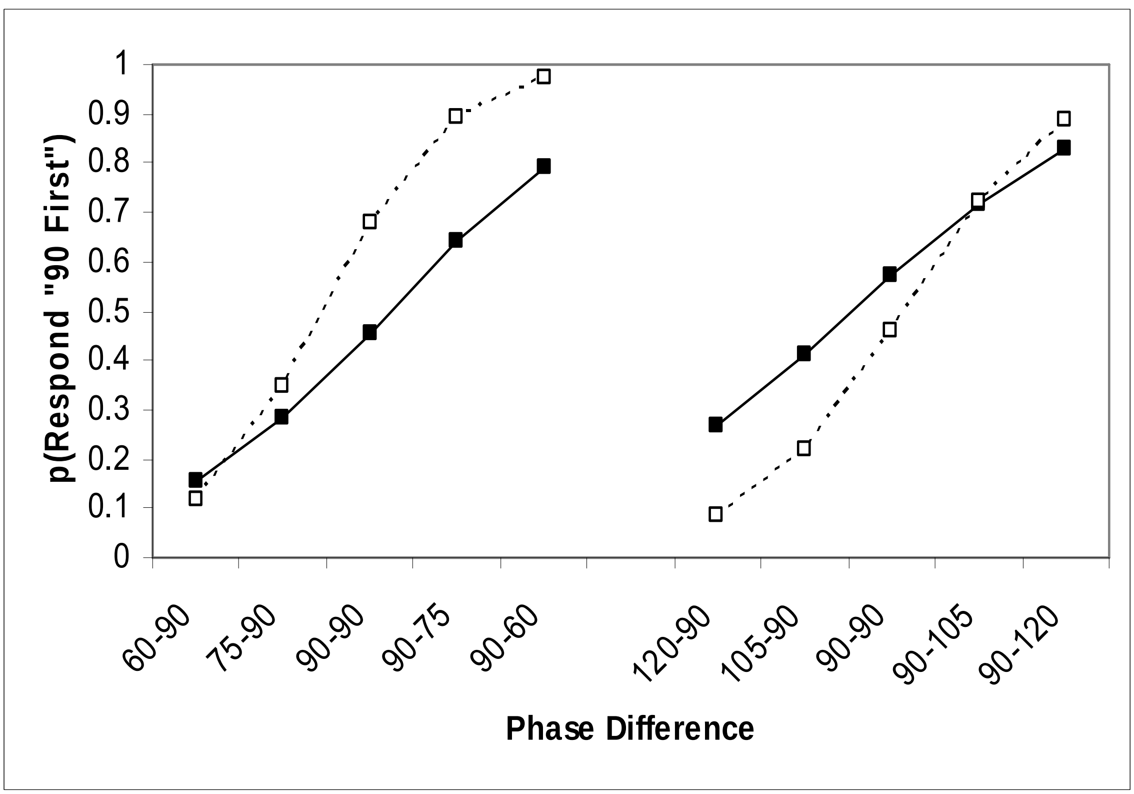


Figure 18. Logistic regression model fits for Perturb Speed v2 (filled squares) and Post Training 3 (open squares) judgment data from all subjects.

