

Half Title Page

POSITION & VELOCITY DEPENDENT LOADS ON BIMANUAL COORDINATION

**The influence of position and velocity dependent loads on bimanual coordination**

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Submitted in partial fulfillment  
of the degree of Master of Science in Kinesiology

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## **DESCRIPTIVE NOTE**

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## **ABSTRACT**

Twelve participants performed a bimanual coordination task with the hands in different force field environments. Both in-phase and anti-phase coordination modes were examined. Mean relative phase absolute error measurements represented how accurate the phase relationship was, and the standard deviation of relative phase indicated how stable the coordination mode was. When the fingers were being moved in the same force environments, coordination was more accurate and stable, compared to when the hands were placed in mismatched force environments. Having one hand in a velocity dependent force-field produced less accurate coordination than when one hand was in a position dependent force-field. When coordinated movements were performed with at least one hand in viscous force-field environment, reduced coordination stability was observed, especially during anti-phase movements. There are several spatial, biomechanical and neuromuscular constraints that could have influenced coordination performance. The proposed mechanisms that affected coordination included the differences in neural compensation for different types of force-fields. As shown in previous studies, elastic loads generated later onset of EMG activity whereas viscous loads generated a higher rate of force production. The inability of the extensors muscles to overcome the load resistance in the viscous force-field affected coordination. These results support a two-tiered extension of the HKB model of bimanual coordination.

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# 1 INTRODUCTION

## 1.1 Interlimb Coordination

In general, coordination can be defined as the organization of several small units into a harmonized whole. In motor control research, this could include coordination between or within limbs, or coordination of a movement to an external stimulus. Interlimb coordination, and more specifically bimanual coordination has been studied extensively. When moving one's hands simultaneously, the hands exhibit both a spatial and temporal relationship (Cardoso de Oliveira & Barthelemy 2005; Kelso et al. 1979; Kennerley et al. 2002; Mechsner & Knoblich 2004; Mechsner et al. 2001; Swinnen 2002; Swinnen & Wenderoth 2004). The coupling between the limbs is adaptive, context dependent and is seen in both periodic movements usually studied in research applications, and in goal-directed, object-oriented movements (Swinnen & Wenderoth 2004, Obhi 2004).

The majority of movement coordination research is concentrated on simple periodic motions such as flexion and extension movements of the wrist or finger (Obhi 2004). Coordination between limbs is characterized by the difference between the phase angles of the limbs' trajectories, known as relative phase ( $\phi$ ). There are two intrinsically stable coordination modes: in-phase and anti-phase. In-phase coordination is defined as a relative phase of zero ( $\phi = 0^\circ$ ), and anti-phase coordination is defined as  $180^\circ$  out of phase ( $\phi = 180^\circ$ ). Depending on the frame of reference of the movement, in-phase and anti-phase coordination modes may be defined differently. For homologous limb

movements, either an egocentric (intrinsic or joint-centered) frame of reference or simultaneous activation of homologous muscles is often used to define in-phase movements. The egocentric frame of reference defines in-phase movements as mirror symmetric movements and anti-phase movements as parallel movements with respect to the midline of the body. In this frame of reference, in-phase movements usually activate homologous muscles simultaneously; whereas anti-phase movements activate homologous muscles in alternation. Coordination modes where homologous muscle groups are activated simultaneously are always more stable than when homologous muscles are activated in alternation. Alternatively, non-homologous limb movements are usually defined in an allocentric (external) frame of reference. In an allocentric reference frame, isodirectional movements are considered in-phase ( $\phi = 0^\circ$ ), and anti-directional movements are considered anti-phase ( $\phi = 180^\circ$ ). Isodirectional movements also present more stable coordination modes than non-isodirectional coordinated movements. A preference for isodirectional movements is also seen when coordinating with a visual stimulus, or coordination between people. This could be a consequence of how spatial data is processed visually since visual stimuli moving in the same direction are more salient (Atchy-Dalama et al. 2005; Baldissera et al. 1991; Carson et al. 2000; Li et al. 2004; Mechsner & Knoblich 2004; Mechsner et al. 2001; Meesen et al. 2006; Obhi 2004; Park et al. 2001; Peper et al. 2004; Spencer et al. 2005; Spencer et al. 2006; Swinnen 2002; Swinnen & Wenderoth 2004; Temprado et al 2003). The Central Nervous System (CNS) has representations of multiple frames of reference, and which reference frame an

action is represented in its context or task dependent (Bays & Wolpert 2006; Meesen et al. 2006).

#### 1.1.1 Differential Stability of Coordination Modes

Inter-limb coordination has been found to have properties of *bistability*, meaning two stable coordination modes exist. In-phase coordination is more stable than anti-phase coordination for all movement frequencies, and for almost all movement tasks. Anti-phase movements display greater relative phase variability, meaning that they are less stable than in-phase movements. With increasing movement frequency, inter-limb coordination shows a *phase transition*, meaning there is a spontaneous switch in coordination pattern, from anti-phase to in-phase. After the phase transition, anti-phase coordination is no longer stable. The phase transition is usually precipitated by greater phase variability and movement trajectory deformations, especially in the non dominant hand (Jirsa et al. 1998; Kennerley et al. 2002; Spencer et al. 2005; Spencer et al. 2006). Inter-limb coordination also demonstrates system *hysteresis*, in that the phase transition is uni-directional. Once the transition to in-phase coordination occurs and the movement frequency is decreased, a phase transition back to anti-phase is not seen. These characteristic behavioural outcomes are often described using Dynamic System Theory (DST) (Amazeen et al. 1998; Beek et al. 2002; Fuchs et al. 1996; Fuchs & Kelso 1994; Haken et al. 1985; Jirsa et al. 1998; Kudo et al. 2006; Mechsner & Knoblich 2004; Mechsner et al. 2001; Obhi 2004; Peper & Beek 1998; Peper & Carson 1999; Peper et al. 2004; Post et al. 2000; Schmidt et al. 1993; Sternad et al. 1995; Swinnen & Wenderoth 2004; Swinnen 2002).

Three possible explanations for the symmetric advantages have been proposed. The symmetry advantage is executional in nature meaning it reflects neural crosstalk between efferent neuronal structures (see section 1.4). The advantage may arise from parameterization of bodily characteristics of movement. Coordination constraints arise cortically during the movement planning stage (Mechsner & Knoblich 2004).

## 1.2 Dynamic Systems Theory

Dynamic Systems Theory (DST) mathematically describes changes that occur to state variables of a system in a time-dependent manner. This treatment has attracted numerous studies in the field of human movement science by attempts to model specific biological systems (Amazeen et al. 1998; Jirsa et al. 1998; Mechsner & Knoblich 2004; Peper et al. 2004; Swinnen & Wenderoth 2004; Swinnen 2002). Models are formulated based on synergetics which states that behaviour of complex systems can be described by very few *order parameters*, instead of a large number of state variables (Haken 2004). The identification of order parameters can be accomplished when the behaviour of the system undergoes qualitative changes. The cooperation or competition between the components of the system creates the order parameters, and the order parameters in turn govern the behaviour of the system (Amazeen et al. 1998; Buchanan et al. 1996; Haken et al. 1985; Jirsa et al. 1998; Kelso et al. 2001; Peper & Beek 1998; Peper et al. 2004; Schmidt et al. 1993). For biological systems, cortical and behavioural dynamics are assumed to be linked to each other. Being able to perform a phase transition gives the system flexibility to maintain stable behaviour over a large range of internal and external parameter values. If the system becomes unstable at any point, it can re-assemble its components into a

new, and stable, pattern of behaviour (Bressler & Kelso 2001; Kelso et al. 2001; Swinnen & Wenderoth 2004). *Behavioural information*, which is stipulated by the environment, or the individual's memory or intention, defines the attraction of the system's dynamics to the new coordination pattern (Atachy-Dalama et al. 2005).

Three different techniques are used as tools to identify the system that captures different biological behaviours. These tools entail stability analysis, which studies the system during phase transitions or perturbations to stable behaviour; space-time analysis, which studies the kinematics (movement frequency, amplitude and peak velocity) during stable steady-state behaviour; and time series analysis. These tools allow researchers to identify both the frictional and elastic contributions to dynamical mass-spring-damper phenomenological models (Beek et al. 1995; Post et al. 2000; Ridderikhoff et al. 2004).

It is important to note that models are idealized and reductionist versions of the systems they represent. They cannot necessarily predict every detail of the behaviour of a system, but are still considered accurate so long as they do not predict behaviour in opposition to experimental findings (Fuchs & Kelso 1994). Therefore, behavioural predictions made from models need to be substantiated by experimental study.

### 1.2.1 **Dynamic Systems Theory Model of Inter-limb Coordination**

Interlimb coordination is perfectly suited to being modeled as a dynamical system since the behaviour of the system is well defined and requires minimal attention to the task. Rhythmic limb movement can be modeled by self-sustained oscillators. The relative autonomy of rhythmic bimanual coordination tasks, suggest the system is

intrinsically dynamical, meaning that the functioning of the subsystems are self-organized. A *self-organized* system contains component control structures that tend towards either an equilibrium point or a steady-state value through mutual influence of subsystem components. As stated above, the behaviour of the inter-limb coordination system is encompassed by the variable of relative phase between the limbs. Relative phase would then be described as the system's *order parameter*. An *order parameter* has three defining characteristics: it completely captures the spatio-temporal organization of all of the system's component subsystems, changes in the order parameter's values occur at a slower time scale than the variables that capture the state of the component subsystems (such as limb displacement), and that abrupt changes occur to the value of the order parameter when phase transitions or bifurcations occur. *Control Parameters* are variables that, when scaled, create large changes in the order parameter's value, and thus the behaviour of the system. Coordination in general is modeled using these assumptions. Unimanual movements to an auditory or visual stimulus, coordination between two subjects and cortical dynamics can also be modeled from the same equations (Amazeen et al. 1998; Beek et al. 1995; Bressler & Kelso 2001; Fuchs & Kelso 1994; Jirsa et al. 1998; Kudo et al. 2006; Peper & Beek 1998; Peper et al. 2004; Post et al. 2000; Schmidt et al. 1993; Swinnen 2002; Swinnen & Wenderoth 2004).

In DST, interlimb coordination is most often described by the Haken-Kelso-Bunz (HKB) Model. The original model was conceptualized as a potential landscape function, and a coupled system of non-linear limit-cycle oscillators. The dynamics of the system can be thought of "as an overdamped movement of a particle" (Fuchs & Kelso 1994, pg.

1089) within the potential landscape function. The model accounts for the stability of two coordination modes at low movement frequencies and for phase transitions seen in inter-limb coordination from anti-phase to in-phase coordination at a critical oscillating frequency. (Baldissera et al. 1991; Beek et al. 2002; Bressler & Kelso 2001; Fuchs & Kelso 1994; Haken et al. 1985; Jirsa et al. 1998; Kudo et al. 2006; Peper & Beek 1998; Peper et al. 2004; Post et al. 2000; Schmidt et al. 1993; Swinnen & Wenderoth 2004; Swinnen 2002). The non-linear limit cycle oscillators represent the kinematics of each limb movements and their interactions (Beek et al. 2002; Haken et al. 1985; Fuchs & Kelso 1994; Peper & Beek 1998; Peper et al. 2004; Post et al. 2000; Schmidt et al. 1993).

$$\dot{\phi} = \Delta\omega - a \sin \phi - 2b \sin 2\phi + \sqrt{Q}\xi_t$$

$$\text{where } \dot{\phi} = \frac{\partial V}{\partial \phi}, \text{ which is integrated to obtain:} \quad (1)$$

$$V(\phi) = -\Delta\omega\phi - a \cos(\phi) - b \cos(2\phi) - \sqrt{Q}\xi_t\phi$$

The potential  $V$ , which is a function of the relative phase ( $\phi$ ), characterizes the stability of coordination modes. The ratio between the coefficients  $a$  and  $b$  represent the mutual oscillating frequencies of the effectors. The model was extended to a stochastic form with additive, not parametric, non-deterministic forces which provide small perturbations to the relative phase, and thus precipitate phase transitions. The low-amplitude stochastic force has size  $\sqrt{Q}$ , where  $\xi_t$  is Gaussian noise of unit size. The additive stochastic force is small compared to the deterministic part of the equation.

Imagining the state of coordination of the system as a particle, the stochastic force will jostle the particle within the landscape function. These ‘pushes’ are random in both magnitude and direction within the landscape (Amazeen et al. 1998; Beek et al. 2002; Bressler & Kelso 2001; Fuchs et al. 1996; Fuchs & Kelso 1994; Haken et al. 1985; Jirsa et al. 1998; Kudo et al. 2006; Peper & Beek 1998; Peper et al. 2004; Post et al. 2000; Schimdt et al. 1993; Sternad et al. 1995; Swinnen & Wenderoth 2004; Swinnen 2002; Zaal et al. 2000).

### **1.2.1.1 Collective and Component Levels of HKB**

The HKB model was developed in two levels: the collective level, represented by the potential function discussed above, and the component level, represented by the coupled oscillators. The collective level formalizes the dynamics of the order parameter of the system ( $\phi$ ), and the component level formalizes the kinematics of the limb movements. Properties of the collective level, such as critical fluctuations and critical slowing down near phase transitions, have been well substantiated empirically; whereas the characteristics of the system at the coupled oscillator level, such as the proper limit cycle model for limb movement and the coupling function between the oscillators, are still under investigation (Beek et al. 2002; Peper & Beek 1998; Peper et al. 2004; Post et al. 2000).

#### **1.2.1.1.1 Collective Level of Model**

Equation (1) holds true for many difference component oscillators as long as said oscillators display stable limit cycle dynamics without strong relaxational tendencies (Sternad et al. 1995). Since the model characterizes the dynamic state of the system as a



whole and is independent of the component oscillators, it is often called the *Collective Level*. Understanding of the coordination dynamics at this level require little or no information about: the parameters acting upon the system, details about how the components within the system interact and the patterns of coordination that emerge from interaction of all the subsystems and the environment (Fuchs & Kelso 1994; Peper et al. 2004). At this level of interpretation the oscillators can be two limbs within a single person, two limbs between two people, a limb and some sort of sensory signal (usually visual or auditory), or even neural population oscillating (both central pattern generators at the spinal level and larger neural networks at the cortical level). The collective level of the HKB model expresses the spatio-temporal relationship between components of the system without having to characterize the exact nature of the interaction of the components; in other words the model is abstract at this level of interpretation (Beek et al. 2002; Bressler & Kelso 2001; Fuchs & Kelso 1994; Peper & Beek 1998; Peper et al. 2004; Swinnen 2002)

In general, the potential function quantifies, and visualizes, both the magnitude and direction of the tendency of  $\phi$  to change as a function of its own value. The collective level takes into account the differential stability of in-phase and anti-phase. Attractors within the potential landscape function, which correspond to stable coordination modes, are represented as local minima. This attractor landscape, or potential function is assumed to be symmetrical such that  $V(\phi) = V(-\phi)$ . The anti-phase attractor well, or function minima, is less deep than the in-phase attractor well (Amazeen et al. 1998; Beek et al. 2002; Fuchs & Kelso 1994; Haken et al. 1985; Jirsa et al. 1998; Peper & Carson

1999; Swinnen 2002). The depth of the function minima characterizes the stability of the point attractor. A deep minimum represents an attractor with a small *relaxation time*; whereas a shallower minimum represents an attractor with longer relaxation time.

*Relaxation time* is the time it takes a system to return to steady state after a perturbation; therefore the smaller the relaxation time, the more stable the attractor. In other words, the depth of the potential function minima represents how easy it is to precipitate a change of coordination mode; the deeper the well the more difficult it is to change coordination, thus the coordination mode is stable. Often the strength of the attractor is characterized by the *Lyapunov exponent*, the slope of the potential well near an attractor. In this way, the Lyapunov exponent is an alternative measurement of the relaxation time of the system near the desired coordination mode (Amazeen et al. 1998; Fuchs & Kelso 1994; Kudo et al. 2006; Post et al. 2000; Schmidt et al. 1993).

When considering empirical studies, the mean relative phase recorded during a trial is considered the position of the attractor in the potential landscape ( $\phi^*$ ). The mean relative phase measured also represents how accurate the coordination pattern is, compared to the intended relative phase ( $\phi_\psi$ ). The standard deviation of the relative phase ( $SD\phi$ ) is a quantification of the stability of the coordination mode at  $\phi^*$ , during system steady-state behaviour. Thus smaller values of  $SD\phi$  measured during a trial represent an attractor or coordination mode that is stable. Larger observed values of  $SD\phi$  represent trials where the coordination mode observed is not as stable. The strength of the relaxation process,

which is inversely related to relaxation time of the system, is also negative correlated to  $SD\phi$  (Kudo et al. 2006; Post et al. 2000; Schmidt et al. 1993).

#### 1.2.1.1.2 Component Level of Model

In the HKB model, the component level of the model represents limb displacement. The oscillators that are used to model the hand movements are autonomous nonlinear limit-cycle oscillators, and they are coupled bi-directionally to each other nonlinearly. A common oscillator that is used in the HKB model to capture limb movement is a hybrid Van der Pol ( $x^2\dot{x}$ ) – Rayleigh ( $\dot{x}^3$ ) oscillator (Beek et al. 2002; Beek et al. 1995; Jirsa et al. 1998; Peper et al. 2004; Schmidt et al. 1993). The oscillator contains both positive and negative damping which creates a self-sustaining oscillator. The Van der Pol damping gives the oscillator the characteristics of increasing peak velocity with increased movement frequency; whereas the Rayleigh damping creates an effect of decreasing movement amplitude with increasing movement frequency (Beek et al. 2002; Beek et al. 1995; Peper & Beek 1998).

$$\begin{aligned}\ddot{x}_1 + \varepsilon\dot{x}_1 + \gamma\dot{x}_1^3 + \delta x_1^2\dot{x}_1 + \omega_1^2 x_1 &= (\dot{x}_1 - \dot{x}_2)\{\alpha + \beta(x_1 - x_2)^2\} \\ \ddot{x}_2 + \varepsilon\dot{x}_2 + \gamma\dot{x}_2^3 + \delta x_2^2\dot{x}_2 + \omega_2^2 x_2 &= (\dot{x}_2 - \dot{x}_1)\{\alpha + \beta(x_2 - x_1)^2\}\end{aligned}\quad (2)$$

Where  $x$  represents the limb displacement, and the time derivatives of  $x$ , represent velocity and acceleration. On the right hand side of equation (2) are the coupling terms between the two oscillators, and the left hand side represents the each oscillator's physical properties. The  $\gamma$  and  $\delta$  terms represent the nonlinearities common to both of the oscillators,  $\varepsilon$  is the damping coefficient,  $\alpha$  and  $\beta$  coefficients determine the strength of

mutual coupling between the oscillators (note: in these oscillators coupling is symmetrical, meaning that oscillator 1 affects oscillator 2 in the same way that oscillator 2 affects oscillator 1) and  $\omega$  is the individual oscillator's inherent frequency (Fuchs et al. 1996; Fuchs & Kelso 1994; Haken et al. 1985; Jirsa et al. 1998; Post et al. 2000).

When modeling limb movements using self-sustained oscillators, it is important to remember that the relative contribution of linear and nonlinear terms of the oscillator equation may change with task context. For example, an oscillator modeling movement of a 'wrist-pendulum system' will have a greater contribution of the stiffness (position dependent, restorative) parameters with greater rotational inertia of the pendulum. Frequency manipulations will also show systematic changes to the stiffness parameters, movement frequencies above the system's eigenfrequency will show increased contribution of the stiffness terms, while movement frequencies below the system's eigenfrequency will show negative contribution of the stiffness parameters. Velocity dependent (damping or frictional) parameters show a decreased contribution to the system dynamics with increased system rotational inertia and movement frequency. Non-linear damping terms (van der Pol and Rayleigh terms) will show increased contributions to the system dynamics in tasks that demand spatial accuracy (Beek et al. 1995; Peper et al. 2004). Therefore it must be concluded that the component oscillators that are used in modeling are task and context sensitive, and that changing the parameters, either stiffness or damping, of either oscillator will change how the oscillators are coordinated.

Also of note, the parameters derived for the limit cycle oscillators are abstract, and do not directly represent the limb biomechanical and physiological parameters. The stiffness and damping terms are calculated using limb kinematics (position and velocity time series), and only indirectly are influenced by changes in muscle recruitment. For example, it is important to keep this in mind that increases in stiffness values can be attributed to both active and passive dynamics of the limb, and these two influences on stiffness cannot be separated using this model (Peper et al. 2004; Peper, Nooji, van Soest 2004).

By making some assumptions, it is possible to derive equation (1) from equation (2). For the original HKB model, it is assumed that if the eigenfrequencies of the oscillators are different, then the differences are small compared to the absolute eigenfrequency of each oscillator. Coupling must be sufficiently strong to keep the oscillators frequency locked at a common frequency (the form the coupling function takes will be discussed in the following section). Lastly, an assumption that amplitude and phase are slowly varying, meaning their dynamics act on much greater time scales than those of the mutual coupling frequency of the oscillators (Fuchs et al. 1996). Unfortunately, an oscillator with damping, as equation (2) has, violates the 'slowly-varying amplitude' assumption, and produces fluctuations in amplitude and phase measurements. These fluctuations will cancel out during in-phase and anti-phase movements, but for any other phase relationship (for example, due to oscillator asymmetry discussed in section 1.2.1.2.2) the relative phase measurement is a complicated oscillating quantity (Fuchs et al. 1996). For experimental considerations, if relative phase is not exactly  $0^\circ$  or  $180^\circ$ , then continuous

relative phase measurements are only an approximation of the theoretical relative phase between the oscillators of the model. To achieve a measure of the theoretical relative phase, either point estimation (also known as discrete relative phase) must be used, a complicated non-linear time transformation must be completed on the time series, or a phase specific to each oscillating frequency component must be calculated (Fuchs et al. 1996).

#### 1.2.1.1.3 Form of Coupling Function

When the HKB model was first proposed, two different possible coupling functions were described: a time derivative coupling function and a time-delay coupling function (Beek et al. 2002; Haken et al. 1985; Kudo et al. 2006; Peper & Beek 1998; Peper et al. 2004; Post et al. 2000).

Historically the time derivative coupling function has been used most often in modeling papers, for it is mathematically simpler than the time delay coupling function. Using this coupling function, the HKB model is reduced from the component oscillator level to the collective level:

$$\frac{d\phi}{dt} = -\frac{dV(\phi)}{d\phi} = (\alpha + 2\beta r^2) \sin \phi - \beta r^2 \sin 2\phi$$

$$\text{Where } -a = \alpha + 2\beta r^2 \text{ and } b = \beta r^2 \quad (3)$$

Therefore if phase transitions occur at  $\frac{b}{a} = 0.25$  then  $r_{critical} = \sqrt{\frac{-\alpha}{4\beta}}$ ,  $\alpha < 0$

where  $a$  and  $b$  are the constants of the HKB model discussed above,  $r$  is the real amplitude of movement oscillation, and  $\alpha$ ,  $\beta$  are adjustable coupling constants that are fixed during a single trial run. For this coupling function, phase transitions are precipitated by movement amplitude reductions, which occur with increasing movement frequency. At the critical movement amplitude, the anti-phase attractor is annihilated, and only the in-phase attractor remains. Therefore, theoretically using this coupling function, movement frequency does not directly influence phase transitions in bimanual coordination, but only influences coordination stability indirectly through movement amplitude modulations (Beek et al. 2002; Kudo et al. 2006; Peper & Beek 1998; Post et al. 2000).

In comparison, the time delay coupling function has a better physiological basis than the time derivative function, although it is not often used in modeling because it is more mathematically complicated. The time delay function theoretically supposes that coupling between the limbs depends upon the limbs' previous positions (Beek et al. 2002; Kudo et al. 2006; Peper & Beek 1998; Post et al. 2000).

$$\frac{d\phi}{dt} = -\frac{1}{\omega^2} [(\alpha + 6\beta r^2) \sin \phi - 3\beta r^2 \sin 2\phi]$$

$$\text{Where } -a = \frac{-(\alpha + 6\beta r^2)}{\omega^2} \text{ and } b = -\frac{3\beta r^2}{\omega^2} \quad (4)$$

$$\text{With } r_{critical} = \sqrt{\frac{-\alpha}{12\beta}}, \alpha < 0$$

The main difference between equation (3) and (4) is that the time delay coupling function is not solely dependent on movement amplitude; in this case movement frequency directly affects stability characteristics. Similar to the time derivative coupling function, only decreases in movement amplitude will lead to abolishment of the anti-phase attractor. The movement frequency term will decrease stability of coordination across the board. Both attractor wells will become less deep, but only the anti-phase well becomes shallow enough that a stochastic fluctuation may precipitate a phase transition (Kudo et al. 2006; Peper & Beek 1998; Post et al. 2000).

Therefore to validate these proposed coupling functions empirically, it must be shown that coordination pattern stability is dependent upon movement amplitude. In other words, if coordination stability does not depend on movement amplitude, then the time derivative theory of oscillator coupling is negated. The time delay theory is not completely disproven because phase transitions are still possible with increasing movement frequency. As mentioned above, movement frequency will make the anti-phase well shallow enough that stochastic fluctuations can precipitate a phase transition (Peper & Beek 1998; Post et al. 2000). Keeping movement amplitude constant, and changing the movement frequency should not influence coordination stability if the coupling function between the limbs is the time derivative form. This assumption was tested using a unimanual tracking task (Peper & Beek 1998) and a bimanual coordination task (Post et al. 2000). Interestingly, though both tasks fit the HKB potential function, they displayed differing dependence on movement amplitude. The stability of coordination of the unimanual tracking task was solely dependent on movement



frequency; therefore the time derivative coupling function, for this task, was excluded, and the time delay function should have displayed a dependency on both movement frequency and amplitude (Peper & Beek 1998). On the other hand, bimanual movement coordination stability displayed reliance on both movement frequency and movement amplitude; therefore supporting the time delay coupling function (Post et al. 2000). These two findings illustrate that coupling between the two oscillators of the HKB is flexible and context dependent. Even though unimanual tracking and bimanual coordination can be described by the same potential function, it is obvious that a more general description of coordination at the oscillator level is not possible (Peper et al. 2004; Post et al. 2000).

Beek et al. (2002) proposed that there are actually four oscillators that must be modeled to accurately account for interlimb coordination. The four oscillators are separated into two coupled 'neural' oscillators that drive two linearly damped oscillators at the 'effector' level (Beek et al. 2002; Peper et al. 2004). The neural oscillators are non-linear limit cycle oscillators that are mutually coupled, using the time derivative form originally proposed by Haken, Kelso and Bunz (1985), phase transitions can be induced without decreasing the effector movement amplitude (Beek et al. 2002, Kudo et al. 2006; Peper et al. 2004). These oscillators then drive the peripheral oscillators, and the peripheral oscillators affect the neural effectors by means of feedback (Beek et al. 2002; Peper et al. 2004). This two-tiered model is reminiscent of the 'neural clock' and 'motor implementation' delays of the Wing-Kristofferson (1973) model of timing (Beek et al. 2002, Wing 2001).

Alternatively, Kudo and colleagues (2006) support the idea that coupling between the limbs is amplitude mediated. They showed that task constraints influence the relative stability of the attractors in the system. Using cross-recurrence quantification (CRQ), they quantified both the magnitude of the Gaussian noise in the system at attractor sites, and the attractor strength for a bimanual pendulum coordination task. The results showed that detuning increases, consequently attractor strength decreases, with the movement frequency, but this effect is moderated when the number of temporal targets is increased (ie: two metronome beats per movement cycle as opposed to one metronome beat) (Kudo et al. 2006). Attractor strength was also decreased with increased detuning of the system, as was expected (Kudo et al. 2006). Surprisingly, the overall stability of the system was lowest at the intermediate movement frequency (as opposed to the lowest movement frequency as predicted by the HKB model) (Kudo et al. 2006). Using the CRQ decomposition, the increased stability was attributed to a lower magnitude of noise in the system due to resonance between the pendulum, with a natural frequency of 1.00 Hz and the desired movement frequency (the attractor strength was the same between the 1.00 Hz movement frequency and the slower movement frequency) (Kudo et al. 2006). Once thought to be constant, it has now been shown that the magnitude of Gaussian noise in the system, and thus coordination stability, is affected by the environment in which the task is performed (Kudo et al. 2006).

### **1.2.1.2 Control Parameters**

Behavioural pattern switching occurs when the complex system reaches a critical value of a control variable. Once the critical value is reached, the behaviour of the

system becomes unstable and component subsystems are disassembled from their current coordination pattern and reassembled in a new, stable coordinative pattern. At these system *critical points* or *instabilities* low dimensional behaviour, and the relevant collective variables or order parameters can be identified (Buchanan et al. 1996; Peper & Beek 1998; Peper et al. 2004; Swinnen 2002). There are two control parameters for inter-limb coordination, the mutual oscillating frequency of the limbs, and the eigenfrequency difference between the limbs (Bressler & Kelso 2001; Fuchs & Kelso 1994; Peper et al. 2004; Schmidt et al. 1993; Swinnen 2002).

#### 1.2.1.2.1 Mutual Oscillating Frequency

Movement frequency is considered the major control parameter of inter-limb coordination because it creates the largest effect on the order parameter. Scaling of the mutual oscillating frequency leads to the phase transition from anti-phase to in-phase at a critical frequency. An individual's critical frequency is unique, although it is correlated with their preferred unpaced movements. In the HKB model, the mutual oscillating frequency between effectors is modeled by the ratio of constants  $b/a$ . Decreases in the ratio of  $b/a$ , correspond to an increase in movement frequency. The critical frequency where phase transitions occur is represented in the model by the annihilation of the anti-phase attractor when  $b/a = 0.25$  (Amazeen et al 1998; Beek et al. 2002; Baldissera et al. 1991; Bressler & Kelso 2001; Fuchs & Kelso 1994; Haken et al. 1985, Jirsa et al. 1998; Peper & Beek 1998; Peper et al. 2004; Post et al. 2000; Schmidt et al. 1993).

Below the critical frequency, both in-phase and anti-phase coordination modes are stable, although the in-phase attractor is stronger than the anti-phase attractor. This is

shown in the HKB potential function as a deeper local minimum for the in-phase coordination mode compared to the anti-phase coordination mode minimum. As mutual oscillating frequency increases, the local minima will become less deep, meaning all the coordination modes become less stable. The in-phase attractor becomes less stable, but at all oscillating frequencies remains an attractor; whereas the anti-phase point attractor is abolished at the critical frequency, at which point any small fluctuations in relative phase will 'bump' the coordination mode from anti-phase to in-phase. Beyond the critical frequency only in-phase coordination is stable (Amazeen et al. 1998; Beek et al. 2002; Bressler & Kelso 2001; Fuchs & Kelso 1994; Haken et al. 1985; Jirsa 1998). The system switching from two stable solutions to only one stable solution is called a *bifurcation* (Bressler & Kelso 2001; Fuchs et al. 1996; Schmidt et al. 1993).

Other empirical changes are observed with increasing frequency. Movement amplitude decreases with increasing movement frequency (Jirsa et al. 1998; Post et al. 2000). Near the transition, when anti-phase coordination mode is unstable, hand movements produce characteristics of dynamic systems that near instabilities: *fluctuation enhancements* and *critical slowing down*. Fluctuation enhancements are signified by a large increase in  $SD\phi$  right before transition. It is usually the increased variability that will 'bump' the coordination mode from one attractor to another. Critical slowing down is a dynamical process where the relaxation time of the system dramatically increases. The system relaxation time is the time that it takes the system to recover to a steady state after a perturbation. The longer the relaxation time indicates that the system is in a less stable attractor state. For inter-limb coordination, as movement frequency is increased, if

the anti-phase coordination is perturbed, the time to re-establish the anti-phase coordination mode is increased (Buchanan et al. 1996; Fuchs & Kelso 1994; Jirsa et al 1998; Peper & Beek 1998; Peper et al. 2004; Post et al. 2000; Schmidt et al. 1993).

#### 1.2.1.2.2 Oscillator Asymmetry

The HKB model was extended to include a symmetry breaking (or detuning) term, used for oscillators with different eigenfrequencies (Amazeen et al. 1998; Beek et al. 2002; Bressler & Kelso 2001; Kudo et al. 2006; Fuchs & Kelso 1994; Peper et al. 2004; Peper, Nooji, van Soest 2004; Schmidt et al. 1993; Sternad et al. 1995). *Eigenfrequency* is described as the inherent or preferred movement frequency of the component oscillator. For interlimb coordination research, system viscosity is assumed to be negligible; therefore the eigenfrequency is assumed to be the *natural frequency* of the system. The *natural frequency* of a system is related to the square root of the ratio of stiffness to mass (Peper, Nooji, van Soest 2004). The difference between the eigenfrequencies of the two oscillators (limbs or effectors) is represented by  $\Delta\omega$  in Equation 1 (Amazeen et al. 1998; Fuchs & Kelso 1994; Kudo et al. 2006; Park et al. 2001; Peper et al. 2004; Peper, Nooji, van Soest 2004; Schmidt et al. 1993; Sternad et al. 1995; Zaal et al. 2000). The modeling assumptions made for the detuning term are that each individual oscillator is in steady-state limit cycle attractor dynamics, and that the instantaneous state of the oscillator can be characterized by the phase of the limit cycle ( $\theta(t)$ , where  $\dot{\theta} = \omega$ ) (Sternad et al. 1995).

Detuning can be quantified as the difference in the relative phase relationship actually produced ( $\phi$ ) and the intended coordination mode ( $\phi_\psi$ ,  $\Delta\phi = \phi - \phi_\psi$ ). Small differences in eigenfrequencies shift the stable fixed points of the potential; whereas large values of detuning abolish all fixed point attractors, meaning no phase-locking of coordination can occur. The system may demonstrate partial attraction to certain phase relationships (phase entrainment coordination), or produce no phase relationship at all, and phase-wrapping, where the phase relationship between the limbs is not stable, will occur (Amazeen et al. 1998; Bressler & Kelso 2001; Fuchs & Kelso 1994; Kudo et al. 2006; Park et al. 2001; Peper et al. 2004; Schmidt et al. 1993; Sternad et al. 1995). Systems that demonstrate these characteristics are said to have *metastability*, in that the degree of coordination can shift over time. Phase relationships between components can strengthen and weaken dependent upon task demands. This makes the system extremely flexible. These metastable systems are used to model cortical dynamics (Bressler & Kelso 2001).

There have been different models proposed to better study the effect that oscillators with different eigenfrequencies have on coordination. The most often cited model was produced by Rand et al. (1998):

$$\dot{\phi} = \Delta\omega + k \sin \phi \quad (3)$$

where  $k$  is the coupling function strength between the two oscillators. The relative phase relationship seen between the two oscillators is a function of each rhythmic unit of the system trying to maintain its own inherent frequency, and the coupling strength

between the two oscillators (Schmidt et al. 1993; Sternad et al. 1995). Note that equation (3) does not accurately model the coordination mode phase transition seen with scaling of movement frequency, nor hysteresis of the system, as Equation (1) does. In fact equation (3) is a special case of equation (1) where the constant  $b$  is set to zero (Fuchs & Kelso 1994).

From equation (1) the following predictions can be drawn from the model (as summarized from Amazeen et al. 1998):

1. When  $\Delta\omega = 0$ ,  $\phi^*$  should be at the intended coordination mode (either in-phase  $\phi = 0^\circ$ , or anti-phase  $\phi = 180^\circ$ ).
2. When  $\Delta\omega < 0$ , then  $\Delta\phi < 0$ ; when  $\Delta\omega > 0$ , then  $\Delta\phi > 0$ .
3. When  $\Delta\omega \neq 0$ , the shift in attractor position is larger at  $\phi = 180^\circ$  than at  $\phi = 0^\circ$ .
4. For a constant movement frequency,  $\Delta\phi$  is larger for larger  $\Delta\omega$ .
5. For a constant  $\Delta\omega \neq 0$ ,  $\Delta\phi$  is greater with increasing movement frequency.
6.  $SD\phi$  is greater at  $\phi = 180^\circ$  than at  $\phi = 0^\circ$ .
7. For a constant movement frequency,  $SD\phi$  increases with increases in  $\Delta\omega$ .
8. For all  $\Delta\omega$  (including  $\Delta\omega = 0$ ),  $SD\phi$  increases with increasing movement frequency.

Using these theoretical predictions, empirical studies have been performed, usually using pendulums of different lengths and weights to create 'wrist-pendulum systems' with different eigenfrequencies. Sternad et al. (1995) tested several of the model

predictions. Firstly, if the coupling coefficient is kept constant, then the attractor position  $\phi^*$  will be dependent only on the sign and magnitude of  $\Delta\omega$ , independent of the actual eigenfrequency values of the component oscillators. Therefore oscillators may have different physical properties (pendulum length, or weight), but if the physical properties are balanced such that the oscillators have the same eigenfrequency, thus creating no eigenfrequency difference, then the intended coordination mode should be produced accurately. Lastly, the increases in  $\Delta\omega$  should show a linear relation to increases in  $\Delta\phi$  from  $\phi^*$  (Amazeen et al. 1998; Park et al. 2001; Peper, Nooji, van Soest 2004; Schmidt et al. 1993; Sternad et al. 1995).

Sternad et al. (1995) tested these model assumptions empirically. It was shown that detuning was dependent only upon the uncoupled, inherent frequencies of the oscillators. But the drift in the relative phase did not necessarily increase in direct proportion to  $\Delta\omega$ . Variation in how  $\Delta\omega$  was composed produced an inverse relationship to  $\Delta\phi$  when the ratio between the two eigenfrequencies was kept constant. The theoretical prediction of  $SD\phi$  increasing with increasing values of  $\Delta\omega$ , was also proven false. These results led Sternad et al. (1995) to conclude that models of detuning at the collective level must include not only the arithmetic difference between the oscillators' eigenfrequencies, but the ratio between them as well (Amazeen et al. 1998).

There is debate on how  $\Delta\omega$  influences the variability of relative phase. Although Sternad et al. (1995) didn't find increases in  $SD\phi$ , Schmidt et al. (1993) did find that  $\Delta\omega$  influenced both the local and global  $\phi$  power spectrum, showing systematic increases in



total and peak power with increases in oscillator asymmetry and movement frequency. The local  $\phi$  power spectrum shows peaks at even integer harmonics of movement frequency. These peaks increase in amplitude, and peaks at higher harmonics appear with increasing  $\Delta\omega$  values. Rhythmically organized  $\phi$  fluctuations suggest that the peaks in the power spectrum represent control processes, or intervals at which perceptual information is used to control coordination. Therefore, increases in the number of peaks with scaling of control parameters (both movement frequency and oscillator asymmetry) suggest that extra control processes are used by the system to maintain coordination stability during a difficult coordination task. Schmidt et al. (1993) suggest that for coordination between asymmetric oscillators, it cannot be assumed that the oscillators are phase-locked, but instead only phase-entrained. For relatively large values of  $\Delta\omega$ , additional control processes, perhaps in the form of increased use of perceptual information, are recruited and the dynamical control regime switches from a point attractor (phase-locked) system to a more flexible phase-entrainment system with periodic components. The periodic control components keep the control structure stable enough to maintain coordination task demands (Schmidt et al. 1993). These interesting spectral components have been replicated from the component level of the HKB model (using Equations (1) and (2)), and support the need for research into how interactions at the component level influence coordination dynamics (Fuchs & Kelso 1994). The results from research into the asymmetrical oscillator control parameter are varied, and not straight-forward.

As will be discussed further in section 1.5, there are different constraints that influence coordination with different eigenfrequency oscillators. In general when  $\Delta\omega \neq 0$ , isodirectional constraints determine the attractor position while muscular constraints determine attractor stability. This means for the same pendulum system, movements in the same direction will produce smaller  $\Delta\phi$  than non-isodirectional movements and movements that are performed with simultaneous activation of homologous muscles will have smaller  $SD\phi$  than movements performed with alternating activation of homologous muscles. The HKB model proposes that the same mechanism that determines attractor position also determines the strength of the attractor, which is contradicted by these results. Obviously, the HKB model does not capture all the dynamics of the system when the system places constraints (in this case directional vs. muscular) in conflict (Park et al. 2001; Peper et al. 2004). These results do not generalize to every coordination task (those without oscillators of different eigenfrequencies), but seem consistent for pendulum tasks (Park et al. 2001; Temprado et al. 2003).

### ***1.2.1.3 Extensions of Haken-Kelso-Bunz Model***

There have been several extensions to the HKB model, but the most important one in terms of the particular study presented in this document, is taking into account handedness and attention. Often a small  $\Delta\phi$  is observed during bimanual coordination, when none should exist. Some have theorized that perhaps the dominant limb had a higher eigenfrequency because most often the dominant hand will lead the non-dominant hand in coordination tasks, but the corresponding increase in  $SD\phi$  (ie: decrease in attractor strength and pattern stability) that is attributed to detuning is not seen in these

circumstances (Amazeen et al. 1997; Amazeen et al. 1998; Donchin et al. 1999; Peper et al. 2004). Therefore Amazeen et al. (1997) hypothesized that handedness effects were not a consequence of the oscillators having different eigenfrequencies, but of an asymmetry in the coupling between the two oscillators. They modeled their assumptions as:

$$\dot{\phi} = \Delta\omega - [a \sin \phi + 2b \sin 2\phi] - [c \cos \phi + 2d \cos 2\phi] + \sqrt{Q}\xi_t \quad (4)$$

where the sine terms are the traditional symmetric version of the HKB model, and the cosine terms produce the asymmetry. The  $c$  constant is often set to zero, and the  $d$  constant is responsible for handedness and attentional effects. Handedness effects on the model are constant, but increasing movement frequency (decreasing  $b/a$  ratio) gives rise to larger phase lag values; in other words it increases the lead of the dominant hand over the non-dominant hand (Amazeen et al. 1997; Peper et al. 2004).