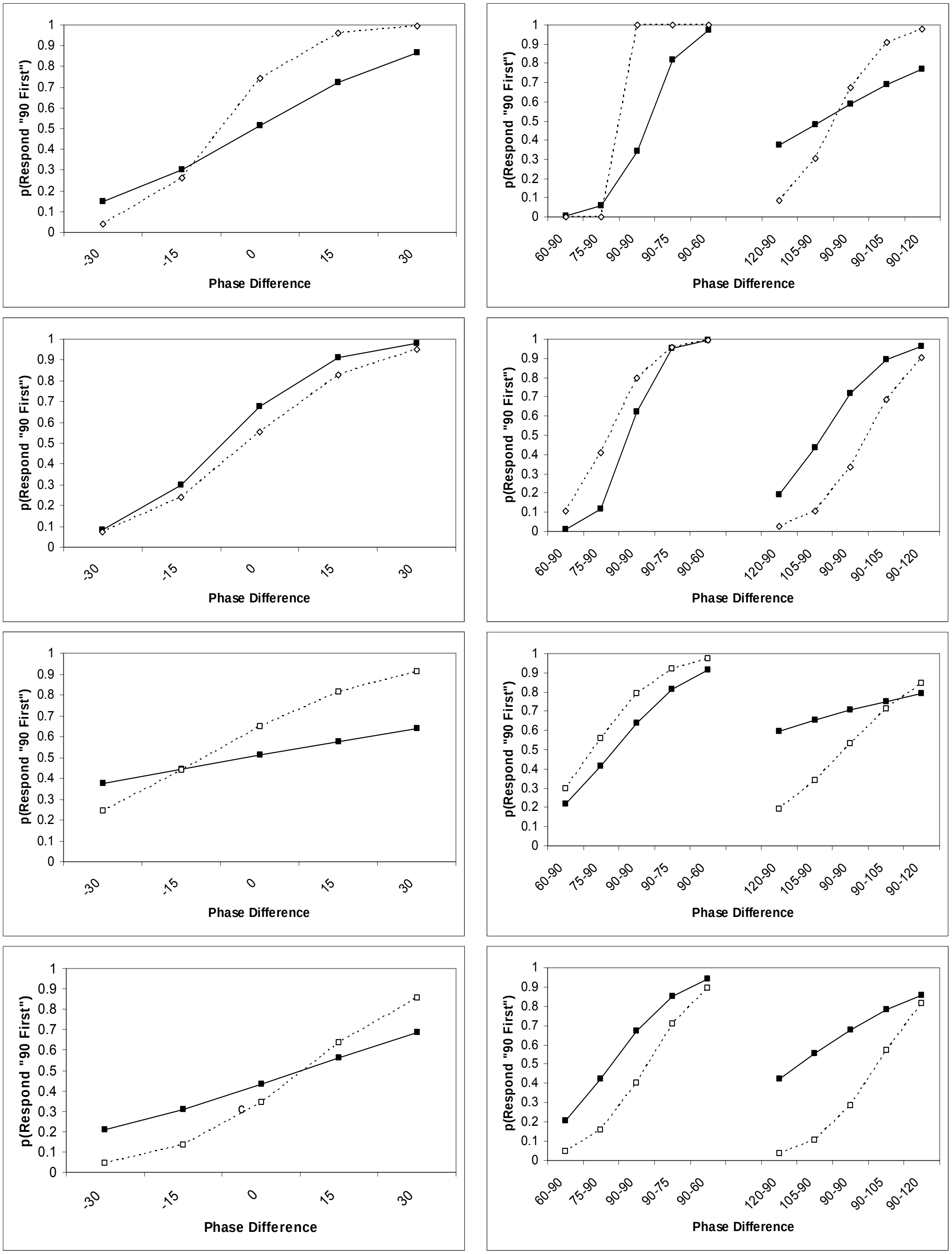


Figure 19. Logistic regression model fits for the compiled (left hand column) and uncompiled (right hand column) for each individual subject, comparing performance in the Perturb Speed v2 (filled square) and Post-Training 3 (open square) judgment tasks.

decrement in threshold was not as pronounced as in the Perturb Position data; however, this perturbation clearly reduced subjects' ability to perform the Choose 90° task.

There was a small difference between the above and below 90° judgments, overall; performance above 90° was slightly poorer. The individual data (Figure 19) shows this quite clearly – all four subjects were worse above 90° than below, the reverse of the pattern found in the other perturbations.

This pattern suggests that the main effect of the perturbation was to add noise, which affected the already hard above-90° displays more but still affected all trials types. The added noise has two related potential sources, the varying frequency and the (therefore) variable relative speed profile. Varying the frequency but not the amplitude meant that the normalization of the velocity information could be done (using the amplitude), but the result would be unstable. The information was available, but its detection would be unstable. This would affect the three subjects who seem to be perceiving relative phase in terms of phase. The magnitude (and, possibly, the variability) of the relative speed simply affects the discriminability of relative direction. With a variable profile, the relative speed would sometimes be higher than the comparable unperturbed display, and hence the display would be noisier; this also reduces the amount of time during a trial during which the relative speed is low enough for the information to be clearly resolved, which would also contribute to the instability of the judgments. This would account for Subject 3 being affected by this perturbation, given that she does not appear to rely on phase for the perception of relative phase. The primary perceptual consequence of this perturbation was therefore to add noise to the displays.