Attentional and handedness effects are not the same in coordinated movements, but they affect the same coefficients in the model. The effect of handedness is taken into account in the model by a constant value of  $d$ . For left-handers, the value of  $d$  is negative (denoting a left hand leading coordination pattern); whereas for right-handers, the value of  $d$  is positive (denoting a right hand leading coordination pattern). Attentional effects do not create a constant effect on  $d$ , they will change given the context of the task.

Attention to the left hand makes  $d$  become more negative, and attention to the right hand makes  $d$  more positive. Therefore, when attention is placed on the dominant hand, a larger  $\Delta\phi$  will be produced, but unlike detuning, the coordination stability is greater.

Thus, although both detuning and asymmetrical coupling produce a  $\Delta\phi$ , they affect  $SD\phi$  very differently. Detuning decreases coordination stability with increasing phase lag; whereas asymmetrical coupling increases coordination stability with increasing phase lag (Amazeen et al. 1997; Amazeen et al. 1998; Peper et al. 2004). These modeling predictions were verified using empirical results. Phase lag decreased when attention was placed on the non-dominant hand, compared to when attention was directed to the dominant hand, and coordination stability was less when attention was placed on the non-dominant hand compared to when attention was placed on the dominant hand (Amazeen et al. 1997; Amazeen et al. 1998; Peper et al. 2004).

Other extensions to the HKB model have included terms for changes within the attractor landscape due to learning, and tasks that include multi-frequency coordination, ratios other than 1:1 movements (Amazeen et al. 1998).

### **1.3 Other Proposed Models of Interlimb Coordination**

The HKB model does describe the potential level of coordination at the abstract level and allows for predictions to be made about general properties of coordination, but cannot capture the details of the neuromuscular physiology that is involved. Thus, expanding upon the two-tier model proposed in Beek et al. (2002), Ridderikhoff et al. (2004), created a biomechanical and physiologically accurate model to investigate bimanual coordination.

Using EMG and movement kinematics, the phase difference between the input signal and output signal was used to create a transfer function that distinguishes between

the contribution of passive joint dynamics (structural biomechanical constraints) and active muscle dynamics (muscular constraints). Using a biomechanically and physiologically accurate model instead of an oscillator (mass-spring-damper model) makes allowances for how musculo-skeletal constraints affect EMG during dynamic movements. Using recordings from both isometric and dynamic contractions it was shown that the same effector can have different phase responses (discussed in section 1.5) dependent upon task requirements. Therefore asymmetry in effector dynamics will create dissonance in frequency responses between the limbs, which in turn will lead to a challenge to coordinate neural signals to create coordination between the effectors. For example, to coordinate an isometric contraction and a dynamic movement in-phase, the required activity of contralateral  $\alpha$ -motorneuron pools must be activated approximately  $45^\circ$  out of phase (Peper & Carson 1999; Ridderikhoff et al. 2004).

#### **1.4 Neural Crosstalk**

Interlimb coordination can be considered a special case of the dual task paradigm. Therefore using the *information processing* theory of dual task paradigms suggests that the detrimental performance of both movement tasks that is often observed is a consequence of limited neural resources. The *neural crosstalk theory* of bimanual coordination supposes that coordination patterns arise from neural interactions, or neural 'leakage', from the cortical level to the spinal level. Neural pathways are theorized to create patterns of mutual interference between the command streams for each limb at different stages of movement planning and organization, resulting in similar spatial and temporal aspects between the limb movements. This is also known as *motor irradiation*.

Motor irradiation refers to the phenomena where contraction of muscles on one side of the body will create increased excitability of the homologous contralateral muscle. The amount of irradiation between the limbs is dependent upon the neural drive that is directed to the engaged muscle. To be able to overcome basic coordination patterns, the neural interference must be suppressed (Atchy-Dalama et al. 2005; Carson 2005; Carson et al. 2004; Spencer et al. 2005; Swinnen 2002; Swinnen & Wenderoth 2004). Further discussion of neural interactions affecting coordination will be discussed as a constraint in section 1.5 Coalition of Constraints.

## **1.5 Coalition of Constraints**

Coordination of multiple limbs into a spatio-temporal relationship can also be conceived as being governed by a set of task and individual dependent musculoskeletal and neural (both perceptual and cognitive) constraints. Constraints can be biomechanical, as in the physical restrictions of joints and ligaments, or they can be more abstract, such as cognitive strategies and the use of sensory feedback. All coordination constraints are weighted dependent on specific task constraints, the constraints are dissociable, and the interplay between constraints creates the coordinative relationship observed. In other words, the greater the number of constraints that are coincident, the more stable and accurate the coordination pattern; conversely, if constraints are in conflict, performance of the coordinated task deteriorates (Carson & Kelso 2004; Carson et al. 2000; Meesen et al. 2006; Swinnen & Wenderoth 2004; Temprado et al. 2003).

### 1.5.1 Temporal and Spatial Constraints

As has been referenced previously, when moving limbs at the same time, they often exhibit a spatio-temporal coupling. Therefore at the most basic level of coordination, spatial and temporal constraints upon the movement of the limbs must exist to couple the limbs.

There are two basic spatial constraints, assimilation and movement direction. Assimilation is the tendency for the movements of the two limbs to become similar. When the limbs perform spatially disparate movements, there is a tendency for each limb's trajectory to be pulled in the direction the other limb is moving. This coupling is detrimental if the required trajectories of each limb are completely different. Direction and amplitude interference do interact. When performing movements of different amplitudes along different directions, the directional interference is decreased compared to when the movement amplitudes are similar; whereas when performing movements of different amplitudes along different directions, the amplitude interference is increased, compared to when the movements are in the same direction. This shows that although these two interference patterns interact, they must also be partly independently controlled since different interference effects are seen when they interact (Meesen et al. 2006; Spencer et al. 2005; Swinnen 2002; Swinnen & Wenderoth 2004; Temprado et al 2003; Wenderoth et al. 2005).

For homologous limbs, the spatial frame of reference for this directional interference seems to be radially egocentric. This means no spatial interference is seen for movements along radial axes with respect to the body, but spatial interference is seen

in coordinated movements where one limb moves in a radial axis while the other limb is moved along a non-radial axis. Coordination of movements when one limb moves orthogonal to the other produce the largest interference effects. These deviations in movement direction can be dissociated from specific patterns of muscle activation; therefore we can presume that directional coding of movements is abstract at the level of movement planning. In fact, the primary motor cortex (M1) codes for movement direction, and if this information is shared across the corpus callosum, this could be a mechanism of spatial constraint on coordination. Therefore if the arms must be moved in different direction, the default coupling (mirror symmetry) must be suppressed so that each arm direction can be encoded independently (Carson 2005; Meesen et al. 2006; Spencer et al. 2005; Swinnen 2002; Swinnen & Wenderoth 2004; Temprado et al 2003; Wenderoth et al. 2005).

In fMRI studies, difficult movement direction tasks, for unimanual and bimanual movements, show increased activity in the superior parietal-dorsal premotor network, in the right hemisphere. This suggests that movement direction characteristics are primarily determined by the right hemisphere then exchanged across both hemispheres (Wenderoth et al. 2005). Re-sectioning of the corpus callosum results in the ability to 'decouple' arm movements, such that spatial interference during bimanual coordination is reduced. Spatial information about limb trajectory is represented within the motor cortex. During bimanual coordination, spatial information about both limbs will be represented in each homologous M1 representation and communicated across the corpus callosum (cortical level neural crosstalk). During asymmetrical (anti-phase) movements, the neural activity



between the two hemispheres will be different, presenting a conflict that generates the instability seen in anti-phase movements (Carson 2005; Kennerley et al. 2002; Spencer et al. 2005).

Spatial constraints become especially important for allocentric coordination tasks. In fact, the preference for isodirectional movements is seen between ipsilateral hand and foot movements both when the hand is pronated and supinated. Isodirectional mode is performed more successfully than non-isodirectional mode. During coordination of the heterolateral hand and foot, there seems to be no difference between isodirectional and non-isodirectional coordination modes (Baldissera et al. 1991; Meesen et al. 2006). Spatial constraints are also seen when individuals with arm amputations perform bimanual movements; therefore these constraints cannot just be biomechanical in nature, but must occur in the cortex. It has been shown that bimanual movements are only transiently affected by lesions in a single hemisphere, or lesions to the corpus callosum, suggesting that bimanual coordination is controlled bilaterally (Carson 2005; Donchin et al. 1998; Jirsa et al. 1998). In fact, bimanual movements performed by split-brain patients do not exhibit the same level of spatial interference, suggesting that the interference arises from the cortico-cortical connections through the corpus callosum and not from neural crosstalk at subcortical levels (as discussed in section 1.5.2) (Carson 2005; Donchin et al. 1999; Kennerley et al. 2002; Spencer et al. 2005; Swinnen & Wenderoth 2004).

The temporal constraints placed upon coordination show that limb movements have a tendency to be initiated and terminated at the same time, even when the limbs are performing separate tasks (Kelso et al. 1979; Swinnen 2002). The type of coordinated movement task will affect the temporal constraints placed upon the task. The timing of discrete coordinated movements is not disrupted by callosotomy and seems to be controlled by the cerebellum; whereas the timing of continuous coordinated movements is disrupted by callosotomy, suggesting a more distributed timing mechanism (Kennerley et al. 2002; Spencer et al. 2005; Swinnen 2002; Swinnen & Wenderoth 2004). There is also a preference for isofrequency movements (1:1 movement ratio), as opposed to more complex temporal relationships (Swinnen 2002; Swinnen & Wenderoth 2004).

### 1.5.2 Neuromuscular Constraints

At the spinal level, the most basic cyclic movement primitives are central pattern generators (CPGs). They are relatively autonomous neural networks that undergo oscillations of their membrane potential, meaning they can function without cortical activation. They can also be flexibly combined to produce a large range of behaviour. Even though they can function without cortical activation, their activity can be modulated by either efferent information from the cortex, or afferent sensory information. Afferent information can modulate interlimb reflexes, whose function is to minimize coordination instabilities. The effect of afferent information upon the reflexes is dependent upon both the task and the phase of the movement cycle. Therefore one constraint placed upon inter-limb coordination is the integration and interpretation of afferent feedback arising from the coordinative task. The afferent signals modulate coordination at both spinal and

supraspinal levels (Carson 2005; Carson et al. 2004; Carson & Kelso 2004; Peper & Carson 1999).

Peripheral signals produced by limb movement may influence coordination stability by modulating the spinal pathways (for example, modulating the Hoffman reflex, which is muscle movement following electrical stimulation of the Ia afferents of muscle spindles, of the contra-lateral limb), and this effect is seen in many different rhythmic movements. This effect is strong enough to entrain both the phase and frequency of a limb's movement when the contra-lateral limb is passively moved, and to disrupt coordination between two limbs when a third limb is moved passively (Carson 2005; Carson et al. 2004; Peper & Carson 1999; Wilson et al. 2003). The afferent signals that influence coordination seem to be produced primarily by muscle spindles, thus seem to be 'movement-elicited'. The faster a limb is moving affects the excitation modulation of the contra-lateral limb. There are several possible mechanisms, both peripheral and cortical, that cause the crossed facilitation effect in homologous muscles. The crossed facilitation must not be completely cortical in nature, as it is preserved in individuals with callosal agenesis. Crossed facilitation appears to be modulated at the spinal level by presynaptic inhibition of Ia afferents, and suggest a specific method by which afferent sensory signals can influence inter-limb, or more specifically bimanual, coordination (Carson 2005; Carson et al. 2004; Peper & Carson 1999). Since the afferent signals modify the Ia spinal reflex pathway, this could create a tendency towards entrainment between the limbs; in other words a tendency to produce mirror movements. Anti-phase movements could become unstable because descending motor commands from the cortex

can no longer compensate for the spinal mechanisms of entrainment (Baldissera et al. 1991; Carson 2005; Carson et al. 2004; Peper & Carson 1999).

Neural responses from the muscle spindle fibers are not the only afferent feedback that affects coordination. In-phase and anti-phase bimanual coordination is also seen in isometric contractions, where movement, and therefore afference from muscles spindle fibers, is minimal, but afference from other sensory receptors will be produced. Differential stability of in-phase and anti-phase, and frequency dependent effects were seen in bimanual isometric contractions, but phase transitions are not observed. This could suggest that many different afferent signals produce most of the characteristic inter-limb stability criteria, but that phase transitions are a product of only muscle spindle afference (Peper & Carson 1999; Wilson et al. 2003). When Peper & Carson (1999) tested the coordination between an isometric movement and a dynamic movement, no difference in stability was seen between in-phase and anti-phase patterns, despite the influence of the isometric limb on the movement (reduction in movement amplitude) and muscle activation profile of the dynamic limb. Therefore it seems that only when similar tasks are performed, for example either both limbs contracting isometrically or dynamically, will characteristic inter-limb coordination stability be produced. From a neurophysiological stand point, this may be due to different regulation of the transmission gain of segmental input to the motoneurone pool, or asymmetries in the recruitment of motor units, which create a large enough disparity between the afference produced from the limb activation to 'de-couple' the limbs (Peper & Carson 1999). The

lack of coupling between an isometric contraction and a dynamic movement was also modeled by Ridderkhoff et al. (2004), and was touched upon in section 1.3.

It is also possible that task context could have influenced stability at many levels of the nervous system, not just the spinal level. At the cerebral level, it is possible that there are task dependent gating mechanisms for the afferent information; therefore if the gating is distinct, there may be little potential for contralateral influences upon homologous neural pathways. Another possible explanation for a lack of differential stability between coordination modes is distinct motor unit recruitment between isometric and shortening contractions. Interactions in the cortical homotopic maps in M1 are modulated by the equivalency of subpopulations of motor units that are recruited for a specific task (Peper & Carson 1999).

Afferent signals not only affect spinal processes, but also may influence coordination stability in the cortex. These constraints will be discussed more in-depth in section 1.5.4 Cortical Constraints.

Afferent information is not the only neuromuscular factor that must be taken into account when studying interlimb coordination. It is well known that initial increases in strength during resistance training arise from neural adaptations, such as increased synaptic effectiveness of connections in M1, and decreased brain activation of premotor areas “upstream” of M1 with learning. Muscle strength can have a direct impact on coordination of a unimanual movement to a metronome. Flex-on-the-beat coordination is more stable than extend-on-the-beat coordination (Carroll et al 2001; Carson & Kelso

2004; Carson et al. 2000; Kelso et al. 2001; Swinnen & Wenderoth 2004). It is known that flexor muscles (especially of the forearm) are stronger than extensors; therefore a smaller proportion of flexor motor units must be activated to create the same amount of force as a larger proportion of extensor motor units. In other words, flexor muscles create a larger torque value for the same degree of motor unit activation compared to the extensor muscles (Carroll et al. 2001; Carson & Kelso 2004). In fact, coordination stability can be influenced by resistance training of the muscles used in the coordinative pattern. When participants increase the muscle strength of forearm extensors, coordination stability of extend-on-the-beat coordination pattern is increased (Carroll et al. 2001; Carson & Kelso 2004). In theory, increased force generating ability decreases the central drive required to perform the coordination pattern (compared to central drive levels before resistance training). A decrease in central drive decreases the interference between motor centers that need to be activated, thus increasing coordination stability (Carroll et al. 2001; Carson 2005; Carson & Kelso 2004). Therefore it is clear that the efficacy of movement imposes a constraint upon coordination, which in turn implies that arm posture, muscle length and moment arm also influence coordination stability (Carson & Kelso 2004; Carson et al. 2000; Li et al. 2004). This constraint is not just seen in finger flexion and extension movements, but also in unimanual and bimanual coordination of forearm pronation and supination. In fact, Carson et al. (2000) found that coordination stability was dependent on mechanical task context; if the axis of rotation about the forearm was changed, the differential stability of pronation-on-the-beat to supination-on-the-beat was reversed. When the task was completed in a bimanual

setting, the relative stability of in-phase and anti-phase was dependent on the mechanical context of the task, in that the stable coordination mode was the composite of the most stable unimanual coordination patterns, even if the bimanual pattern was anti-phase as opposed to in-phase. The constraint governing the coordination during this task was the mechanical constraint placed upon each limb, not the coupling between limbs (Carson et al. 2000). Therefore this suggests that changes in arm posture also change the muscle length and fiber orientation, which in turn influence the muscle activation patterns, ultimately changing the stability of interlimb coordination (Li et al. 2004; Swinnen & Wenderoth 2004).

### 1.5.3 Cortical Constraints

Motor irradiation, has cortical mechanisms as well. The crossed facilitation seen in homologous motor pathways is dependent upon the neural drive, or contraction effort being exerted by the active muscle. Using Transcranial Magnetic Stimulation (TMS) to study motor evoked potentials of a resting limb, while the contralateral limb was actively moved, it was shown that there is a phase-dependent potentiation of the corticospinal pathway. In other words, when one limb is moving, it is easier to evoke a movement in the contralateral limb due to a potentiation created by the contralateral component of a descending efferent signal (Peper & Carson 1999). Because the potentiation volley is phase locked to the movement of the active limb, it is possible that this may be disruptive to coordinative patterns that require asynchronous activation of homologous muscles. This phase-dependent potentiation also lends itself to entrainment, and probably works in tandem with the entrainment process at the spinal level discussed in section 1.3.1 (Peper

& Carson 1999). If the muscle is the prime mover of an action, the motor evoked potential (MEP) elicited from a TMS test pulse is higher than when the contralateral homologous muscle is at rest; whereas if the muscle is not the prime mover, the MEP is smaller than when the contralateral homologous muscle is at rest. These effects are not elicited from stimulation of the descending neural tract during electrical stimulation of the cervicomedullary junction. Therefore homologous motor pathway potentiation must have a cortical mechanism (Carson 2005; Carson et al. 2004).

From an anatomical point of view, there are many neural levels at which the spatio-temporal coupling of coordination may occur. Motor commands from M1 can take direct or indirect routes to the spinal cord. The neurons of the lateral corticospinal tract cross in the medulla and terminate on the ventral horn of the spinal cord providing contralateral motor control, specifically to distal portions of limbs. Conversely, the neurons of the ventral corticospinal tract run uncrossed through the brainstem region and terminate at the medial regions of the spinal cord. The neural fibers of the ventral tract may terminate either ipsilaterally or contralaterally, and provide control of proximal limb and axial muscles (Carson 2005; Spencer et al. 2005; Swinnen 2002). In fact, it has been shown that proximal muscles groups are more strongly coupled than distal muscle groups. This proximal muscle group effect was even seen in non-homologous limbs where coordination of iso-functional muscle groups produced more stable coordination than non-isofunctional muscle groups (Meesen et al. 2006). Therefore each limb could receive discordant motor commands from each hemisphere during anti-phase coordination, which in turn, could decrease stability of the anti-phase coordination mode.



Inter-hemispheric interactions play a significant role in homologous motor pathway potentiation as well. The primary motor areas (M1) in each hemisphere are connected through the corpus callosum, and are known to exchange information between the two hemispheres, but it seems that most of the crossed facilitation is actually mediated by common inputs from motor planning areas, which are discussed below, with denser callosal connections. Excitatory connections between homotopic M1 areas, are surrounded by inhibitory connections, which through selective activation create patterns of facilitation or inhibition that are spatially, temporally and functional separate (Carson 2005).

Lesion and imaging work completed in both human and non-human primates show that bimanual coordination predominantly activates a distributed network including: the primary motor cortex (M1), primary sensory cortex (S1), lateral premotor cortex (PMC), supplementary motor area (SMA proper, primarily the dorsal part behind the VCA line), dorsal cingulate motor area (CMA) and the anterior corpus callosum. Activation of the posterior parietal cortex (PPC) is dependent upon task complexity and familiarity (Carson & Kelso 2004; Donchin et al. 1998; Jirsa et al. 1998; Peper & Carson 1999; Swinnen 2002; Wenderoth et al. 2005). Activation in the PMC is usually seen bilaterally in the caudal portion of the dorsal PMC (PMCd), near the precentral sulcus. The activity in this area is thought to involve integration of both the limbs' motor plans into a unified sequence of muscle contractions, and the suppression of easier motor plans, such as mirror movements. In fact, when the arms are completing the same movement, the neural activity in each hemisphere could be mutually reinforcing, producing stable

coordination, and each movement is performed better bimanually than their composite unimanual movement (Swinnen & Wenderoth 2004; Wenderoth et al. 2005).

Spatial aspects of coordination are encoded in a distributed network. Activation within the PMCd, medial and lateral superior parietal gyrus and the supramarginal gyrus is sensitive to both limbs moving in distinct directions and the limbs having different movement amplitudes. Previous research has attributed sensorimotor transformations for motor actions to these areas. The activation observed was greater in the right hemisphere, historically said to process spatial information, relative to the left hemisphere. Completing movements of differing amplitudes simultaneously also has unique activation in the dorsolateral prefrontal cortex – anterior cingulate cortex – supramarginal gyrus circuit. Activation in these areas has traditionally been attributed to cognitive operations such as updating of working memory, shifting between environmental stimuli and inhibition of unwanted, competing motor responses (conflict situations similar to the Stroop effect). Areas that were specific to controlling simultaneous movements in different directions included the posterior portion of the inferior temporal gyrus, extending from the middle temporal gyrus to the middle occipital gyrus, and the globus pallidus. Globus pallidus activation is often attributed to somatosensory information about disparate directions. Traditionally, activation of the inferior temporal gyrus is attributed to imagery, which the authors of the study propose was used to estimate orthogonal directions (Wenderoth et al. 2005).

The temporal aspect of coordination, for discrete movements, is usually attributed to activation in the cerebellum (Carson & Kelso 2004; Kennerley et al. 2002; Swinnen 2002). Lobule VI, in both the vermis and the hemisphere, seems to be responsible for movements with a predictable rhythm. Activity in the posterior regions of the cerebellum (lobule VI, Crus I, vermis lobule VII and VIII), is present when limbs not moved in synchrony, but must maintain an exact time delay between the limbs. Traditionally, activity in the cerebellum is also attributed to error monitoring (comparing the predicted sensory feedback from the efference copy of the motor command to the actual sensory feedback), and error correction. The activity seen in these temporal tasks could also be attributed to these functions as well (Swinnen & Wenderoth 2004).

Increased activation is seen in difficult coordination tasks, and is usually attributed to augmented requirements for central control. Higher activation is seen in the medial brain areas, SMA and CMA, during internally generated movements; whereas externally guided movements activate more lateral brain areas such as the PMC (Swinnen 2002; Swinnen & Wenderoth 2004; Wenderoth et al. 2005). Anti-phase movements generally show higher activation of the SMA, S1, M1, CMA and PMC compared to in-phase movements. Non-isodirectional movements also show higher activation of the SMA and CMA than isodirectional movements (Swinnen 2002). The 'spread' of neural activation may in fact impede proper coordination, as areas of the cortex not directly related to the motor task are recruited. Therefore the increases in central drive, due to increasing force or velocity demands to maintain coordination stability, may actually create interference via extraneous muscle activity to the coordinative task. Activation levels decrease with

learning or familiarity with a coordination task, which also supports the decreased activation – higher stability theory. During novel coordination tasks, there are increases in activation of prefrontal, parietal and subcortical areas above and beyond the activation of ‘coordination’ brain areas mentioned above (Carson & Kelso 2004; Swinnen 2002; Swinnen & Wenderoth 2004; Wenderoth et al. 2005). Activation of the pre-SMA, caudal anterior cingulate cortex (ACC) and prefrontal areas suggest an increase in working memory and attentional requirements. The ACC is often thought of as the interface between cognition and action; therefore activation of the ACC and the lateral prefrontal cortex during novel coordinated movements is probably responsible for the suppression of competing or unwanted movement responses, such as default coordination modes (Swinnen 2002).

Neural activation in M1, PMC and SMA has been attributed specifically to bimanual movements in single cell recordings in monkeys (Donchin et al. 1998; Peper & Carson 1999). Interesting neural activation patterns have been found in primate single cell recording studies that prove that bimanual movements are more than just the addition of two unimanual movements. Originally, it was thought that ‘bimanual related activity’ was only seen within the SMA. Specific activation for bimanual movements, different from unimanual activation, is seen for all bimanual movements (fingers, hands, arms, ect.) (Donchin et al. 1999; Donchin et al. 1998).

Recently it has been found that the SMA is not the only motor area that displays specific bimanual related activity. 69% of cells within M1 are direction specific. Most

of these cells fire with the movement of the contralateral arm in a specific direction, although some cells are activated by movements of the ipsilateral arm. Interestingly, some M1 cells that show direction specific activation during unimanual movements, show different activation during direction specific bimanual movements as well. This 'bimanual activation' exhibited within M1 does not exhibit different characteristics, such as activation latency, strength, or duration, than activity seen in the SMA bimanual cells, and the movement kinematics and arm EMG does not significantly affect the 'bimanual activation' in these M1 cells. The 'bimanual activity' seen in M1 was more pronounced in hand and arm movements compared to finger movements because M1 has a higher proportion of bilateral movement control for more proximal musculature compared to the classic contralateral control of more distal musculature. In other words, homologous M1 areas are strongly connected for the arms, but not the fingers; therefore bimanual related activity in M1 was more pronounced in arm movements (Donchin et al. 1999; Donchin et al. 1998).

Jirsa et al. (1998) extended the HKB model to hopefully predict temporal brain dynamics, and how they change with changes in coordination. Using Magnetoencephalography (MEG), the temporal dynamics of brain behaviour were shown to be strongly dominated by the movement frequency of the limbs. Brain activation pattern also showed a distinct transition when the behavioural phase transition between the limbs occurred.

#### 1.5.4 Perceptual-Cognitive Constraints

Neuromuscular factors are not the only constraints that influence coordination accuracy and stability. Perceptual constraints, including multimodal sensory integration, and cognitive constraints including intention, attention, effort, task conceptualization and learning affect coordination as well. These perceptual and cognitive constraints also change the pattern of distributed cortical activation (Atachy-Dalama et al. 2005; Carson & Kelso 2004; Li et al. 2004; Swinnen & Wenderoth 2004).

Coupling between the two limbs is mediated by sensory feedback of many different modalities. For example, when coordinating movements to a visual stimulus or between people, the coupling must only be visual; whereas coupling of movements within a person may have both visual and proprioceptive components. This suggests that stability of coordination is dependent upon the stability of the perception of relative phase between the moving parts (Atachy-Dalama et al. 2005; Temprado et al. 2003; Wilson et al. 2003; Zaal et al. 2000). For visual coupling, isodirectional movements are more stable, since visual stimuli that move in the same direction are more salient. In fact, for coordination of movements between people isodirectional movements were more stable than non-isodirectional movements regardless of homologous muscle activation; therefore stability of coordination with purely visual coupling is defined by allocentric constraints (Temprado et al. 2003). For intraperson interlimb coordination, anti-phase movements (specifically alternation of homologous muscle groups) show greater deficits when sensory feedback is limited, for example a blind fold is used to restrict visual information. This implies that multimodal sensory integration is more important for

control of (muscular) anti-phase coordination than in-phase coordination (Temprado et al. 2003).

Using finger abduction and adduction movements with congruent and incongruent forearm postures (pronated and supinated), Mechsner et al. (2001) attempted to dissociate perceptual constraints from neuromuscular constraints. The research showed that regardless of forearm posture, non-isodirectional movements showed more accurate and stable coordinative structure than iso-directional movements. The non-isodirectional coordination partiality was seen both when the forearms were in the same posture (simultaneous activation of homologous muscles) and in different postures (alternating activation of homologous muscles); therefore they attributed this finding to a perceptual preference for mirror-symmetric movements (Atachy- Dalama et al. 2005; Li et al. 2004; Mechsner et al. 2001; Mechsner & Knoblich 2004). They did fail to take into account that placing the arms in different postures would change the mechanical context of the arm, thus changing the muscle activation patterns of the muscles, by changing the muscle length, moment arm, and torque generating ability (Carson et al. 2000; Li et al. 2004). The experiments were repeated using wrist abduction-adduction (horizontal plane) movements, yielding the same results, but the recruitment of extraneous biomechanical degrees of freedom was also observed. The abductors and adductors of the wrist are also the wrist flexors and extensors; therefore recruitment of extra degrees of freedom will result in unintended movements in the vertical plane. The most accurate and stable coordination mode, that also demonstrated the least amount extraneous movements, was when homologous muscles were simultaneously activated. The conditions with that did

show movement in the vertical plane, the flexion or extension movements tended toward activation of homologous muscles with the abduction and adduction movements.

Therefore, perceptual constraints are important, but are difficult to dissociate from neuromuscular constraints, and are not the only factors that govern coordination as Mechsner et al (2001) claimed (Li et al. 2004).

Sensory feedback from perceptual cues, such as an auditory metronome or haptic information can stabilize coordination. If sensory input is coincident with the 'goal' of a movement, for example flex-on-the-beat, then coordination is stabilized, and if there are two sensory cues for each movement cycle (metronome beat at flexion and extension), the coordination pattern is further stabilized. Conversely, if sensory input is counter-phase to the 'goal' of the movement, for example flex-between-the-beat, then coordination is destabilized, and often phase transitions to a coordination pattern where the goal of the movement and the sensory input coincide are seen (Carroll et al. 2001; Carson & Kelso 2004; Kelso et al. 2001; Kudo et al. 2006; Swinnen & Wenderoth 2004). When feedback is provided in more than one sensory modality, at higher movement frequencies, phase transitions occur to coordination patterns where the two sensory modalities and movement goal become 'bound' together into a single coherent action-perception unit. A single coherent action-perception unit will also require less attentional resources, which also increases coordination stability (Carson & Kelso 2004; Kelso et al. 2001; Swinnen & Wenderoth 2004). Obviously, perceptual constraints upon coordination are just as salient as neuromuscular constraints, and depending on the task requirements may even override the neuromuscular constraints on coordination. In fact,



trying to coordinate only visual information about limb movement can allow for completion of difficult coordination tasks (such as a 4:3 coordination between the limbs) that cannot be accomplished without augmented feedback. Augmented feedback also facilitates learning a new difficult coordination mode (Atachy-Dalama et al. 2005; Mechsner & Knoblich 2004; Mechsner et al 2001; Swinnen & Wenderoth 2004). Another possible strategy to perform difficult coordinated movements would be intermittent control of the movements. Performance is monitored at key kinematic markers of movement called *anchor points*. These anchor points usually coincide with a sensory cue, such as an auditory metronome beat, or haptic contact with a surface (Swinnen & Wenderoth 2004).

How relative phase is perceived may also affect the ability to produce a coordinative relationship. Both visual and proprioceptive judgments of relative phase variability (which was artificially manufactured in a visual display and a haptic tracking movement) are dependent upon the mean phase relationship. For example, in both modalities during in-phase movements, different levels of phase variability are discernible at all oscillating frequencies. Conversely, during anti-phase movements, at low oscillating frequencies, different levels of oscillating frequency are discernible, but at higher movement frequencies, estimations of variability of the phase relation increase. The ability to perceive phase variability at higher frequencies during anti-phase movements is different between the visual and proprioceptive systems. During a 90° phase relationship, judgments of relative phase variability is much higher and different levels of variability cannot be distinguished visually, and can only be separated

proprioceptively at lower oscillating frequencies. These results lead to two different conclusions. First, that the proprioception system percept is more sensitive to relative phase variability than the visual system percept. Second, that perception of relative phase seems to be dependent upon relative direction of limb movement. For the visual system, the ability to perceive movement direction is dependent on the velocity of the movement. In-phase (isodirectional) movements have a constant relative velocity of zero, but anti-phase and a  $90^\circ$  phase relationship involve a variable relative velocity; therefore in-phase movements are perceived as less variable than other phase relationships (Atachy-Dalama et al. 2005; Wilson et al. 2003). It is important that proprioception is sensitive to relative phase variability because it seems to be used for coordination error correction, especially for spatial movement characteristics (Spencer et al. 2005).

It is the sensory consequences of movement that helps stabilize and learn new coordination patterns. Atachy-Dalama et al. (2005) had two groups learn a new  $30^\circ$  phase coordination relationship. The control group had to learn the new coordination mode using only two auditory metronomes for each arm. This group would have to change the relative timing of outgoing motor commands to produce the proper phase relationship and sensory feedback. The experimental group had an inertial load placed upon one hand so that the  $30^\circ$  phase relationship was produced by simultaneous timed motor commands. This group was able to produce the new phase relationship more accurately and stably quicker because they did not need to learn a new outgoing motor command relationship, but were still able to receive the same sensory feedback from their movements. Once the inertial load was removed, the experimental group was still able to

produce the new phase relationship. The second group couldn't have learned the outgoing motor command pattern; therefore the learning must have been of the sensory consequence of the movement, not the motor command relationship (Atachy-Dalama et al. 2005).

Intention can stabilize and destabilize coordination. The phase transition from anti-phase to in-phase can be delayed by cognitive strategies, and intentional switching from anti-phase to in-phase is easier than switching from in-phase to anti-phase. It is clear that cognitive strategies influence coordination stability, but that intention in turn is influenced by relative stability of coordination patterns. Attention effects during coordination are also a cognitive constraint upon coordination (Carson & Kelso 2004). The effects of attention have already been discussed above in section 1.2.1.4.

How coordinated tasks are conceptualized will also affect performance. For example, the amplitude interference discussed in section 1.5.1 can be reduced by using visual cues for the participant to follow. The decrease in spatial interference can be attributed to how the participant perceives the task, but changing the perception will also change the neural network used to complete the task. The visual cues will activate the parietal-premotor network for externally guided movements; whereas the same task with no visual cues will activate the basal ganglia – supplementary motor area circuit attributed to internally generated movements (Swinnen & Wenderoth 2004).

## 1.6 Force-field or Load Experiments

Insight into how the CNS controls movement can be gleaned by observing how it compensates for changing external environments. In research, often loads, both 'real' and 'virtual', are placed upon moving limbs to elucidate the compensatory mechanisms.

It is important to discuss how adding a load to a limb affects the limbs movement before exploring the consequences of loads placed upon the limbs in a coordination task. Mackey et al. (2002) placed 'compliant' loads upon the participants' dominant hand during wrist flexion and extension movements. In this context, compliant loads mean that there was resistance placed upon the movement, but the movement was not arrested in any way; therefore the loads used in the Mackey et al. (2002) experiment are very similar to the virtual force-fields used in the present study. Mackey et al. (2002) found no differences in the amplitude or movement frequency between the load conditions and no load condition, but there were differences in the Flexor Carpi Radialis (FCR) and Extensor Carpi Radialis (ECR) muscle activation profiles as measured by electromyogram (EMG). Elastic (position-dependent) loads, and inertial (acceleration-dependent) dependent loads changed the timing of the EMG bursts in both the FCR and ECR. Muscle activation showed delayed onset and offset in elastic load conditions compared to the no load condition. Inertial load conditions showed earlier onset of muscle activation compared to the no load condition. The viscous (velocity-dependent) load condition did not change the timing of muscle activation, but did change the rate of force-production. The rate of force production increased with increasing viscous load on the hand. From these results Mackey et al. (2002) concluded that motor commands sent

from CNS are modified contingent on both load character and magnitude, so that properties of the load may be utilized such that desired kinematics are produced.

Alteration to mechanical properties of limb segments during bimanual coordination is not novel. Often, an inertial perturbation is applied to the limb, by adding a weight of some sort, or having the subject swing a pendulum. Using inertial loads during interlimb coordination, the same early onset of EMG was seen, and the anticipatory effect was larger in anti-phase than in-phase coordination, during coordination between hand movements and movement of the ipsilateral foot. The earlier onset of arm EMG during anti-phase coordination actually created a more accurate phase relationship during the loaded anti-phase coordination compared to the unloaded anti-phase condition and the loaded in-phase coordination condition. The elastic load in-phase and anti-phase conditions did not show differences from the unloaded conditions in terms of phase relationship, but the EMG of the hand muscles were delayed, as the CNS took advantage of the stored elastic forces (Baldissera et al. 1991; Baldissera & Cavallari 2001). The more accurate phase relationship seen in anti-phase coordination was attributed to the attention-heavy CNS motor commands that must over-ride the entrainment tendencies created by afferent feedback (as discussed in 1.5). Any small attentional disturbance during anti-phase coordination resulted in a transition to in-phase coordination (Baldissera et al. 1991). The mechanism of load compensation was to change the onset timing of EMG activation to maintain coordination pattern and the time shift of the EMG onset seems to be dependent upon afferent sensory signals (Baldissera et al. 1991; Baldissera & Cavallari 2001). In unloaded conditions, the timing of EMG onset is also

influenced by oscillating frequency, which suggests that the control mechanism for the timing of muscular activation must monitor limb dynamics in order to maintain coordination between limbs (Baldissera & Cavallari 2001).

There are two possible hypotheses of neuromuscular control for the accommodation of asymmetrical effector dynamics: one, EMG phasing is based solely upon sensory afference from the limbs; or two, that the default timing of neural control signals are modified to adapt to different task contexts (Baldissera et al. 1991; Baldissera & Cavallari 2001; Mechsner et al 2001; Ridderikhoff et al. 2004).

If coordination of asymmetrical effectors was based solely upon the feedback signals from movement, then deviations from the intended relative phase would be independent of the degree of asymmetry between the effectors, and depend solely upon the accuracy of the perceptual system and movement frequency. As discussed earlier, it is often reported that  $\Delta\phi$  is dependent upon  $\Delta\omega$  in pendulum studies, which arises from phase shifts between the control signals and the rhythmic movement of the unequally loaded limbs. Therefore, this lends more support to the second hypothesis, that there is both a feedforward and feedback component to interlimb coordination with asymmetrical effectors (Ridderikhoff et al. 2004).

Feedforward control mechanisms, for example a set neural pattern for in-phase coordination where descending motor commands to the effectors are sent simultaneously, fail to compensate for changes in the frequency response of asymmetric effectors (be that different effectors, same effectors with different loads, or different tasks given to each

effector, ie.: isometric contraction and dynamic movements). Large relative phase errors should be seen at the behavioural level; but under various asymmetric effector conditions, coordination can be achieved more accurately than would be predicted from feedforward mechanisms alone. The decrease in the relative phase shift observed at the behavioural level then signifies that there is an active involvement of sensory afference in modifying the control structure to maintain intended coordination patterns. Therefore the behaviour observed would be the result of two competing subsystems, a feedforward mechanism that would favour in-phase and anti-phase because neural control signals seem to be attracted to these activation patterns, and a feedback mechanism that allows for compensation for asymmetries in effector dynamics (Ridderikhoff et al. 2004).

## 2 Purpose of Study

The interaction of the environment and the oscillating effector is an important factor in coordination, but how manipulated environments affect coordination needs to be determined. It has been shown that *velocity* is an important informational source of proprioceptive information, and this information about limb movement is intrinsic to coordination (Peper & Carson 1999; Wilson et al. 2003). Previous research has manipulated the inertial forces during coordination, but it is of interest to understand how different types of loads would affect interlimb coordination. Using velocity and position dependent force-fields to perturb the fingers' movements during a continuous finger flexion-extension task would help elucidate issues within the HKB modeling literature, as well as biomechanical and physiological constraints upon bimanual coordination.

The *overall objective* of this thesis was to clarify how mechanical perturbations to the effectors' movement trajectory would affect interlimb coordination, by studying the stability of the phase relationship achieved. The stability of the phase relationship was quantified by measurements of mean relative phase absolute error and variability of relative phase. Mean relative phase described the placement of the attractor in the potential landscape ( $\phi^* = 0^\circ$  or  $180^\circ$ , for in-phase and anti-phase respectively) (Amazeen et al. 1998). Variability or standard deviation of the relative phase ( $SD\phi$ ) described the strength of the attractor at the mean relative phase measured (Amazeen et al. 1998).

The *specific predictions* of the study were to confirm the predictions made by the classical Haken-Kelso-Bunz model (Amazeen et al. 1998):



1. Force-fields applied to the fingers will change the eigenfrequency of the finger-PHANToM system (see section 3); thus if different force-fields are applied to each finger symmetry breaking would occur. Theoretically, the position dependent force-field should increase the eigenfrequency of the system, and the velocity dependent force-field should decrease the eigenfrequency of the system.
2. With detuning, the position of the attractor would be shifted from its original position on the potential landscape.
3. When the oscillators have different eigenfrequencies, the strength of the attractor (mutual oscillator cooperation) must overcome individual oscillator competition; thus the attractor strength is diminished. This should result in higher relative phase variability during mismatched force-field conditions.
4. During anti-phase coordination mode (reduced attractor strength) both coordination accuracy and stability would be reduced compared to in-phase coordination mode.
5. Larger  $\Delta\phi$  and  $SD\phi$  should be observed in velocity dependent force fields as compared to position dependent force fields because velocity based proprioception information helps control coordination (Peper & Carson 1999; Wilson et al. 2003). Velocity dependent loads also produce a higher rate of force-production as measured by EMG; whereas position dependent loads delay onset of EMG activity (Mackey et al. 2002). Coordinating two different rates of

force production is hypothesized to be more difficult than coordinating the onset timing of two different muscle activations.

## 3 Methods

### 3.1 Experimental Design

Twelve self-reported right handed graduate students (7 male) gave informed consent according to the ethical procedures of McMaster University before participating in this study. Handedness was confirmed using a modified version of the Edinburgh Handedness Inventory (Oldfield 1971). Participants were seated comfortably in an adjustable chair in front of two independent Sensable™ PHANToM 6 DoF (Woburn, MA) haptic devices. Participants placed their forearms in a semi-pronated posture with their index fingers inserted into thimble-like interfaces attached to individual haptic devices. The experiment was completed in two sessions of approximately one and a half to two hours each.