Summary – Perturb Speed (version 2): Performance was hurt by this perturbation, but not to the same extent as in the Perturb Position condition. The pattern of data suggests that, perceptually, the perturbation added noise to the displays which affected detection of the information required to perform the judgment, but did not perturb the information itself. Given the stability of amplitude, participants likely relied on it for normalization, and hence were able to do the task (albeit noisily; the changing frequency would make the constant amplitude an inappropriate scaling parameter for much of the trial).

Procedure - Perturb Direction

Relative direction is a measure of whether two oscillators are moving in the same or opposite direction (it is either +/-1, in other words). 0° is characterized by the oscillators moving in the same direction 100% of the time; 180° is characterized by the oscillators moving in the same direction 0% of the time; and 90° is the point of maximum variability in relative direction (50% same, 50% opposite direction).

Bingham's model predicts that this is the information variable modifies the perceived phase used to drive a coordinated rhythmic movement, and that judgments about relative phase entail integrating relative direction over time (relative phase is specified, mod 180°, by the proportion of time the oscillators move in the same versus the opposite direction).

The noisy detection of relative direction (with the noise a function of the speed difference) is required in the driver in order to generate the HKB attractor layout.

Relative direction was perturbed in two ways. First, we added a sinusoidal component to the y-axis of the dots. By manipulating the relative phase of the y-component sinusoids, we could vary whether the two dots were traveling in the same or the opposite direction, independently of the mean relative phase along the x-axis. Pilot data, however suggested that the perturbation had no effect; the displays had produced a motion which could be decomposed by the visual system into the two component sinusoids (c.f. Johansson, 1950) nullifying the perturbation.

The second method had the dots move in a square wave trajectory (refer to Figure 20). The top dot moved along trajectory (1); the bottom dot moved along one of the other trajectories (2-5). The initial difficulty with a square wave is that each corner is an abrupt discontinuity, to which the visual system is likely to be highly sensitive and which may add noise that is not specific to the task. However, the 0° condition served as a control for the effects of the corners; all the corners are present, but there is no variability from either relative direction or relative speed. One clear advantage of the square wave was being able to perturb relative direction very precisely, without the visual decomposition problem.

The proportion of time spent moving in the same or in different directions could now be varied. The square wave trajectory has motion along the x-axis (left to right) and the y-