The participants were asked to move the fingers in a continuous flexion-extension movement in the horizontal plane (See Figure 1). Both in-phase (mirror symmetric) or anti-phase (spatial symmetric) coordination patterns were performed. Visual targets (not shown in Figure 1), were placed on the PHANToM devices, so that participants maintained constant movement amplitudes of approximately eight centimeters. Participants were asked to synchronize with a metronome of either 1 Hz or 2 Hz for twenty movement cycles then to continue moving at the same speed for another thirty movement cycles; therefore 1 Hz trials were 51 s and 2 Hz trials were 25.5 s long. For the in-phase coordination mode, the participants were told to synchronize the fingers pointing inwards to the metronome. For the anti-phase condition, participants

synchronized both fingers pointing rightwards to the metronome (right hand maximal extension, left hand maximal flexion). Participants were not warned of the specifics of the force-field, but were encouraged to keep to the movement goals despite any perturbation they might feel. The 2 Hz condition produced several trials that did not include a stable coordination mode (either phase wandering or phase wrapping), and thus were excluded from further analysis.

The PHANToMs were each controlled by an individual Pentium Class IV computer, using the Handshake VR toolbox for Simulink in MATLAB™ (Natick, MA). The PHANToM devices recorded a time stamp, three axes of the end effector position of the robot and three axes of the force the devices produce at a frequency of 1000 Hz. The haptic devices produced two different types of force-fields, a position-dependent or elastic (E) force field, and a velocity dependent or viscous damping (V) force-field. The elastic force-field creates a resistive force that is similar to a virtual spring. The further the spring is stretched away from its resting length, the more force it exerts to return to the resting length.

$$\vec{F}_E = -k(D_s - D_f) \quad (5)$$

where  $\vec{F}_E$  is the force produced by the haptic device,  $k$  is the proportionality constant of 1.5 N/m,  $D_s$  (m) is the anchor of the virtual spring one meter from the centre of the PHANToM's workspace in the direction of finger extension, and  $D_f$  (m) is the instantaneous finger position. Therefore the participant 'felt' a resistive force during flexion and an additive force during extension.

The velocity dependent force-field creates a resistive force that is similar to moving through a thick substance similar to honey. Faster movements create larger resistive forces compared to slower movements.

$$\vec{F}_V = -c\vec{v} \quad (6)$$

where  $\vec{F}_V$  is the force produced by the haptic device,  $c$  is the proportionality constant of 6 Ns/m, and  $\vec{v}$  is the instantaneous velocity of the finger. While the hand was placed in a damping force-field, the participant 'felt' a resistive force during both flexion and extension.

A no force (null, N) condition was also included. This created nine different permutations of force-field conditions, three where the force-field conditions matched, and six where the force-field conditions were mismatched. The mismatched conditions were used to create detuning between the two fingers. Participants completed four trials of each of the nine force-field conditions, in each coordination mode. For each movement frequency and coordination mode, the nine conditions were randomized. The movement frequency and coordination mode that a participant experienced first was counterbalanced over participants. In the first testing session, two trials of each condition were completed (seventy-two trials), followed by a repeat of the same number of trials, in the same order, on the second day, for a total of one hundred forty four trials.

### 3.2 Data Analysis

All data analysis was completed in MATLAB<sup>TM</sup> (Natick, MA), using custom scripts. Only the continuation portion of the data from the 1 Hz trials was further analyzed. Both mean and standard deviation of discrete relative phase were calculated.

The first 20 s (the synchronization phase) of each trial were removed, so that only the continuation phase was used. All of the participants were able to achieve the desired movement frequency. The maxima and minima peaks of position were identified, using an in house peak picking algorithm in MATLAB. The inter-response interval was calculated as the time between minima. In general, the discrete relative phase (DRP) formula was defined as:

$$DRP_n = \frac{t_{rn} - t_{ln}}{IRI_{r(n-1)}} \times 360^\circ \quad (7)$$

where  $t_{rn}$  and  $t_{ln}$  for in-phase trials represent the time at which both fingers are at the target (maximal flexion). For anti-phase movements the variables represent the time where the right finger is at the target (maximal extension), and the time at which the left finger reaches the equivalent position in its trajectory (also maximal extension). Thus, for in-phase trials, the DRP values should be close to  $0^\circ$ , and for the anti-phase trials DRP should be close to  $180^\circ$ . The denominator of the equation is the inter-response interval of the right hand of the previous interval. This resulted in a time series of approximately 30 values of discrete relative phase. There were only approximately 30 responses because the trial was a continuation task, and some subjects either sped up or slowed down, changing the number of responses in each trial. Each DRP time series was

inspected manually for phase wandering or phase wrapping. If clear phase wrapping, where a hand completes a whole extra cycle compared to the other hand, occurred the trials were excluded. Once summary statistics of each trial were completed, trials were also excluded if mean relative phase error was greater than  $45^\circ$ , and mean standard deviation for a single trial was greater than  $30^\circ$ . There were no trial exclusions based upon movement amplitude reductions. For the 1 Hz in-phase data, 1.9% of trials were not included, 0.8% due to technical difficulties in the data recording of one of the PHANTOMs, and 0.8% due to larger mean relative phase errors ( $\phi$ ) that the  $45^\circ$  tolerance. For the 1 Hz anti-phase data, 5.3% of trials were excluded, 1.9% due to technical difficulties, 1.4% due to  $\phi > 45^\circ$ , and 1.9% of trials that exceeded the stability criteria of standard deviation of relative phase ( $SD\phi$ ) less than  $30^\circ$ . For the 2 Hz in-phase data, 0.9% of trials were excluded, 0.7% due to technical difficulties, and 0.2% due to  $\phi > 45^\circ$ . For the 2 Hz anti-phase data, 19.2% of trials were excluded, 0.2% due to technical difficulties, 3.2% due to  $\phi > 45^\circ$ , and 15.7% due to  $SD\phi > 30^\circ$ . Since there were significantly more trials excluded from the 2 Hz anti-phase conditions, all of the 2 Hz trials were excluded from further statistical analysis.

Two different Analyses of Variance (ANOVA) were performed in SPSS (Chicago, IL), on the mean relative phase error and relative phase standard deviation. The ANOVA designs were a 2 Coordination Mode (in-phase, anti-phase)  $\times$  2 Force-field conditions (matched vs. mismatched) and a 2 Coordination mode (in-phase, anti-phase)  $\times$  9 Force-field conditions (NN, NE, EN, NV, VN, EE, EV, VE, VV). ANOVAs were also

performed on movement kinematics. Movement amplitude measurements were placed in a 2 Coordination Mode (in-phase, anti-phase)  $\times$  2 Hand (right, left)  $\times$  2 Movement Phase (flexion, extension)  $\times$  9 Force-field conditions ANOVA. Peak force measurements, for the trials with a force-field, were placed in a 2 Coordination Mode (in-phase, anti-phase)  $\times$  2 Hand (left, right)  $\times$  2 Movement type (flexion, extension)  $\times$  6 Force-field conditions ANOVA.



## 4 Results

### 4.1 General Kinematic Results

#### 4.1.1 Movement Amplitude Effects

Movement amplitude was calculated for both the flexion and extension phases of the movement task. Flexion movement amplitude was calculated as the absolute value of the difference in position of maximal extension to maximal flexion, and extension movement amplitude was calculated as the absolute value of the difference in position from maximal flexion to maximal extension.

Movement amplitude in the in-phase ( $M = 0.080$  m) coordination mode was significantly greater than the anti-phase ( $M = 0.073$  m) coordination mode ( $F(1,11) = 16.812, p = 0.002, \eta^2 = 0.604$ ). Movement type factor was also significant ( $F(1,11) = 12.516, p = 0.005, \eta^2 = 0.532$ ), showing that extension movement was 0.2 mm larger than flexion movement. The force-field factor was also significant ( $F(2.085, 22.936) = 3.475, p = 0.046, \eta^2 = 0.240, \text{Huynh-Feldt corrected}, \epsilon = 0.261$ ). Applying a force-field to the hand decreased the movement amplitude compared to a no force-field condition.

Amplitude in an elastic force-field was reduced only slightly (1-3 mm); whereas the reduction in a damping force-field was much greater (6-9 mm). This evidence supports the hypothesis that coordination will be disrupted more by a damping force-field than an elastic force-field. The reduction in amplitude in a damping force-field is similar to that seen between in-phase and anti-phase coordination modes, and it is widely acknowledged that anti-phase coordination exhibits higher mean relative phase error, and less

coordination stability than in-phase coordination. The interaction of coordination mode  $\times$  hand was also significant ( $F(1,11) = 20.183, p = 0.001, \eta^2 = 0.647$ ).

Post-hoc pair-wise means comparisons were performed on the interaction using Tukey's Honestly Significant Difference (HSD). None of the differences were significant, but in the in-phase coordination mode, the left hand ( $M = 0.082$  m) had greater movement amplitudes than the right hand ( $M = 0.078$  m); whereas in anti-phase coordination, the right hand movements had larger amplitude ( $M = 0.074$  m) than the left hand ( $M = 0.072$  m). The larger difference in movement amplitude of the left hand (compared to the movement amplitude differences seen in the right hand) between in-phase and anti-phase coordination was the driving factor of this interaction. The only other significant interaction was the coordination mode  $\times$  movement type interaction ( $F(1,11) = 22.437, p = 0.001, \eta^2 = 0.671$ ). The driving factor of the interaction was the differences between the coordination modes in both flexion (*in-phase* – *anti-phase*,  $0.0069$  m,  $p < 0.05$ ) and extension (*in-phase* – *anti-phase*,  $0.0071$  m,  $p < 0.05$ ). The difference between flexion and extension movements in a single trial must be very little or movements would drift over time, but the difference between flexion and extension was larger in the in-phase coordination mode (*flexion* – *extension*,  $-0.00031$  m) compared to the anti-phase coordination mode (*flexion* – *extension*,  $-8.65 \times 10^{-5}$  m).

#### 4.1.2 Force – field Effects

For the force-field conditions the PHANToM recorded the forces it exerted during a trial. From the force time series, mean peak force values were calculated for both flexion and extension movements. For the elastic conditions, these peak forces were

created at maximal flexion and extension. For this particular experimental task, the position dependent nature of the force-field produced absolute maximal force at the point of maximal flexion, and absolute minimal force at the point of maximal extension. For the damping conditions, peak forces are created at peak velocity in each movement trajectory; therefore, the peak forces for flexion and extension should be similar, and only dependent upon the movement velocity of each movement. Only the trials with a force-field were placed in a 2 Coordination Mode (in-phase, anti-phase)  $\times$  2 Hand (left, right)  $\times$  2 Movement type (flexion, extension)  $\times$  6 Force-field conditions ANOVA. The six force-field conditions varied with respect to hand. For the left hand, the force-field condition order was EN, VN, EE, VE, EV, and VV and for the right hand the force-field condition order was NE, NV, EE, VE, EV, VV; therefore for each force-field level in the ANOVA, the conditions had the same type of force-field on the hand in question, and the same force-field on the other hand.

The in-phase coordination mode ( $M = 0.981$  N) had significantly higher forces than the anti-phase coordination mode ( $M = 0.937$  N) ( $F(1,11) = 5.738, p = 0.036, \eta^2 = 0.343$ ). During the flexion phase ( $M = 0.983$  N) the PHANToM created more force than the extension phase ( $M = 0.935$  N) ( $F(1,11) = 23.869, p = 0.000, \eta^2 = 0.685$ ). This difference could come from two possible sources: one, the peak elastic force at extension will always be lower than the peak elastic force at flexion, and two, flexion movements may have been faster than extension movements, creating a larger damping force during the flexion movement phase. The main effect of force-field was not significant ( $F(1.427, 15.697) = 0.666, p = 0.479, \eta^2 = 0.057, \text{Huynh-Feldt corrected}, \epsilon = 0.285$ ).

The interactions of coordination mode  $\times$  hand ( $F(1,11) = 8.620, p = 0.014, \eta^2 = 0.439$ ), coordination mode  $\times$  movement phase ( $F(1,11) = 6.206, p = 0.030, \eta^2 = 0.361$ ), hand  $\times$  movement type ( $F(1,11) = 9.120, p = 0.012, \eta^2 = 0.453$ ), coordination mode  $\times$  force-field condition ( $F(5,55) = 2.856, p = 0.023, \eta^2 = 0.206$ ), movement type  $\times$  force-field condition ( $F(1.187, 13.060) = 7.534, p = 0.014, \eta^2 = 0.407, \text{Huynh-Feldt corrected}, \epsilon = 0.237$ ) and hand  $\times$  movement type  $\times$  force-field condition ( $F(1.716, 18.878) = 8.471, p = 0.003, \eta^2 = 0.435, \text{Huynh-Feldt corrected}, \epsilon = 0.433$ ) were all significant. Post-hoc means comparisons were completed on all interactions using Tukey's Honestly Significant Difference test, with significance set at  $p < 0.05$ .

None of the pair-wise comparisons were significant in the coordination mode  $\times$  hand interaction, but the interaction can be explained by a smaller mean force created by the left hand in the anti-phase coordination mode. For both hands, forces seen in the in-phase coordination mode are higher than the anti-phase coordination mode. In the right hand, the difference between the two conditions is small (*in-phase*,  $M = 0.978$  N, *anti-phase*,  $M = 0.960$  N), while in the left hand the difference is much greater (*in-phase*,  $M = 0.984$  N, *anti-phase*,  $M = 0.914$  N). This created a situation where the forces produced by the left hand were larger than those produced by the right hand in the in-phase coordination mode, and smaller in the anti-phase coordination mode, which in turn created the significant interaction.

The coordination mode  $\times$  movement type interaction was significant due to the differences in the amount of force produced in the flexion phase of movement between

coordination modes. Again, none of the pair-wise comparisons were found to be significant during post-hoc testing, but clear trends could be seen to explain the interaction. Flexion movements always produced a higher force independent of coordination mode, and in-phase always produced higher forces independent of movement type. But the difference in force produced in flexion (*in-phase – anti-phase*, 0.054 N) was greater across coordination mode than the difference in produced force in extension (*in-phase – anti-phase*, 0.032 N). Conversely, the differences between movement types were greater during in-phase coordination (*flexion – extension*, 0.058 N) than anti-phase coordination (*flexion – extension*, 0.036 N). The differences found in the flexion phase could have been caused by either larger amplitude movements during in-phase movements, causing larger elastic forces, or by faster flexion movements during the in-phase coordination mode compared to anti-phase, which would cause larger damping forces. Larger amplitude movements were seen throughout in-phase movements, suggesting that the elastic force explanation is valid; however, one must also take into consideration that if the participant moved further in approximately the same amount of time, then movement velocity must have increased, thus increasing the damping force as well.

The hand × movement type interaction was driven by the difference between the left hand and right hand forces being exerted in the extension phase of the movement. Once again, no significant pair-wise comparisons were found using Tukey's HSD test. The difference between the hands in the flexion phase of movement was very small (*Left – Right*, -0.004 N); whereas the difference between the forces produced by each hand in

the extension phase was an order of magnitude larger (*Left – Right*, -0.036 N). Since all of the subjects in this study were right handed, the difference seen in the extension phase of the movement probably reflects strength differences between the hands. In right hand dominant people, often the extension muscles of the right hand are stronger than the left hand due to the right hand's use in daily living activities (Incel et al. 2002). The differences between the forces produced by the hands in each phase of movement was also larger in the left hand (*flexion – extension*, 0.063 N), compared to the right hand (*flexion-extension*, 0.031 N).

The coordination mode  $\times$  force-field interaction is driven by the differences between coordination modes, seen in the forces produced when a hand was in a viscous force-field. None of the pair-wise comparisons conducted were significant, but Figure 2 shows that the conditions where the hand was in an elastic force-field have less difference between the coordination modes, than do the conditions where the hand was in a viscous force-field. In fact, the anti-phase conditions where a hand was placed in a viscous force field produced much less force than all the other conditions. The only possible exception is when both hands were in a viscous condition. A decrease in the amount of force seen in a viscous force-field is directly proportional to the speed at which the finger was moving. This could be foreshadowing some of the later results which demonstrate that subjects had larger relative phase errors in mismatched conditions that included a viscous force-field, but that the matched viscous condition did not show these coordination difficulties.

The movement type  $\times$  force-field interaction is driven mainly by the differences in the elastic force field between mean peak flexion force and mean peak extension force. Once again there were no significant means comparisons from post-hoc testing, but for all conditions where the hand in question is in an elastic force-field there is a difference between flexion and extension (*other hand in no force-field*, 0.114 N, *other hand in an elastic force-field*, 0.118 N, *other hand in a viscous force-field*, 0.116 N) that was an order of magnitude larger than the difference seen in all conditions where the hand is in a viscous force-field (*other hand in no force-field*, 0.016 N, *other hand in an elastic force-field*, 0.025 N, *other hand in a viscous force-field*, 0.015 N). The smaller difference in the viscous conditions means that the velocities of the flexion and extension movements were approximately equal, although flexion is consistently faster (higher force). The difference between movements phase that was seen in the elastic force-field conditions was simply a matter of how the force-field was constructed.

The hand  $\times$  movement type  $\times$  force-field interaction produced a single significant pair-wise comparison. There was a significant difference between the forces produced during the extension movement of the left hand in a viscous force-field (while the right hand was not in a force-field) and forces produced by the right hand during extension movements, while the left hand was not in a force-field ( $p < 0.05$ ). Although this was the only significant difference, there were other trends that led to the interaction being significant. Similar to the movement type  $\times$  force-field interaction, the difference between the forces recorded at flexion and extension were larger in the elastic force-field than in the viscous force-field. The differences between the forces recorded for each

hand during flexion movements, in both elastic and viscous force-fields, were quite small; however the differences between the hands were much larger during extension movements, especially in the viscous conditions.

## 4.2 Matched and Mismatched Force-field Results

### 4.2.1 Mean Relative Phase Error ( $\phi$ )

For mean relative phase error, both the main effect of Coordination Mode ( $F(1, 11) = 5.855, p = 0.034, \eta^2 = 0.347$ ) and Force-field condition, matched or mismatched ( $F(1, 11) = 29.441, p = 0.000, \eta^2 = 0.728$ ) were significant. In-phase coordination produced significantly smaller error values than anti-phase coordination, and matched force-field conditions produced significantly smaller errors than mismatched force-field conditions. The interaction of coordination mode and force-field condition was not significant ( $F(1, 11) = 3.266, p = 0.098, \eta^2 = 0.229$ ).

### 4.2.2 Relative Phase Standard Deviation ( $SD\phi$ )

For the relative phase standard deviation, the effect of coordination mode was significant ( $F(1, 11) = 17.946, p = 0.001, \eta^2 = 0.620$ ). The in-phase coordination trials had significantly lower standard deviations, and thus are more stable, than the anti-phase coordination mode. The main effect of force-field condition, matched vs. mismatched ( $F(1, 11) = 3.670, p = 0.082, \eta^2 = 0.250$ ) and the interaction of coordination mode and force-field condition ( $F(1, 11) = 0.242, p = 0.632, \eta^2 = 0.022$ ) were not significant.



### 4.3 Individual Force-field Results

#### 4.3.1 Mean Relative Phase Error ( $\phi$ )

The results of the mean relative phase error 2 Coordination mode  $\times$  9 Force-field condition ANOVA, showed that the main effect of coordination mode was not significant ( $F(1, 11) = 4.060, p = 0.069, \eta^2 = 0.270$ ). The main effect of force-field was significant ( $F(3.539, 38.927) = 10.960, p = 0.000, \eta^2 = 0.499, \text{Huynh-Feldt corrected}, \epsilon = 0.442$ ), as was the interaction between coordination mode and force-field factors ( $F(8, 88) = 5.086, p = 0.000, \eta^2 = 0.316$ ).

From the Bonferroni corrected means comparison in SPSS, the significant differences between the levels of the force-field factor can be identified (and are summarized in Fig. 6). For the force-field condition, the matched conditions were not significantly different from each other. Two mismatched conditions produced significant differences from the majority of the other force-field combinations. In both of these conditions, the left hand was placed in a viscous force-field, and the right hand was placed in either a null (VN) or elastic (VE) force-field. The VN condition was significantly different from both hands in no force-fields (NN,  $p = 0.006$ ), elastic force-fields (EE,  $p = 0.008$ ), viscous force-fields (VV,  $p = 0.006$ ), and when the left hand was in a null force-field and the right hand is in an elastic force-field (NE,  $p = 0.004$ ). The difference between VN and when the left hand was in an elastic force-field and the right hand was not in a force-field (EN,  $p = 0.067$ ) was close to significance. The VN condition was not significantly different from the other conditions when one hand was in

a viscous force-field and the other hand in a different environment (VE, NV, EV, all conditions  $p = 1.000$ ). The VE condition was significantly different from all the matched conditions (NN,  $p = 0.005$ , EE,  $p = 0.003$ , and VV,  $p = 0.002$ ), as well as both mismatched conditions where one hand was in an elastic force-field and the other hand was not in a force-field (NE,  $p = 0.001$ , EN,  $p = 0.031$ ). Similar to the VN condition, the VE condition was not significantly different from the other detuning conditions with one hand in a viscous force-field and the other hand in a different force-field environment (VN, NV,  $p = 1.000$ , EV,  $p = 0.921$ ). Although the mean relative phase error ( $\phi$ ) was greater than the matched conditions and elastic – no force-field conditions for the detuning conditions with the right hand in a viscous force-field (NV, EV), this difference was not significant. These two conditions were also not significantly different from the detuning conditions with the left hand in a viscous force-field. This finding points to a handedness effect when the left hand is in a viscous force-field, which magnifies a more general effect of an increase in mean relative phase error due to detuning with one hand in a viscous force-field.

Planned comparisons with Tukey's HSD post-hoc tests were used to identify the means that were significantly different for the coordination  $\times$  force-field interaction. First, the differences between in-phase and anti-phase coordination modes were compared for each force-field condition (Figure 7A). In general,  $\phi$  was smaller for in-phase coordination than anti-phase coordination, as is predicted by the HKB model. The matched conditions (NN, EE,  $p < 0.05$ ) showed stereotypical HKB results with in-phase showing smaller values of  $\Delta\phi$  than anti-phase, but this difference was not significant for

the matched VV condition. The results of the mismatched force-field conditions were not as clear. The mismatched conditions where one hand was in an elastic force-field and the other hand was in a viscous force-field showed the similar results to the matched force-field conditions, where in-phase  $\Delta\phi$  was less than anti-phase  $\Delta\phi$  (EV, VE,  $p < 0.05$ ). The mismatched conditions where one hand was not in a force-field produced opposite results to what is expected from the HKB model. Two conditions (NE and VN) showed much smaller differences in  $\phi$  between in-phase and anti-phase coordination mode, and the other two conditions (NV, EN) showed that the anti-phase condition had smaller error than the in-phase condition, for NV this difference was significant ( $p < 0.05$ ).

Next, the differences between force-field conditions within a particular coordination mode were considered. Please note that only related conditions were compared. All of the matched conditions were compared. For the mismatched conditions, each condition was compared to four other force-field conditions: the two matched conditions that comprise the mismatched condition, the mirror condition (where each hand is in the opposite force-field), and the mismatched condition where the force-field of the hand in question was kept constant, and the other hand's force-field varied. For example, the condition EN was compared to the two matched conditions EE and NN, the mirror condition of NE, and the mismatched condition EV, where the hand that was in the null condition was then placed in the viscous condition.

For all the matched conditions (NN, EE and VV), none of the conditions had significantly different  $\phi$  measurements for both in-phase and anti-phase coordination modes, as tested by Tukey's HSD.

Next, the differences between the matched conditions and the mismatched conditions were checked for significant differences. The trials where one hand was not in a force-field were compared to the no force-field condition. The results are summarized in Figure 7B and 7C. The in-phase trials showed that the two conditions where one hand was placed in a viscous force-field, and the condition where the left hand was placed in an elastic force-field, resulted in significantly greater values of  $\phi$  from the no force-field condition (NV, VN, and EN,  $p < 0.05$ ); whereas the condition where the right hand was placed in an elastic force-field (NE) was not. In the anti-phase trials only one condition produced significantly higher values of  $\phi$  from the matched condition (VN,  $p < 0.05$ ), and the other three conditions were not significantly different.

Next, means comparisons were performed upon the conditions with at least one hand in an elastic force-field. For the in-phase coordination mode, of the two conditions where one hand was not placed in a force-field, the left hand in an elastic force-field (EN) had higher  $\phi$  values compared to the right hand (NE) in the elastic force-field, but not significantly so. The NE condition did not show significant differences from the no force-field and elastic force-field matched conditions, but the EN condition produced significantly more error than both matched conditions (NN, EE,  $p < 0.05$ ). The EN condition was also not significantly different from its counterpart, EV; however, NE

produced significantly less error than VE ( $p < 0.05$ ). The EV condition was not significantly different from the mirror condition, VE, and the matched condition, EE, but was significantly less accurate than VV ( $p < 0.05$ ); however, the VE condition produced larger  $\phi$  values than both matched conditions (EE, VV,  $p < 0.05$ ). For the anti-phase coordination mode, the two conditions where one hand was placed in an elastic force-field (EN, NE) produced approximately the same values of  $\phi$ . The two conditions were also not significantly different from the matched no force-field and elastic force-field conditions. When the other hand was placed in a viscous condition, the  $\phi$  errors were much larger. EN and NE produced significantly less error than their viscous counterparts EV and VE, respectively ( $p < 0.05$ ). Both EV and VE conditions had larger errors than the matched conditions (EE and VV,  $p < 0.05$ ), even though EV had smaller error than the mirror condition VE ( $p < 0.05$ ).

The means comparisons were performed between conditions where at least one hand was placed in a viscous force-field. Please note that some of the comparisons have been reported in the previous paragraphs, and will not be reviewed again. During in-phase coordination, the mismatched conditions with one hand in a viscous force-field and the other hand not in a force-field (VN and NV) both produced significantly larger  $\phi$  values than the matched viscous force-field condition ( $p < 0.05$ ). As well, these two conditions were not significantly different from each other. These two conditions also produced larger  $\phi$  values than their corresponding conditions with the other hand in an elastic force-field, but only the difference between NV and EV reached significance ( $p < 0.05$ ). In the anti-phase condition, a handedness effect can be seen. When the right hand

was in a viscous force field and the left hand was not in a force-field, there was no significant difference to  $\phi$  values then when both hands were in the matched viscous force-field condition. There was a larger difference between NV and EV, which reached significance ( $p < 0.05$ ). On the other hand, there was a significant difference between  $\phi$  values for conditions VN and VV ( $p < 0.05$ ) and  $\phi$  values for NV were significantly smaller than VN ( $p < 0.05$ ). The error was even greater when the right hand was in an elastic force-field (VE), but the difference between VN and VE still reached significance ( $p < 0.05$ ).

#### 4.3.2 Relative Phase Standard Deviation ( $SD\phi$ )

The results of the relative phase standard deviation, 2 Coordination mode  $\times$  9 Force-field conditions ANOVA, showed that the main effect of coordination mode was significant ( $F(1,11) = 17.391, p = 0.002, \eta^2 = 0.613$ ). In-phase coordination was significantly better (meaning  $SD\phi$  was lower) than anti-phase coordination ( $p = 0.002$ ), as predicted by the HKB model. Sphericity was violated for the force-field factor, but was not significant with or without sphericity correction ( $F(8, 88) = 1.452, p = 0.186$ , not corrected,  $\eta^2 = 0.117$ ). The interaction between coordination mode and force-field was significant ( $F(8, 88) = 5.894, p = 0.000, \eta^2 = 0.349$ ).

Post-hoc pair-wise comparisons were performed on the interaction using Tukey's HSD. Following the same format as above, first the differences between in-phase and anti-phase coordination mode for each force-field condition was examined (summarized in Figure 9A). Significant differences in coordination stability were seen for all

conditions that included a viscous damping force-field (NV, VN, EV, VE, VV,  $p < 0.05$ ). The matched elastic force-field condition also displayed significantly more stable coordination during the in-phase coordination compared to anti-phase coordination (EE,  $p < 0.05$ ). The matched no force-field condition, and the mismatched conditions with no force-field and elastic force-field (NE and EN) did not show significant differences between in-phase and anti-phase coordination mode, although the in-phase coordination mode was more stable.

During in-phase coordination the matched no force-field condition was not significantly more or less stable than the matched elastic force-field conditions. The matched viscous force-field condition was significantly more stable than the matched no force-field and elastic force-field condition ( $p < 0.05$ ). In other words, the matched viscous condition was the most stable, the matched no force-field condition had medium stability, and the elastic condition was the least stable. During anti-phase coordination, the no force-field condition was significantly more stable than the EE and VV conditions ( $p < 0.05$ ). The difference between the matched elastic and viscous conditions was not significant. During anti-phase coordination, the no force-field condition was the most stable, the elastic condition exhibited medium stability and the viscous condition was least stable.

Next, pair-wise comparisons were completed on the mismatched conditions. First, the mismatched conditions where one hand was not in a force-field were studied. During in-phase coordination the stability was not noticeably different between the

matched no force-field condition (NN) and all the mismatched conditions with one hand not in a force-field (NE, EN, NV and VN). During anti-phase coordination, again there was no discernible difference in stability between the matched no force-field condition (NN) and the conditions where one hand was in an elastic force-field (NE and NE); however, the conditions where one hand was in a viscous force-field (VN, NV) were significantly worse ( $p < 0.05$ ).

Subsequently, mismatched conditions where one hand was placed in an elastic condition were compared and no significant pair-wise differences were found. As reported above, during in-phase coordination, there was very little difference in stability between the mismatched conditions EN and NE, and the matched no force-field condition. There was also no difference between the two mismatched elastic condition (EN and NE), and between the mismatched conditions and the matched elastic force-field condition. The mismatched conditions with one hand not in a force-field condition, EN and NE, were less stable than their counterparts with one hand in a viscous force-field, EV and VE, but not significantly so. The mismatched conditions EV and VE did not show significant differences in stability from each other. Both were slightly, but not significantly, more stable than the matched elastic condition, but less significantly stable than the matched viscous condition (EV, VE,  $p < 0.05$ ). During the anti-phase coordination mode, the mismatched conditions EN and NE did not demonstrate significantly different stability from each other. These two conditions, EN and NE, were both more stable than the matched elastic force-field condition (EE,  $p < 0.05$ ) and the corresponding mismatched condition with one hand in a viscous force-field (EV, VE,



respectively,  $p < 0.05$ ). Similarly, the mismatched elastic and viscous conditions, EV and VE, did not exhibit differential stability from each other, nor the matched elastic and matched viscous conditions.

Finally, the mismatched conditions with one hand placed in a viscous force-field were examined. During in-phase coordination, the matched viscous condition was significantly more stable than the mismatched conditions with one hand not in a force-field (VN, NV,  $p < 0.05$ ). The stability of the two no force-field mismatched condition, NV and VN, were not significantly different from each other. There also was no significant difference in stability between NV and VN and their respective elastic mismatched counterparts EV and VE. The stability between all the viscous conditions (VV, NV, VN, EV and VE) during anti-phase coordination showed no differences.

In conclusion, if one hand was in a viscous force-field it didn't matter whether the other hand was in an elastic force-field, no force-field or in a matched viscous force-field, the coordination stability was equally affected. This suggested that effector damping had a larger effect on coordination stability, especially in the anti-phase coordination mode, than effector stiffness.

## 5 Discussion

### 5.1 Discussion of Major Findings

Our results show that the force-fields used in this experiment influenced coordination stability. Movement frequency was also a major factor in this coordination paradigm. This experiment was designed to examine the steady-state system coordination dynamics, thus any trial that showed transitional behaviour was excluded. The 2 Hz movement data was not presented in this study because many trials showed phase transitions and this made the data unreliable. The increased number of phase transitions maintains that coordination becomes unstable with increases in movement frequency.

#### 5.1.1 Movement Kinematics

As stated in the introduction, movement amplitude is not the sole determinant of coordination stability, but it does factor into stability of bimanual coordination (Peper et al. 2004; Post et al. 2000). There were visual targets to define approximate movements amplitudes, but participants were told that these were guidelines, and that movement amplitude was not strictly enforced; therefore it was free, within limits, to vary. Historically when movement amplitude is free to vary, decreases in movement amplitude are seen when coordination becomes less stable. Conversely, smaller amplitude movements could indicate less stable movements.

Movement amplitude was decreased during anti-phase movements compared to in-phase movements, supporting the idea that smaller movements are seen during less stable

coordination. Applying a force-field to the hands decreased movement amplitude, but the decrease in movement amplitude was much larger for the velocity dependent force. Obviously with a resistive force, movement amplitude will tend to decrease due to the increasing force required to move the finger at the desired tempo. This could also suggest that velocity dependent forces decrease the stability of the coordination.

The peak force results mirror the movement amplitude results. There were no significant differences between the peak force magnitudes between elastic and viscous conditions. In-phase movements created higher forces than anti-phase movements. This means that in elastic force-fields that movement amplitude was larger during in-phase movements compared to anti-phase movements, and in viscous force-fields that movement velocity was higher during in-phase movements compared to anti-phase movements. It can also be inferred that higher forces were produced during the more stable coordination patterns.

The peak forces generated by the right and left hands during in-phase movements were very similar. Although the forces produced by both hands were reduced in the anti-phase condition, the left hand force difference was larger than the right hand force difference. As all the subjects were right hand dominant, this reduction in force is similar to the non-dominant hand trajectory deformations that precede a phase transition (Kennerley et al.2002), and suggest that coordination instability may be caused by the non-dominant hand's inability to produce the same magnitude of force, given the same level of effort, as the dominant hand (Carroll et al. 2001). More specifically, from the

hand × movement type interaction, it's clear that the left hand extensors were producing less force than the right hand extensors, especially in a viscous force environment. It is known from work by Carroll et al. (2001), that the strength of a muscle, and the level of neural drive that is attributed to a coordination task, will influence the stability of said task. Therefore, the decreased stability, especially during anti-phase movements in a viscous environment, seems to stem from the extensor muscles of the left forearm being weaker than the right extensors. Unfortunately, this cannot be confirmed, as no measurements of participant's forearm muscle strength were taken during testing.

#### 5.1.2 Coordination Accuracy

Mean relative phase error reflects the accuracy of the coordination pattern produced. Coordination, on average, was more accurate during in-phase movements compared to anti-phase movements, and when the hands were in similar force-field environments compared to when they were in two different force-field environments. This is unsurprising from a dynamic system point of view because when the hands are in similar environments, there should be very little differences between the two oscillators, and any  $\Delta\phi$  could be attributed to handedness or attentional effects (Amazeen et al. 1997; Amazeen et al. 1998; Donchin et al. 1999; Peper et al. 2004). This also holds true from a more neurophysiological point of view, where if both hands are in a similar environment, then any shifts in timing onset of EMG, or rate of force production would be the same for both hands, and thus should not interfere with the accuracy of coordination.

When the mean relative phase absolute error was examined with the separate nine force-field conditions, the effect of coordination mode was no longer significant, but the main effect of force-field and the interaction between force-field and coordination mode was significant.

Having one hand in an elastic force-field and the other hand in a null force-field did not significantly increase or decrease the errors produced during coordination. Although the in-phase matched conditions did show less error, the accuracy of both in-phase and anti-phase coordination modes for one hand in an elastic environment, were of similar value to the anti-phase matched conditions. It is known that elastic forces applied to a limb during a coordinative task delays the onset of EMG (Baldissera & Cavallari 2001; Mackey et al. 2002), but it appears that changes to the timing of the onset of EMG activity to one limb did not affect the accuracy of the coordinative task between homologous limbs.

Having one hand in a viscous force environment decreased coordination accuracy, especially when the left hand was in the viscous force-field. There are several different factors that could have contributed to these results. First, the general decrease of coordination accuracy was only seen when one hand was placed in the viscous environment. Previous research has shown that movements executed with a velocity dependent load will produce a larger rate of force production (Mackey et al. 2002). From the results of this study, it seems that coordination accuracy was decreased when the hands had to create two different rates of force production. Coordination accuracy was

even worse when the left hand was in the viscous environment, compared to when the right hand was in the viscous environment. There are two possible explanations. First, that since all the subjects were right hand dominant, their attention could have been focused upon their right hand (Amazeen et al. 1997; Amazeen et al. 1998; Donchin et al. 1999; Peper et al. 2004). When the hand was in a viscous force environment, there was extra emphasis placed upon achieving the proper phase relationship; whereas when the left hand was in the viscous force-field the attention was still placed upon the right hand, and subjects were less aware if the left hand lagged and created larger relative phase errors. Secondly, as discussed above, the left hand extensors typically produced less force than the right hand extensors in a viscous environment, and the larger relative phase errors could be attributed to the fact that the left hand was not strong enough to create the desired phase relationship.

Considering the three interaction of mean relative phase absolute error, some of the results were not clear, and again, had several factors that could have determined coordination accuracy. For the matched conditions, in-phase coordination was always more accurate than anti-phase coordination, which is predicted for homologous limb movements by the HKB model. The results of the mismatched conditions were more variable. The conditions NE and VN had similar mean relative phase error results for both in-phase and anti-phase; whereas for EN and NV the anti-phase coordination pattern was more accurate than in-phase coordination. Anti-phase coordination exhibited smaller  $\Delta\phi$  when the hand was loaded (inertial and elastic) during coordination of the ipsilateral hand and foot (Baldissera et al. 1991; Baldissera & Cavallari 2001). The researchers

concluded that anti-phase coordination may be more accurate (but not more stable) because of a greater reliance on sensory feedback and cognitive resources to maintain the more difficult coordination mode. On the other hand, in-phase coordination relies more heavily on the timing of feedforward efferent motor commands to homologous muscles, than afferent feedback; therefore is less accurate when a load is placed on one of the effectors.

A second factor that could have influenced coordination accuracy was the interaction of muscular and spatial constraints. The task was organized such that muscular and spatial constraints were in conflict. In-phase movements were defined as simultaneous activation of homologous muscles, but in extrinsic space, the movements were anti-phase. The movements where there was alternate activation of homologous muscles were defined as anti-phase, but were spatially in-phase. Park et al. (2001) showed that when the principle of homologous muscle coupling is in conflict with principle of isodirectional coupling, the accuracy of the relative phase relationship is determined by the spatial constraints. Obviously, this did not hold true for all of the conditions in this experiment, but could be a contributing factor to the mean relative phase errors that were observed in the mismatched conditions where the anti-phase coordination mode was just as or more accurate than the in-phase coordination mode.

### 5.1.3 **Coordination Stability**

Coordination mode and movement frequency had a greater influence on coordination stability than the force-field environment. As mentioned above, the 2 Hz movement data could not be used due to phase transitions induced by unstable

coordinative states. It is clear that movement frequency had a significant impact upon coordination stability.

Anti-phase coordination produced significantly higher values of  $SD\phi$ , meaning that coordination stability was less. This was true for every force-field condition. The differences in  $SD\phi$  between coordination modes varied between the force-field conditions, leading to a significant coordination mode by force-field interaction. Conditions NN, EN and NE did not produce in-phase  $SD\phi$  values that were significantly different from their anti-phase  $SD\phi$  values. The matched elastic condition (EE) did show a significant difference between in-phase and anti-phase, but this difference was less than the viscous conditions. Similar to the mean relative phase error values, it seems that elastic force-field conditions do not exert a strong influence on coordination accuracy or stability compared to the null condition. All the conditions with a viscous force environment (VV, NV, VN, EV, VE) produced much larger values of  $SD\phi$  during anti-phase coordination compared to in-phase coordination.

Interpretation of the coordination stability results was easier than for the accuracy of coordination. Again there were several factors that could have influenced coordination stability. First, according to the HKB model, anti-phase coordination should be less stable than in-phase coordination (Amazeen et al. 1998; Haken et al. 1985). Second, muscle strength affects coordination stability, as well as coordination accuracy. During the viscous conditions, the extensors had to work against resistance, which they did not have to do in the null and elastic conditions. The increased effort to extend the finger



against resistance could have increased the neural drive required, and thus destabilized coordination (Mackey et al. 2002). If resistance to the extensors had been the only cause of coordination instability, there should have been a corresponding decrease in stability of the in-phase coordination mode while the fingers were in a viscous force environment. Third, it has been shown that multisensory feedback is more important for control of anti-phase coordination mode than in-phase coordination (Baldissera et al. 1991; Temprado et al. 2003). Previous research has shown that proprioceptive information from muscle spindles about movement velocity is important for maintenance of difficult coordination modes, error correction, and learning of new coordination modes (Atchy-Dalama et al. 2005; Peper & Carson 1999; Spencer et al. 2006). Therefore it is possible that velocity dependent resistance creates a mismatch between the expected afferent information given the efferent commands and actual afferent feedback received, which in turn disrupts coordination, specifically of anti-phase movements. It is also possible that with more trials participants could have learnt to compensate for the viscous force and the stability of coordination would have improved. Finally, although participants did not seem to have trouble coordinating with an elastic load, which influences the timing of EMG onset (Baldissera & Cavallari 2001; Mackey et al. 2002), the coordination stability in a viscous force-field was much worse. The stronger the viscous load, the higher the rate of force required to compensate for the load. Therefore, from the results, it seems that coordinating movements with two different rates of force production creates unstable coordination.

## 5.2 General Discussion

### 5.2.1 Classical HKB Models

The first four hypotheses presented in Section 2 are all taken from the classical Haken-Kelso-Bunz (1985) model. In this model, the force-field environments would affect the component oscillators of the model, creating an eigenfrequency difference, which in turn produces a detuning effect. A pure detuning effect would create larger mean relative phase error values ( $\Delta\phi$ ) and relative phase standard deviation ( $SD\phi$ ) in the mismatched force-field conditions compared to the matched force-field conditions, and anti-phase coordination compared to in-phase coordination.

The hypotheses presented in Section 2 were proven true for the most part. In general, the mismatched force-field conditions produced higher levels of relative phase error and  $SD\phi$ , compared to the matched force-field conditions. This suggests that the force-fields did create an eigenfrequency difference between the finger-PHANToM systems.