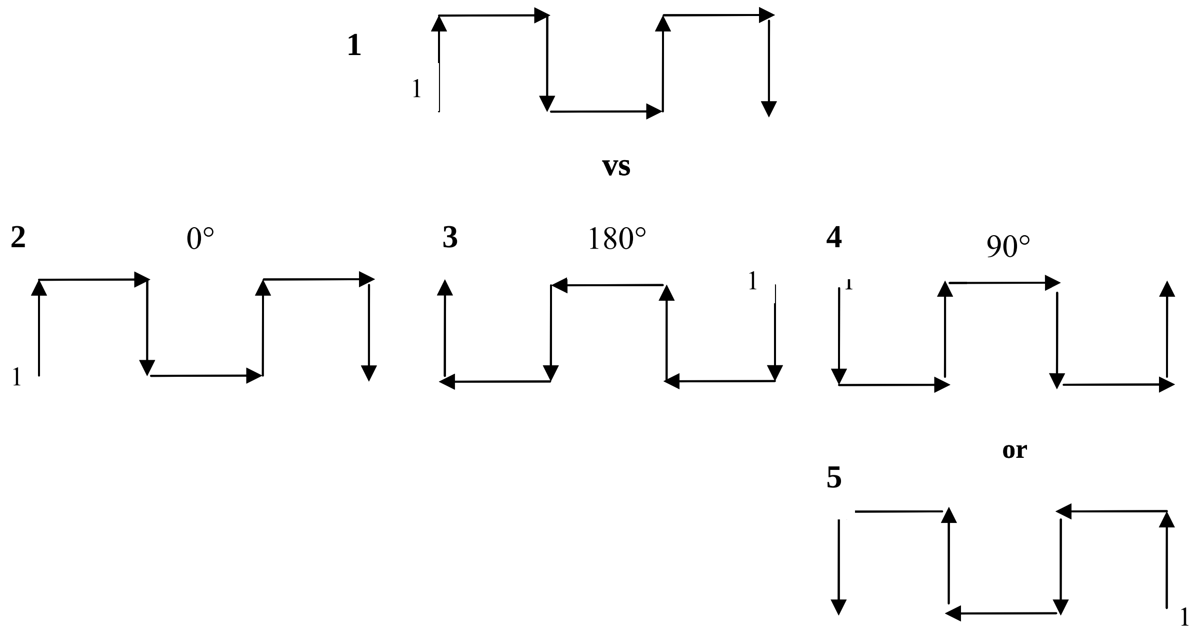


Figure 20. The top row is a schematic of the path followed by the top dot. The second row shows the path the second dot followed to produce relative direction behavior consistent with 0° (1 & 2), 180° (1 & 3) or 90° (1 & 4 or 1 & 5). There are two ways of producing 90°-like behavior - having the x-components moving the same direction and the y-component moving in the opposite direction, or vice versa.

axis (top to bottom). Each dot's motion was always parallel to the motion of the other dot (so that relative direction is defined) but it could move in the same direction or the opposite direction. Look at the schematic path at the top of Figure 20 (representing the movement of the top dot), and compare it first to the '0°' trajectory (2) for the bottom dot. Note that both x and y components were moving in the same direction at all times. Now compare it to the '180°' trajectory (3). Both components were at all times moving in the opposite direction.

Now compare the top dot's trajectory (1) to the first '90°' trajectory (4). Both dots started at the same x location, but began moving in the opposite y directions. When they began moving along x, they are moving in the same direction, and so on. In this way relative direction is the same half the time, and different half the time, as is the case in 90°. The other example (5) is when the same direction motion is along the y-axis.

The problem now was to get a slightly different pattern of relative direction, while maintaining the parallel motions. We needed to be able to make 'different' displays for the judgment task, something analogous to 60°, for instance. Such patterns were created by using the '90°' trajectories (numbers 4 and 5 in Figure 20) and varying the speed of the dots from segment to segment. For example, if, when moving in the same direction, the speed of the two dots is reduced half the speed of the two dots when they are moving in the opposite direction, the display will spend twice as much time moving in the same direction as moving in the opposite direction. This is how relative direction behaves at

45°. By calibrating this difference carefully, the temporal pattern of relative direction for any arbitrary mean relative phase can be generated.

We showed subjects examples of ‘0°’. ‘90°’ and ‘180°’ (refer to Figure 20), and then showed them a series of displays showing ‘0’, ‘90°(x)’ and ‘90°(y) (displays 4 and 5 respectively, from Figure 20[4]), 180’, and ‘45’, ‘60’, ‘120’ and ‘135’, with the latter four conditions calibrated so that the slow segment was either on the x axis or the y axis. For ‘45’ and ‘60’, the slow segment was whichever segment (x or y) along which the dots were currently moving in the same direction; for ‘120’ and ‘135’, the slow segment was whichever segment (x or y) along which the dots were currently moving in the opposite direction. There were therefore twelve different trial types; each was presented once per block, and there were five blocks

The task for this section was slightly different. There was no way to do a version of the Choose 90° task using these displays, because strictly speaking the dots were never moving at 90°; they were moving such that a specific characteristic of their motion (relative direction) behaved as it does at 90°. Additionally, the method used to generate non-90° displays meant that a Choose 90° task could be reduced to detecting when the speeds along the segments was the same versus different. Instead, we reverted to having subjects judge mean relative phase using a slider bar, a task which was used in many of the previous judgment studies (e.g. Bingham et al, 2000; Wilson, Bingham & Craig, 2003). We showed subjects examples at the beginning, and then gave them a slider bar

[4] By convention, the ‘x’ label will refer to displays in which the dots moved in the same direction on x-axis segments (and therefore in different directions on y segments), and vice versa for the ‘y’ label.

and asked them to rate the mean relative phase of the display they had just seen. The slider bar went from 0 to 100, but the monitor displayed '0°' at 10, '90°' at 50 and '180°' at 90. This left some room at the end of each slider bar so subjects were forced to place the slider bar in all trials. After they made their judgment, they then used a second slider bar to provide a measure of their confidence in their judgment of mean phase. This slider displayed 'Not Confident', 'Somewhat Confident' and 'Very Confident' at 0, 50 and 90 along the slider bar, again requiring the subjects to place the bar.