Coordination accuracy did not produce consistent results across the mismatched conditions. There was a clear effect of hand on the accuracy of coordination, especially when the hand in question is in a viscous force environment. The effect of attention and handedness could have interacted with the detuning effect to confound the results. There wasn't a handedness effect upon the coordination stability. Therefore it is possible that when the right hand was placed in a force-field it decreased the lead it usually displays during bimanual coordination resulting in lower mean relative phase absolute error;

whereas when the left hand was placed in a force-field, the lag it usually displays during bimanual coordination was increased, resulting in higher mean relative phase absolute error. Therefore the coordination accuracy was dependent upon the interaction of the  $\Delta\omega$  term and the  $d$  coefficient (Amazeen et al. 1997).

Conflict between the spatial and muscular task requirements could have affected the coordination accuracy. Park et al. (2001) showed that for a task with detuning, the attractor position ( $\Delta\phi$ ) was dependent upon spatial constraints, and the attractor strength ( $SD\phi$ ) was determined by muscular constraints. This effect was not robust during other coordination tasks (Temprado et al. 2003). It is possible that spatial constraints did affect coordination accuracy, by producing a more salient multimodal afferent error signal to estimate the error in the phasing relationship (see section 5.2.2). The HKB model does not capture these spatial and muscular interactions; therefore the model does not fully explain the coordination dynamics of this task (Park et al. 2001; Peper et al. 2004).

The muscle strength of the left hand probably influenced the coordination accuracy and stability as well. Unfortunately, the HKB model is phenomenological in nature, and there is no direct way to model the difference in strength between the forearms. The component oscillators of the HKB model do not directly represent the mechanical properties of the limbs, but are formulated based upon the kinematics, position and velocity trajectories, of the limbs. Therefore, in dynamics systems theory, the effect of the force-field upon coordination would not have a direct impact upon the

component oscillators, but would affect the oscillators abstractly by changing the trajectories of the coordinated limbs (Peper et al. 2004).

It has become clear in recent years that the HKB model is an excellent basic, but abstract, model of coordination, but cannot describe all the biomechanical and neurophysiological interactions that occur during bimanual coordination. The results reported above also cannot be explained solely by the classical HKB model, and other explanations, such as muscle strength and afferent feedback must be considered.

#### 5.2.2 **Biomechanical and Physiological Interpretations**

There are three important biomechanical and neurophysiological constraints that had possible influences upon coordination accuracy and stability in force-field environments. The timing and strength of efferent motor commands to compensate for the force-field loads, the strength of the forearm muscles used in the coordination task, and the use of afferent information for error correction, all influenced the results.

Previous research by Mackey et al. (2002), using a unimanual task with similar load forces as were used in this task, showed that elastic loads influenced the timing of EMG onset, and viscous loads influenced the rate of force production. Assuming for a moment that coordination is controlled purely in a feedforward manner (which it is not), then the force-field conditions provide very different challenges to coordination. The elastic force-field would require shifts in the relative timing of efferent commands; whereas the viscous force-field would require sending different strength motor commands simultaneously to achieve the required relative phase pattern. The elastic

force-field conditions were more accurate and stable than the viscous conditions which imply that producing a change in the relative timing of muscle activation is more easily accomplished by the central nervous system than producing two different rates of force production.

The neural drive required to produce force is influenced by muscle strength. Carroll et al. (2001) showed that increasing muscle strength stabilizes coordination. Due to the nature of the force-fields, the elastic force-field provided resistance to the flexor muscles, not the extensor muscles. On the other hand the viscous force-field produced resistance on both the flexor and extensor muscles. Extensor muscles are known to be weaker than flexor muscles (Carroll et al. 2001). Therefore conditions where resistance is placed on the weaker extensors will require increased neural drive to the muscle to complete the required movement. Increased neural drive will increase the cortical activation, which in turn increases the neural interference between hemispheres (Carson 2005). The crossed facilitation would be useful during simultaneous activation of homologous muscles, as the neural activation in both hemispheres will be mutually reinforced (Swinnen & Wenderoth 2004). In fact, this effect is suggested by the relatively stable in-phase movements in viscous force-fields, and the higher force exerted by the left hand extensor during in-phase movements in viscous force-fields. During anti-phase movements, where the activation of homologous muscles was in alternation, the neural interactions between hemispheres were a detriment to coordination stability. This was demonstrated by the marked decrease in the force exerted by the left hand extensor (which in right hand dominant subjects is most often weaker than the right hand

extensors) during anti-phase coordination, and the corresponding decrease in coordination stability during anti-phase movements in a viscous force-field.

Unfortunately, these conclusions can only be inferred, as neither EMG nor cortical imaging, such as fMRI, were recorded during the experimental task.

As stated previously, coordination is not simply a feedforward system, but also uses afferent feedback to control the relative phasing between the limbs. Multimodal sensory integration of perceived relative phase plays an important role in maintaining coordination stability. During more difficult coordination tasks, increased activation in S1 and S2 has been reported (Atachy-Dalama et al. 2005; Kelso et al. 2001; Peper & Carson 1999; Spencer et al. 2006; Wilson et al. 2003). It has been proposed that proprioceptive information about the relative velocity between the two limbs' movement trajectories may help control coordination. When only one finger is placed in a force-field, especially a velocity dependent force-field, there is a marked difference in the movement kinematics for a given level of force input compared to a no force-field condition. If the efferent motor commands to each limb are the same, then the limbs would have different trajectories, thereby creating a conflict between the sensory afferences from each limb. This error signal would then be used to correct the phasing relation between the two finger movements. This type of sensory information has been shown to be more important for anti-phase coordination (Baldissera et al. 1991) and difficult coordination tasks. Sensory consequences of movement are important for learning new coordination tasks (Atchy-Dalama et al. 2005). Given more practice in each force-field condition,

improvements on coordination accuracy and stability would probably have been observed.

### 5.2.3 Interlimb Coordination Model

From the conclusion drawn from the previous two sections, the classical Haken-Kelso-Bunz model could not explain the results presented. The current results would be modeled better using the two-tiered model of Beek et al. (2002), which, while still a phenomenological model, is less abstract than HKB (Peper et al. 2004). The ‘neural’ oscillators are coupled in the non-linear the same way the original oscillators were coupled. Previous research has shown that neural activity does exhibit the same phase transitions from anti-phase to in-phase as seen in limb movements (Bressler & Kelso 2001; Jirsa et al. 1998). The bidirectional coupling between the neural oscillators would model neural crosstalk and crossed facilitation or inhibition. The forcing signal sent to linearly damped oscillator, representing the ‘effector’, would be the efferent motor commands and feedback signal from the linear oscillator to the ‘neural’ oscillator would be the sensory afference error signal. Each ‘effector’ oscillator could be modeled upon the mechanical attributes of each limb, as a second-order linear oscillator, or a more physiological, biomechanical model (Peper et al. 2004; Peper, Nooji, van Soest 2004; Ridderikhoff et al. 2004). Therefore the forces applied to each finger by the PHANToM would change parameters of the effector oscillator, but would influence coordination in general by way of afferent feedback.

#### 5.2.4 Future Directions

This study was a first step towards understanding bimanual coordination in different force environments. These environments provide an important tool for investigation into how efferent and afferent neural signals (or feedforward and feedback control strategies), and neuromuscular constraints affect coordination accuracy and stability.

Further studies of this nature would benefit from EMG of the wrist flexors and extensors, similar to Mackey et al. (2002), Baldissera & Cavallari (2001), as well as muscle strength measurements, to be able to tease apart the muscular strength and neural compensation affects on coordination in the force-field environments. Since, these measurements were not taken during this experiment; it was difficult to conclude which constraints were responsible for the results, and inferences could only be made from previous research.

Since the 2 Hz movement coordination was not stable enough to analyze, it would be beneficial to perform a 'time to transition' protocol using the same forces while increasing the metronome frequency. This way the influence of movement frequency on the force-field coordination could be determined.

Lastly, modeling the results based upon Beek et al. (2002) two-tiered model proposed in section 5.2.3, could provide insights into the behavioural results reported here.



## 6 Conclusion

Performing bimanual coordination with the hands in different force field environments affected both the coordination accuracy and stability. When the fingers were being moved in the same force environments, coordination was more accurate and stable, compared to when the hands were placed in mismatched force environments. The effect of having one hand in a velocity dependent force-field produced larger mean relative phase absolute error than having one hand in a position dependent force-field. Similarly, when placed in a viscous force-field environment, coordination stability was reduced, especially during anti-phase coordination. There are several spatial, biomechanical and neuromuscular constraints that could have controlled coordination performance. The proposed mechanisms that influenced coordination included: the differences in neural compensation for the force-fields, where elastic loads shows later onset of EMG activity and viscous loads show a higher rate of force production; the strength of extensors muscles, and their ability to (not) overcome resistance and how that affects coordination; and sensory information used in error correction and how that could influence coordination.

## 7 References

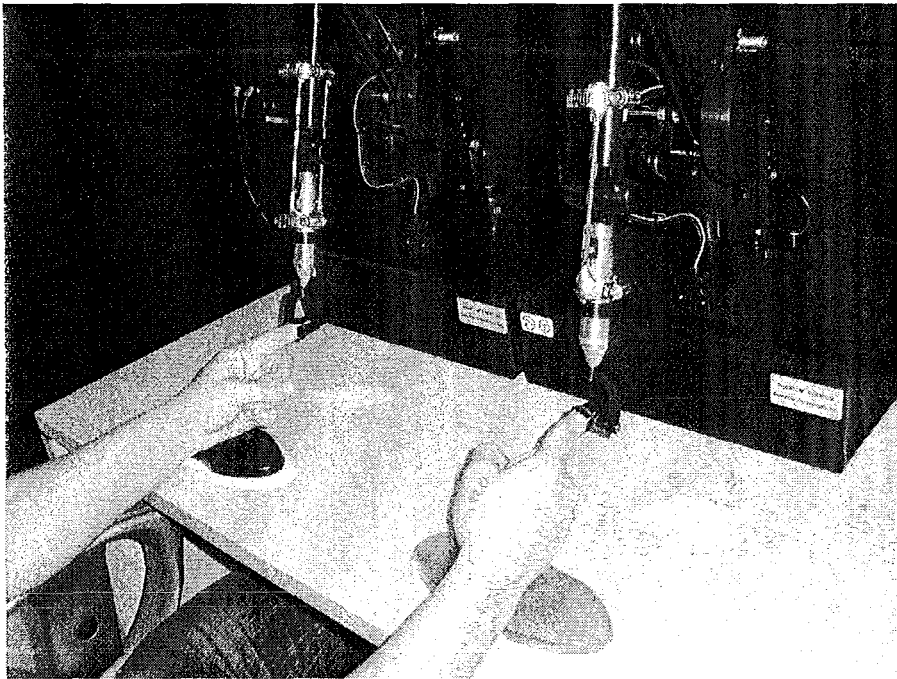
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**Figure 1: The experimental equipment and participant arm posture.**

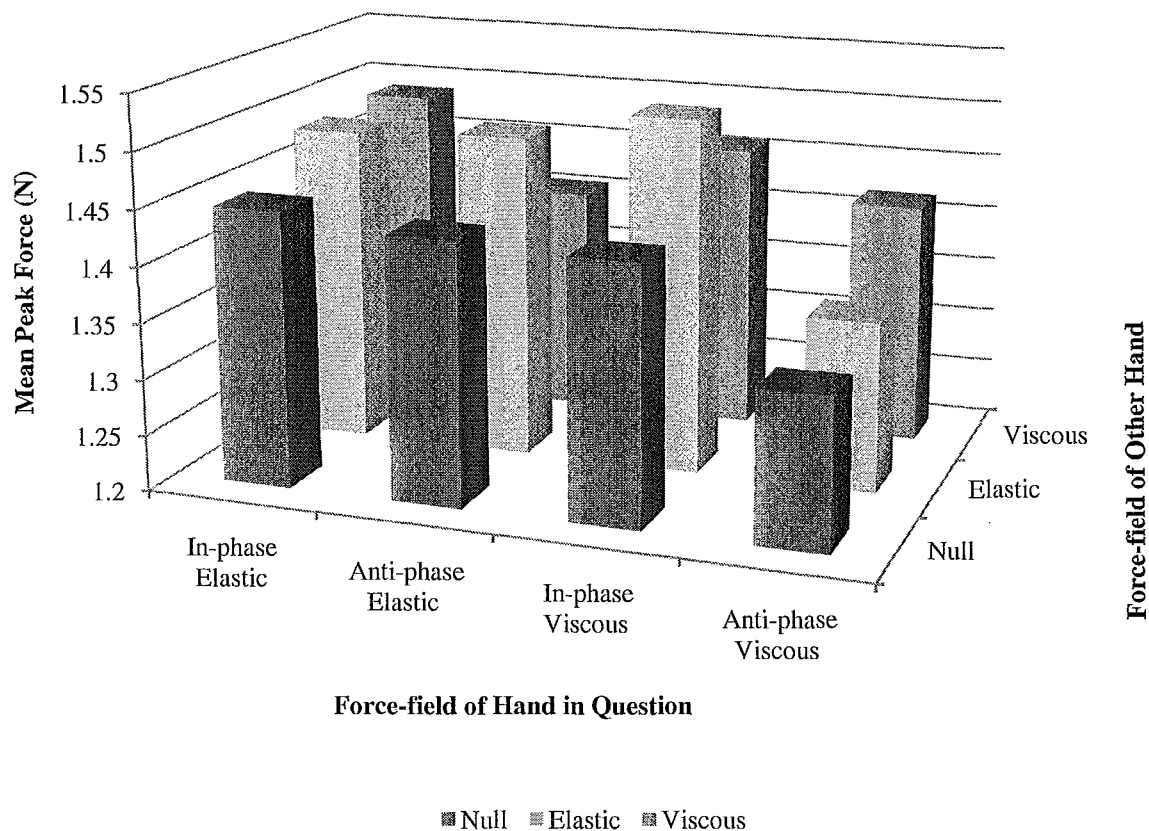


Figure 2: Coordination mode  $\times$  force-field interaction on forces produced during each condition ( $F(5, 55) = 2.856, p = 0.023, \eta^2 = 0.206$ ). Although there were no significant differences seen in post-hoc testing, the trend shows that during anti-phase coordination with only one hand in a viscous force-field, the force produced by that hand was much smaller. This suggests that movement speed was reduced, which could have led to larger errors in coordination and lower coordinative stability.



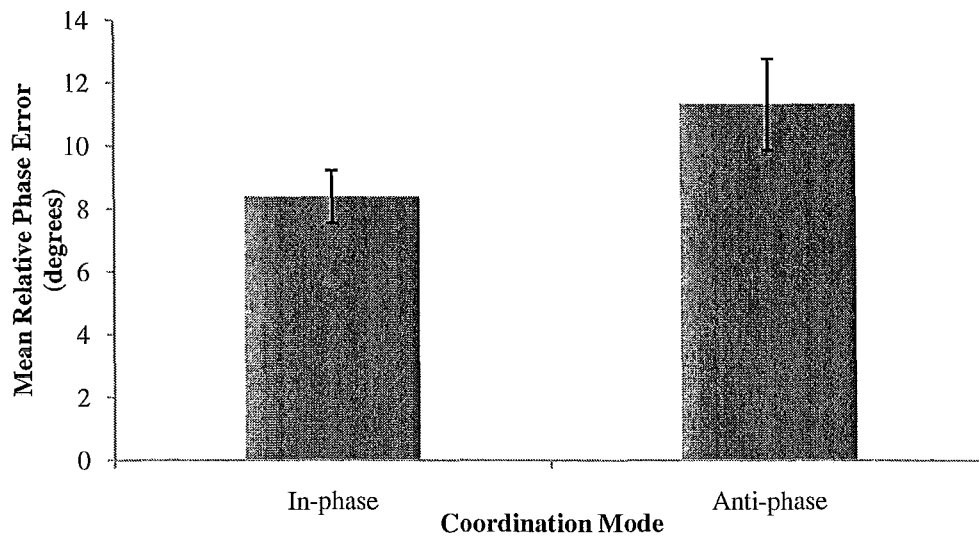
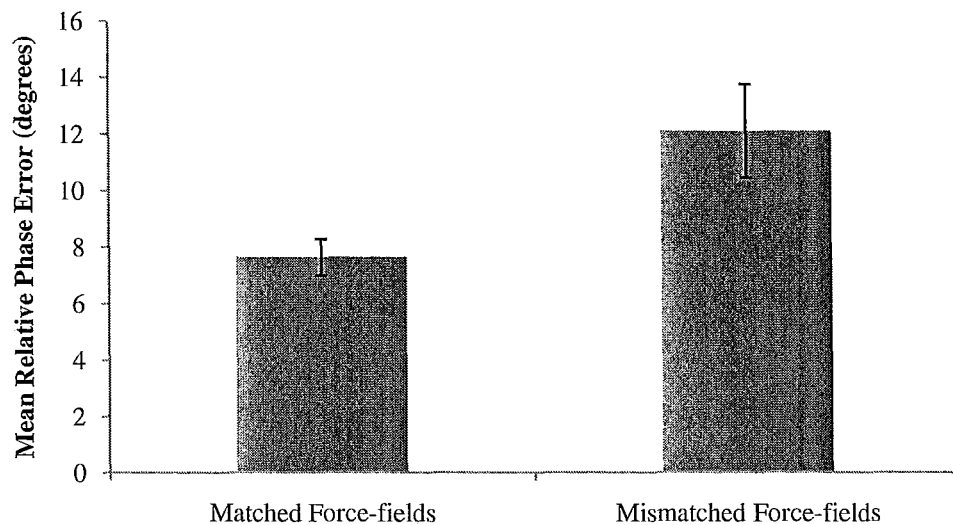
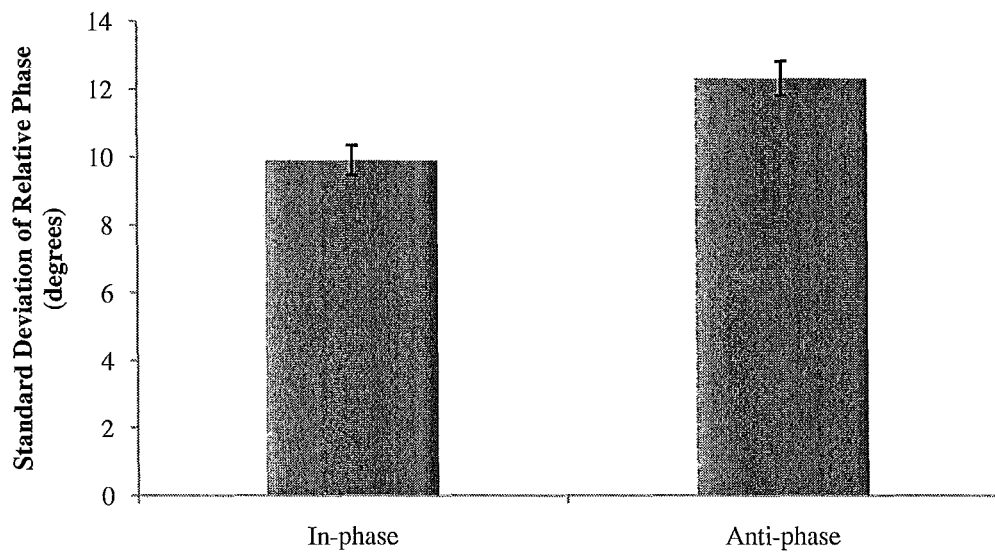


Figure 3: Main effect of coordination mode on mean relative phase error ( $\phi$ ). The error bars represent one standard error of the mean value. The in-phase coordination mode produced significantly less mean relative phase error than the anti-phase coordination mode ( $F(1, 11) = 5.855, p = 0.034, \eta^2 = 0.347$ ).



**Figure 4: Main effect of matched vs. mismatched force-field conditions on mean relative phase error ( $\phi$ ). The error bars represent one standard error of the mean value. The matched force-field condition produced significantly less error than the mismatched conditions ( $F(1, 11) = 29.441, p = 0.000, \eta^2 = 0.728$ ).**



**Figure 5: Main effect of coordination mode on the relative phase standard deviation ( $SD\phi$ ). The error bars represent one standard error of the mean. The in-phase coordination mode was significantly more stable than the anti-phase coordination mode ( $F(1, 11) = 17.946, p = 0.001, \eta^2 = 0.620$ ).**

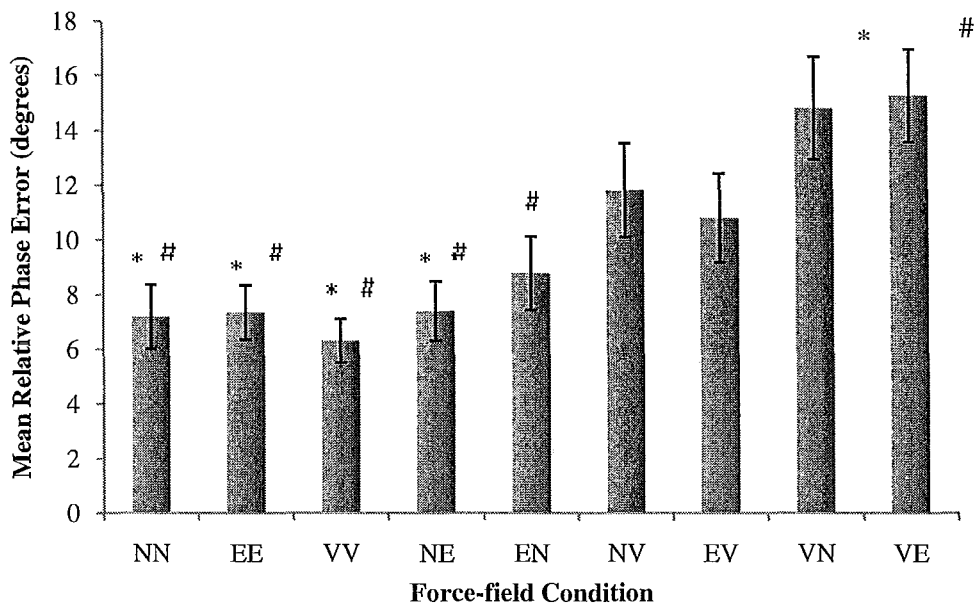
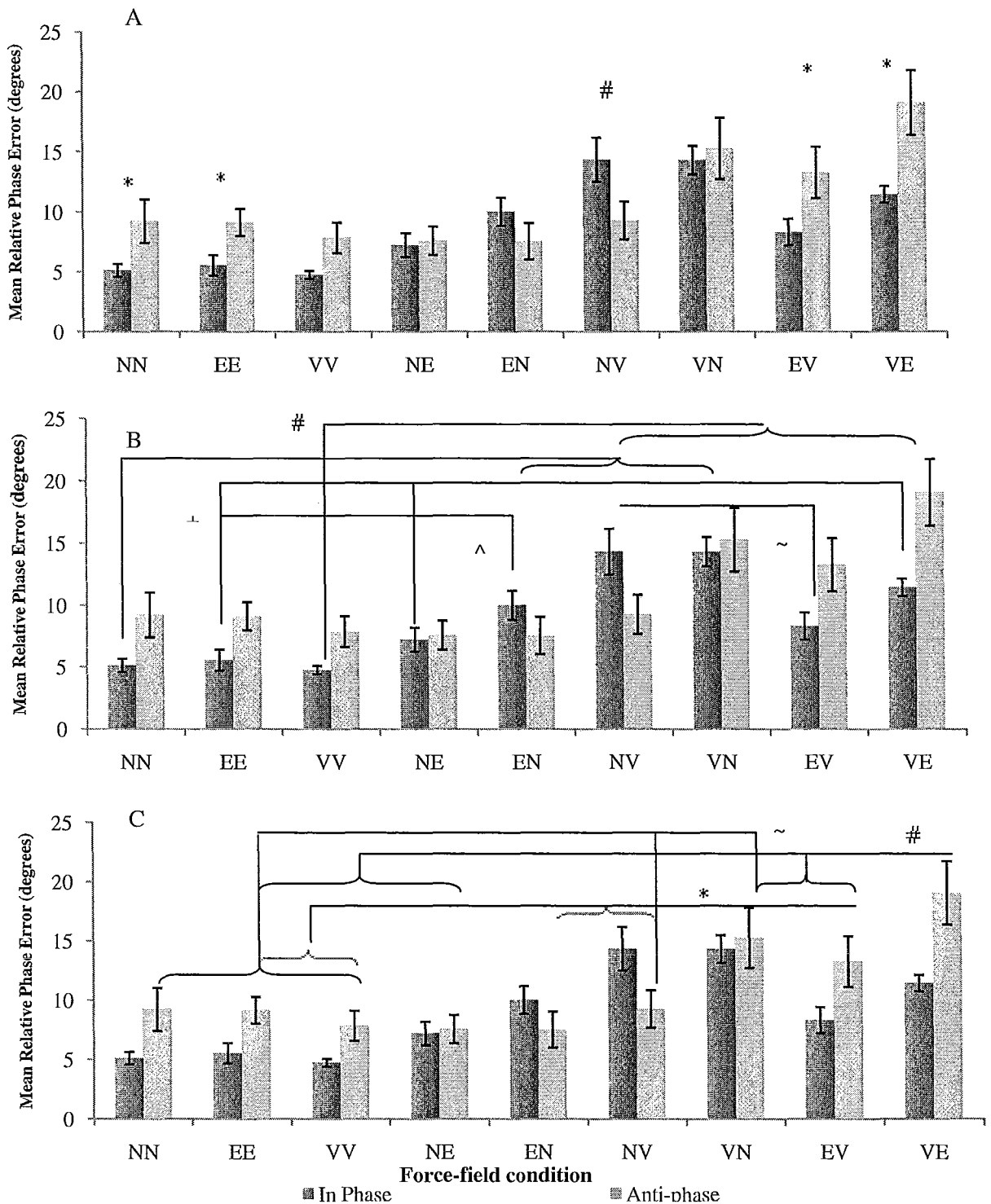
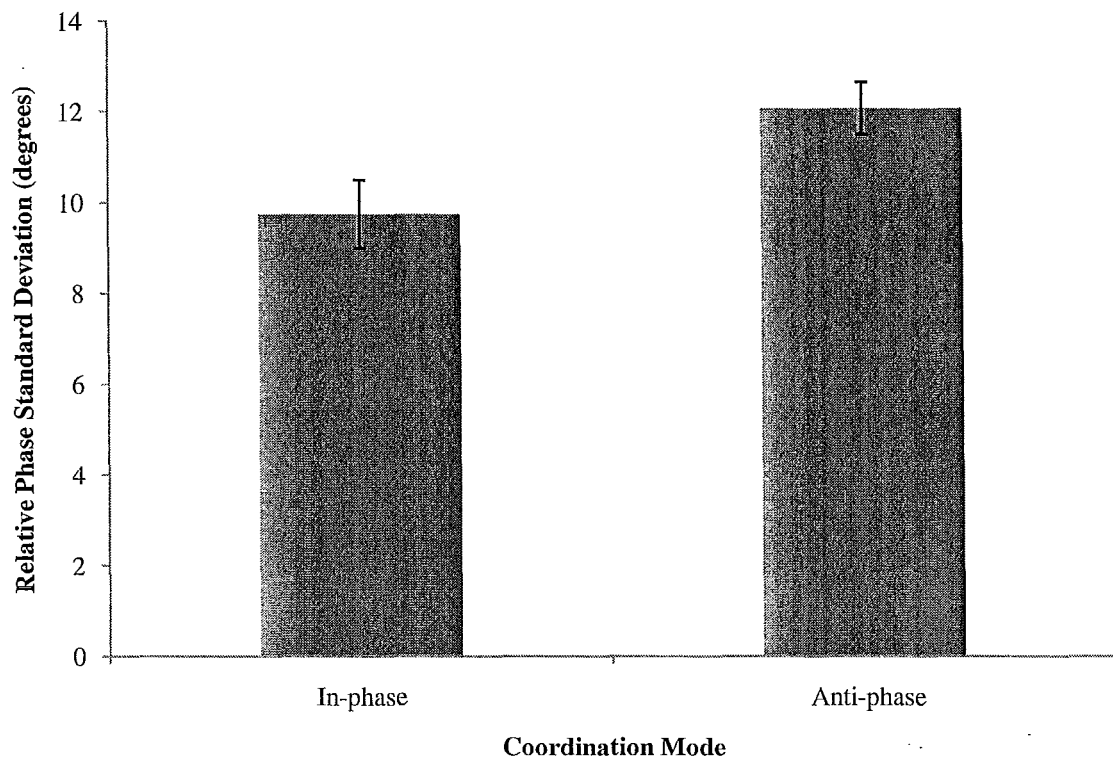


Figure 6: Main effect of Force-field condition ( $F(1, 11) = 10.960, p = 0.007, \eta^2 = 0.499$ , *Huynh-Fleldt corrected*,  $\epsilon = 0.442$ ) on Mean Relative Phase Error ( $\phi$ ). The error bars represent one standard error of the mean. An asterisk denotes a significant difference between the left hand viscous, right hand null force-field (VN) condition and four other conditions ( $p < 0.05$ ). A pound sign denotes a significant difference between the left hand viscous, right hand elastic force-field (VE) condition and five other conditions ( $p < 0.05$ ).

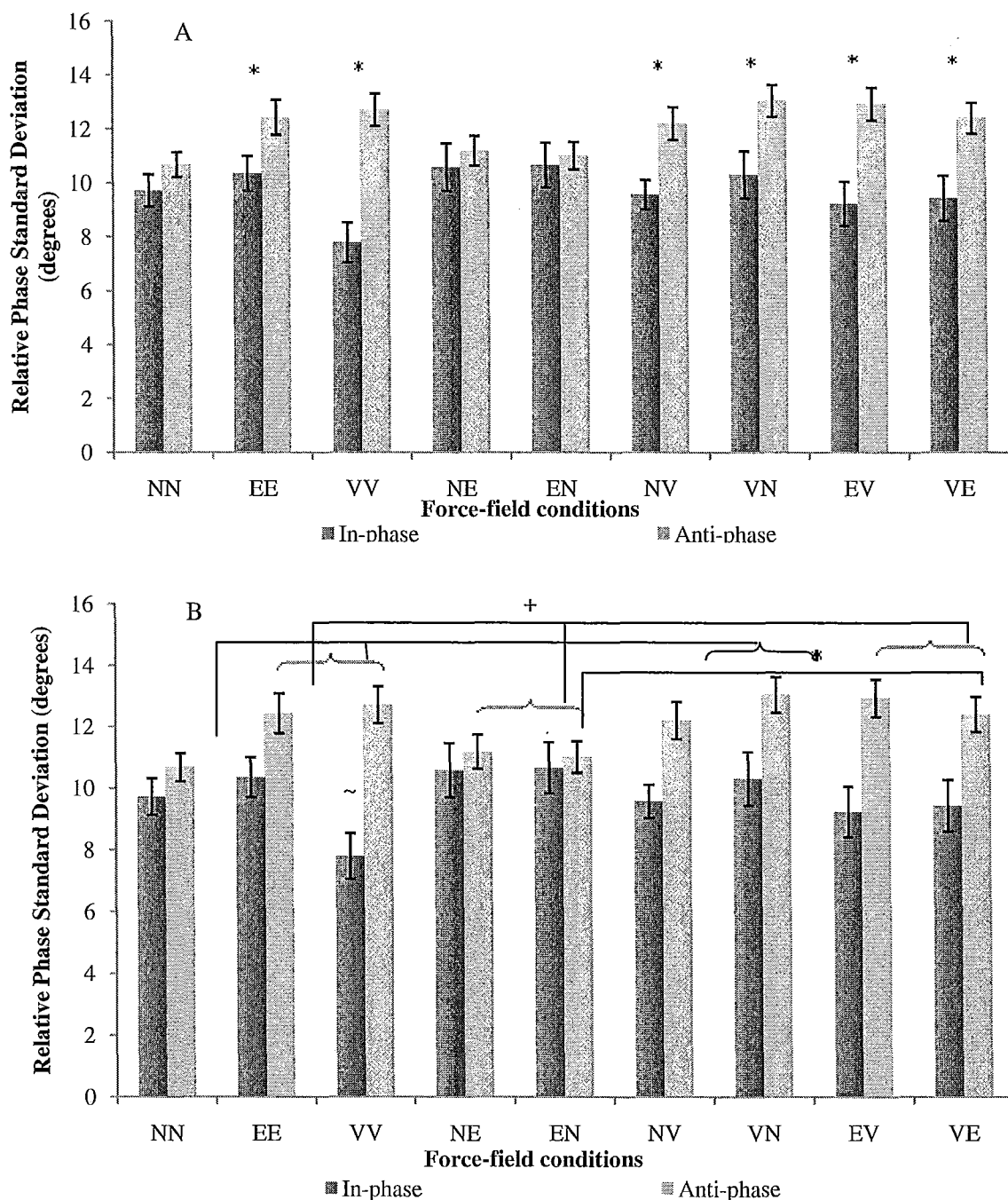


**Figure 7:** The interaction effect between Force-field condition and Coordination Mode ( $F(8, 88) = 5.086, p = 0.000, \eta^2 = 0.316$ ) on mean Relative Phase Error ( $\phi$ ). All post-hoc pair-wise significant difference tested with Tukey's HSD ( $p < 0.05$ ) A: The asterisk denotes the conditions where in-phase  $\phi$  was less than anti-phase  $\phi$ , and the pound sign denotes the conditions where anti-phase  $\phi$  was less than in-phase  $\phi$ . B (in-phase coordination comparisons): The pound sign signifies the significant differences between the VV condition and the VN, NV, VE and EV conditions. The asterisk

signifies the significant difference between NN and the EN, NV and VN conditions. The plus sign denotes the difference between VE and the conditions NE and EE. The circumflex denotes the difference between EN and EE. The tilde symbol represents the difference between EV and NV. C (anti-phase coordination comparisons): The VN condition produced significantly more error than NV, NN and VV as revealed by the tilde. The VE condition produced significantly larger error values than EE, VV, NE, VN and EV (pound sign). EV produced larger errors than NV, EN, EE and VV, as shown by the asterisk sign.



**Figure 8:** The main effect of Coordination Mode on Relative Phase Standard Deviation ( $SD\phi$ ) for the 2 Coordination Mode  $\times$  9 Force-field Conditions ANOVA. The in-phase coordination trials were significantly more stable than the anti-phase coordination trials ( $F(1, 11) = 17.391, p = 0.002, \eta^2 = 0.613$ ).



**Figure 9: Relative Phase Standard Deviation ( $SD\phi$ ) interaction between coordination mode and force-field condition ( $F(8, 88) = 5.894, p = 0.000, \eta^2 = 0.349$ ). A: Shows the results of post-hoc tests conducted on differences between in-phase and anti-phase coordination modes for each force-field condition, significance set at  $p < 0.05$  (as indicated by an asterisk). B: shows the differences within a coordination mode. For in-phase coordination, VV was significantly more stable than all other conditions (tilde), and VE was more stable than EN (asterisk). For the anti-phase coordination, NN was significantly more stable than EE, VV, VN and NV (pound sign); the conditions NE and EN were more stable than EE and their mismatched viscous counterparts, VE and EV respectively (plus sign).**



## Appendix A1:

*Edinburgh Handedness Inventory*

Please indicate your preferences in the use of hands in the following activities *by putting a check in the appropriate column*. Where the preference is so strong that you would never try to use the other hand, unless absolutely forced to, *put 2 checks*. If in any case you are really indifferent, *put a check in both columns*.

Some of the activities listed below require the use of both hands. In these cases, the part of the task, or object, for which hand preference is wanted is indicated in parentheses.

Please try and answer all of the questions, and only leave a blank if you have no experience at all with the object or task.

	Left	Right
1. Writing	┌ ┌	┌ ┌
2. Drawing	┌ ┌	┌ ┌
3. Throwing	┌ ┌	┌ ┌
4. Scissors	┌ ┌	┌ ┌
5. Toothbrush	┌ ┌	┌ ┌
6. Knife (without fork)	┌ ┌	┌ ┌
7. Spoon	┌ ┌	┌ ┌
8. Broom (upper hand)	┌ ┌	┌ ┌
9. Striking Match (match)	┌ ┌	┌ ┌
10. Opening box (lid)	┌ ┌	┌ ┌
<b><u>TOTAL(count checks in both columns)</u></b>		

Difference	Cumulative TOTAL	Result

**Scoring:**

Add up the number of checks in the “Left” and “Right” columns and enter in the “TOTAL” row for each column. Add the left total and the right total and enter in the “Cumulative TOTAL” cell. Subtract the left total from the right total and enter in the “Difference” cell. Divide the “Difference” cell by the “Cumulative TOTAL” cell (round to 2 digits if necessary) and multiply by 100; enter the result in the “Result” cell.

**Interpretation (based on Result):**

- below -40 = left-handed
- between -40 and +40 = ambidextrous
- above +40 = right-handed

Edinburgh handedness inventory (2006). York University. [http://www.cse.yorku.ca/course\\_archive/2006-07/W/4441/EdinburghInventory.html](http://www.cse.yorku.ca/course_archive/2006-07/W/4441/EdinburghInventory.html). Retrieved: Thursday November 6, 2008 (3:00pm).

## Appendix A2:

**INFORMED CONSENT TO PARTICIPATE IN A STUDY ENTITLED:**

*Influence of external mechanical perturbations on bimanual coordination and timing*

I, \_\_\_\_\_, consent to participate in a research study entitled  
*Influence of external mechanical perturbations on bimanual coordination and timing.*

**Investigators:**

**Principal Investigator:** Ramesh Balasubramaniam,

Canada Research Chair in Sensorimotor Neuroscience

Department of Kinesiology

McMaster University

1280 Main St. West

L8S 4K1

**905-525-9140 x. 21208**

Student/Co-Investigator: Courtney Bridgewater

M.Sc. Student

Department of Kinesiology

McMaster University  
1280 Main St. West  
L8S 4K1  
**905-525-9140 x. 27390**

Funding Organization: N/A

**Purpose of the Study:**

The objective of the experiment is to examine the differences in spatial and temporal coordination using mechanical perturbations to a repetitive tapping task.

**Procedures Involved in the Research:**

Participation will require attending approximately 2.5 hours of testing over 1-2 sessions, in the Sensorimotor Neuroscience Laboratory (AB104, IWC). I will be asked to sit in front of two robots, and place my fingers within the thimbles attached to the robots. I will be asked to synchronize tapping my index finger to a metronome, then asked to try to continue moving my finger at the same frequency until the trial has completed. I will be asked to move my fingers together or in opposition to the beat. The robots will sometimes create forces in response to my movements. If I have further questions about the procedure of the experiment, I will ask the student investigator prior to beginning testing.

**Potential Harms, Risks or Discomforts:**

It is not likely that there will be any harms or discomforts associated with this study. I may experience some muscle fatigue or soreness in the hands or the forearms from the repeated tapping movements. If you feel any discomfort at any time, you can let the investigator(s) present know and are welcome to take a rest. You can take as many rest periods as needed throughout the experiment, and they can be of any duration needed.

**Potential Benefits:**

There will be no immediate benefit to me resulting from participation in the study. This study may help further our understanding of the neural mechanisms that control timing and coordination.

Participants can request a copy of any publications or formal reports that uses the data acquired from their participation. Please contact the student or principal investigator for further details.

**Payment or Reimbursement:**

I will not receive any compensation for my participation in this study.

**Confidentiality:**

Information obtained from the testing session(s) will be held in the strictest confidence and will not be used except for the purposes of research. I understand that my data will be coded in a way that ensures anonymity. All data will be associated with an alphabetic or numeric code only. I also understand that any published results will be presented with complete anonymity. Data will be pooled for analysis, and identifying documents will be kept separate from data. I understand that any personal data will be kept in a separate file and securely stored in a location accessible only by the principle investigator within his office in room 203 of the Ivor Wynne Centre. I understand that all experimental data will be saved on a PC or archived on CD, DVD or External Hard Drive and stored and accessible only by the researchers responsible for this study in our laboratory facility, room AB104 of the Ivor Wynne Centre.

**Withdrawal from the Study:**

I understand that my participation in this study is completely voluntary, and that I may withdraw from the study at any time for any reason (which does not need to be provided). In the event of my withdrawal, I understand that all information gathered will be destroyed and will not be used.

**Questions Concerning this Study:**

I understand that I may ask all my questions about this study and that they will be answered. These questions may be directed to Ramesh Balasubramaniam (905-525-9140 x. 21208), principle investigator or Courtney Bridgewater (905-525-9140 x. 27390), student investigator.

This study has been reviewed and approved by the McMaster Research Ethics Board. If I have concerns or questions about my rights as a participant or about the way the study is conducted, I may contact:

McMaster Research Ethics Board Secretariat

Telephone: (905) 525-9140 ext. 23142

c/o Office of Research Services

E-mail: [ethicsoffice@mcmaster.ca](mailto:ethicsoffice@mcmaster.ca)

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**Consent:**

I, \_\_\_\_\_, consent to participate in this study. My questions have been answered to my satisfaction. Two copies of this consent form have been signed and I have received one signed copy.

Appendix A3:  
Participant Instructions

- Please sit in the chair
- place your wrists on the supports comfortably, with your forearms in a neutral position where your palms face each other
- place your index finger in the thimbal attached to the phantom
- now move your fingers to the right and left pointing the thimbals at the goals provided
- when the trial starts you will hear a beep
  - some trials the beeps will be fast, other trials the beeps will be slow
- your goal is to either:
  - move your fingers between the targets such that they are closest together on the beep
  - move your fingers between the targets such that they both point to the right on the beep
- the beep will stop half way through the trial, please continue at the same pace that you were moving at with the beep
- continue moving until the end of the trial (the trial will end with a different tone or when the experimenter says stop)