Results – Perturb Direction (Square Wave)

Refer to Figure 21, which shows data from all four subjects compiled. The top left graph shows the mean judged mean relative phase. Subjects quite readily judged '0°' and '180°' to be those phases (not surprisingly, as they had seen examples of these exact displays).

The next five data points are for the 'x' conditions (i.e. when the dots were moving in the same direction along the x segments). All five phases in the 'x' condition ('45', '60', '90°', '120' and '135') were judged to have the same mean relative phase (all pairwise comparisons $p>.5$) and were at the 0° end of the scale. Judgments were variable in these trails, but consistently so; Subject 1 rated all these conditions to be 90°, Subjects 2-4 showed the average pattern.

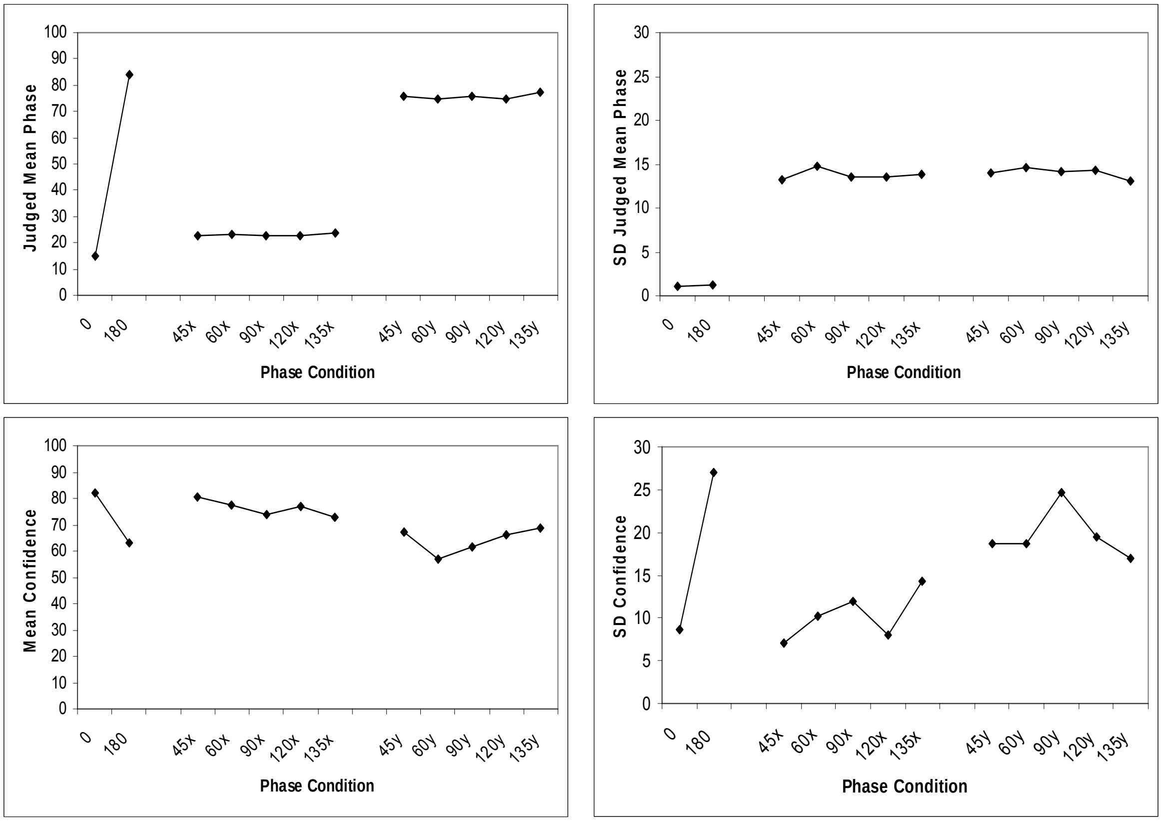


Figure 21. Data from the Perturb Direction condition for all subjects.

Top: Mean judged mean phase (left) and the standard deviation of the mean judged phase (right)

Bottom: Mean confidence (left) and the standard deviation of the mean confidence (right)

The next five data points are for the ‘y’ conditions (i.e. when the dots were moving in the same direction along the y segments, and crucially, moving in the opposite direction on the x segments). All five phases in the ‘y’ condition were judged to have the same mean relative phase (all pairwise comparisons, $p>.5$) and were at the 180° end of the scale. Judgments were again variable, but again, consistently so and for the same reason as the ‘x’ trials.

Mean confidence was high for all judgments, however ‘180°’ and the ‘y’ conditions showed high variability in the confidence judgments.

Subjects were insensitive to the y-axis segments and responded solely as a function of the behavior along the x-axis. If the dots were moving in the same direction along the x-axis, the displays were judged to be 0°; if they were moving in the opposite direction along the x-axis, they were judged to be 180°. Subjects were not completely unaware of the speed manipulation used to generate the various phases; their confidence fluctuated over the various trial types, but not in any systematic way. It seems to be the case that they were simply unable to integrate information across orthogonal dimensions, and chose the more salient x-axis.

The motion along the x-axis was more pronounced; the dots moved across the x-axis in 5 100 pixel segments, and only up and down over a range of 100 pixels. The two subjects who did this condition last were asked to repeat the task, this time paying explicit attention to the y-axis. One subject (2) reversed his judgments, and rated the displays to be 0° when the dots moved in the same direction along the y axis, and 180° when they moved in the opposite direction along the y-axis. However, the other subject (3) was unable to attend to the y-axis and replicated her previous results. So while it is clearly not impossible to detect what is occurring on the y-axis, it is also clearly not easy.

Discussion – Experiment 2

The first part of this project had established that learning in a perceptual discrimination task transferred to a movement task; this second part asked what it was that had been learned. We employed a perturbation method, and systematically perturbed candidate information variables suggested in part by Bingham's perception-action model of rhythmic movement coordination. A perturbation that made normalization of velocity impossible (Perturb Position) completely undermined the ability of three subjects to do the task, while perturbations of relative speed (Perturb Speed, versions 1 & 2) added noise to performance.

Bingham's model predicted that during a coordinated movement, each oscillator is driven by the perceived phase of the other. The information for phase is a normed velocity signal (Eq. 2). That driver is modified by P (Eq. 3), an informational term that instantiates relative phase as relative direction. This modification is required to generate the HKB landscape, which it does by virtue of the way in which detection of relative direction is modified by relative speed (the cubed term in Eq. 2).

In the model, relative phase is specified by relative direction, and therefore phase itself does not have to be detected for judgments about relative phase. In order to model the judgment of mean phase and phase variability (see Bingham 2004a and 2004b), Bingham simply integrated P over a 2-second window. None of the terms in P require normalization, however; in fact, the actual magnitude of the relative speed difference in the noise term is required to simulate the effect of frequency changes on movement stability, and normalization would cancel that out. The model therefore predicted that a perturbation that affects normalization but preserves relative direction should have no effect on judgments about relative phase. This was not the case – performance was hit hardest in the Perturb Position condition. It therefore seems clear that both the coordinated movement and perception of coordinated movements require the same information, and that that information is both phase and relative phase, i.e. something like the driver in Eq. 1.

That information must still involve relative direction, however, because without it you cannot generate the HKB attractor layout. If relative phase is perceived solely as a difference of phases, there is no reason why any phase should be privileged or distinguishable over any other phase. Even if the detection of phase was modulated by the speed difference (i.e. if the noise term from Eq. 3 was modulating phase instead of relative direction), this still wouldn't account for the observed movement characteristics because a given pattern of speed differences is only specific to a given mean relative phase for a specific combination of amplitudes – change that (e.g. by making one oscillation bigger than another) and the resulting pattern of speed differences will now be associated with a different mean relative phase.

The current evidence supporting relative direction's role in the perception of relative phase is quite clear. First, we found evidence that subjects could not integrate information from orthogonal axes. Second, the actual act of perturbing relative direction independently of mean relative phase proved to be virtually nonsensical. The square wave patterns did replicate the behavior of relative direction, but as noted in the Methods, the dots were never actually moving at, for instance, 90°, and subjects' judgments reflected that. Previous data showed that making feedback about a motion parallel was more important than making it in-phase for stabilizing movement (Bogaerts et al, 2003), and that orthogonal components of motion do not have phase specific effects on movement stability (Wilson et al, 2005b). Relative direction must be definable for the coordination phenomena to emerge.

Given all this, however, it is still clear from the current results that relative direction is not the entire story. We found evidence that only one subject had learned to rely only on relative direction to perceive relative phase, but her performance in the judgment tasks from the first study was not as good as that of the other three subjects, who seem to use both phase and relative direction. While relative direction does specify relative phase, it may be that Bingham's model is correct when it assumes that judgments of relative phase require integration of relative direction over time, and that this process by itself is less efficient than when combined with information about the phase of each oscillator.

The current results support a perception-action approach to studying rhythmic movement coordination. They suggest that the information used in both the production and perception of coordinated rhythmic movement is identical: the relative direction of motion (relative phase) and the normalized velocity (phase). In a dynamical systems approach, if perturbing a given component requires the (functional) disassembly of the system under study, that component can be sensibly thought of as necessary. Relative direction was impervious to perturbation (without completely changing the task from rhythmic movement coordination to some other domain). This is strong evidence that relative direction is a necessary and constitutive component of the rhythmic movement coordination perception-action system. However, it is equally clear that phase itself, perceived as normalized velocity, is equally important, which future modeling work should take into account.

General Discussion

Perceptual information is an integral part of the organization of any perception-action dynamical system. This project set out to investigate the identity and role of perceptual information in a well understood movement task, rhythmic movement coordination. The results support the analysis of this task as fundamentally a perception-action task, and also support the analysis of a perception-action task as a dynamical system, whose entire organization can be explored via perturbation methods.

Experiment 1

A key part to any perception-action account is an account of the learning process. Attention, in Gibson's (1969) terminology, requires education – a perceiver-actor must learn to become sensitive to information that specifies functionally relevant parts of the world. But learning is not just perceptual – learning also entails forming the action part of the perception-action system, and integrating the perception and action components into a functional whole. We identified some elements of this process in the first experiment.

90° is proposed to be unstable because it is the location in the space where the information is maximally difficult to detect. We trained four people to be better able to discriminate 90° from neighboring phases, and this indeed allowed them to improve, maintaining stable movement at 90°. Movement stability is a function of perceptual stability.

This improvement took some time, however – there was no change in movement stability until the second post-training session. The judgment data clearly showed that subjects' discrimination of the space had improved, but it was not until the subjects had a chance to use this new skill in service of a perception-action task that the process of integrating the new skill could begin. We are not arguing, therefore, from a position of 'perceptual dominance' – it is not the case that perception is the only meaningful part of this task. What matters is its relation to the rest of the system.

One interesting aspect to the training was that we weren't forcing them to learn one particular variable; their exploration of the space of possible information was guided by themselves and by the 'Correct' or 'Incorrect' feedback. We did see some evidence in the first experiment that one subject had learned a different variable than the rest. This finding supports the admonition in Jacobs and Michaels (2001) that averaging over subjects may be misleading if different subjects are relying on different variables. Attention must be paid to the details of individual variation in learning, because this can provide important information about the makeup of the perception-action system being studied.

Experiment 2

The other important goal of this type of study is to identify the information variable being used. Bingham's model predicted that relative direction is the information for relative phase, with relative speed playing the role of noise. However, while relative direction is indeed a constitutive part of the perceptual information, the normalized velocity that is the perceptual instantiation of phase plays a key role as well.

It was impossible to perturb relative direction independently of relative phase – the former defines the latter. Relative direction is also the only variable to specify relative phase under all conditions of frequency and amplitude (mod 180°, which is plausible given that the perception-action system treats symmetry partners such as 90° and 270° as identical states). Relative direction must be definable for the movement phenomena to emerge, but it is not, itself, the specifying variable.

The implications for modeling

Bingham's model proposed that the perception of relative phase entails only the detection of relative direction, which is integrated over time to form the basis for judgments about relative phase. Relative direction is used in movements in a slightly different fashion – it modifies the perceived phase of each oscillator which is used as the driver for the other oscillator. This task specific use of the same information was noted as a strength of the model's predictions.

However, the current data clearly show that phase matters for the perception of relative phase as well as for the coordination of movement, and that the information used in both movement and perception tasks is therefore identical. This is actually a stronger claim than the model's original claim of 'same information, task specific use'. The claim is that the two tasks, perceptual judgments about coordinated movements and the production of coordinated movement are functionally identical. This has actually been an important assumption of all the previous perceptual judgment studies – if the information was not the same, then the validity of the conclusions about the role of perception is weakened. It now remains to model the perceptual judgment data using both perceived phase and perceived relative phase.

Taking a perception-action approach to the study of rhythmic movement coordination has proved to be the best way to address many of the questions in the field. For instance, the HKB pattern of behavior is a clearly established phenomenon, but many questions remained. What is an attractor? Why is there one at 0° and 180° but not 90°? Why is the 0° more stable? Perception-action systems are dynamical systems, with action and informational components. Attractors emerge due to the properties and organization of the components in a dynamical system – it is therefore vital to study the properties and organization of the perception-action system in question in order to be able to answer these important questions.

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Editorial Activities

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Teaching Experience

Research Methods in Psychology (P211, Indiana University)
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Publications

Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005b) Human movement coordination implicates relative direction as the information for relative phase. *Experimental Brain Research.*

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Conference Presentations

Wilson, A. D., & Bingham, G. P. (2005). The perceptual information for rhythmic movement coordination. *Talk presented at the International Conference on Perception and Action, Monterey, CA.*

Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005). Relative direction is implicated as the information for relative phase. *Poster presented at Vision Sciences Society, Sarasota, FL.*

Wilson, A. D., Bingham, G. P., & Collins, D. R. (2003). Contributions of visual and haptic perception to stability in movement coordination. *Poster presented at Vision Sciences Society, Sarasota FL.*

Wilson, A. D., Bingham, G. P., & Collins, D. R. (2003). Phase perception and coordinated rhythmic movement. *Talk given at Indiana University & Brown University.*

Wilson, A. D., Bingham, G. P., & Craig, J. C. (2002). Visual and haptic perception of relative phase and phase variability. *Poster presented at International Society for Ecological Psychology (ISEP), Oxford, OH.*

Wilson, A. D., Bingham, G. P., & Craig, J. C. (2002). Visual and haptic perception of relative phase and phase variability. *Talk given at Indiana University.*

Wilson, A. D. (2001). A methodological alternative to the assumption of mental representation. *Paper presented at the Society for Philosophy and Psychology, Cincinnati, OH.*

Service

2003-2004: *Student Member, Gay, Lesbian, Bisexual & Transgender (GLBT) Alumni Association Board, Indiana University*. Met regularly to plan events and fundraising; participated in Membership committee and an ad hoc committee to investigate how the AA could better serve its transgendered members (which involved constructing a survey and reporting the results to the full board).

2000 – 2003: *Student Member, GLBT Student Support Services Office Advisory board*. Met twice a semester to hear news from the Office and advise on future directions and actions.

2000 – 2002: *President, Allys student group*. Restarted group (for the straight allies of the GLBT community) in summer of 2000 after it had been inactive for some years. Worked with GLBT Student Support Office & OUT with programs and activities centered on encouraging diversity, including two Valentine's Day Balls which were fundraisers for Bloomington's Community AIDS Action Group (2000 & 2001); National Day of Silence (2000-2); and a Pride Rally (2001). Planned and participated in a weekend long training session (involving workshops on communication, diversity, awareness, etc; 2001).