MULTIFREQUENCY COORDINATION DYNAMICS

by

WINSTON D. BYBLOW

B.H.K. Human Kinetics, University of Windsor
Ontario, Canada, 1988

M.Sc. Kinesiology, Simon Fraser University
B.C. Canada, 1990

DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

in the School
of
KINESIOLOGY

SIMON FRASER UNIVERSITY
April, 1994

APPROVAL

NAME: Winston D. J. Byblow

DEGREE: Doctor of Philosophy

TITLE OF THESIS: MULTIFREQUENCY COORDINATION DYNAMICS

EXAMINING COMMITTEE:

Chair: Dr. G. Tibbits

Dr. D. Goodman
Co-Senior Supervisor

Dr. J. Dickinson
Co-Senior Supervisor

Dr. R. Marteniuk

Dr. H. Weinberg
Internal Examiner
Psychology, S.F.U.

Dr. M. Turvey
External Examiner
University of Connecticut
Center for the Ecological Study of Perception & Action

Date Approved: April 11, 1994

PARTIAL COPYRIGHT LICENSE

Title of Thesis/Project/Extended Essay

Multifrequency Coordination

Dynamics

Author:

(signature)

Winston Dean John Byblow

(name)

07/12/94

(date)

ABSTRACT

Human coordination was studied using paradigms of rhythmic movement. Four experiments were conducted. In Experiment 1, the intrinsic dynamics of bimanual coordination were examined under predefined hand and frequency assignments. Four subjects performed movements of rhythmic forearm pronation and supination. Performance asymmetries were confirmed between conditions of hand and frequency assignment. Phenomena regarded previously as a feature of attentional limitations were shown to be a feature of inherent (in)stability at the level of the collective variable, relative phase. Contrasting conditions in which the left hand versus the right hand adopted the dominant frequency in multifrequency relation, the "left-hand-fast" assignment demonstrated greater instability in measures of relative phase variability, time-to-transition, and phase attraction. The individual limbs did not differ with respect to variability of frequency, suggesting that asymmetries in multifrequency coordination were better reflected in the collective behaviour, rather than in differences at the component level. In Experiment 2, temporal variability in rhythmic movement was examined under the constraints of multifrequency coordination. Four subjects participated in tasks of rhythmic finger flexion and extension. Analyses derived from the model of response timing of Wing & Kristofersson (1973) were modified such that the cycle-to-cycle variability of rhythmic movement could be partitioned into sources attributable to timekeeping i.e., pattern generation, and neuromuscular delay. The basic predictions of the two-component model were confirmed. Asymmetries were not manifest at component levels, although they were again evident at the level of the collective variable, relative phase. There was minimal support that collective variable dynamics were significant predictors of timekeeping and delay variances. In Experiment 3 a novel assessment of multifrequency coordination dynamics was provided in a paradigm of person-environment coordination. Three subjects maintained unimanual oscillations of forearm pronation and supination at sub-maximal frequencies of oscillation in the presence of an auditory stimulus. An abrupt shift in stimulus frequency provided means for assessment of dynamic stability and flexibility near low-order frequency mode-locks. There was limited support for the expression of asymmetries through flexibility, in that person-environment coordinations prepared with the dominant limb better maintained regions of phase space inaccessible to interlimb coordination. The relation of stimulus frequency to limb frequency determined the collective variable dynamics to a greater extent than limb preference. Examinations of stability of bimanual coordination were provided in Experiment 4 using perturbation techniques. Four subjects completed rhythmic wrist rotations (pronation and supination). Mechanical perturbations were applied unexpectedly to either limb. Analyses of relaxation time confirmed the phenomenon of critical slowing down for 1:1 coordination in all subjects. There were limited data to assess the effects of asymmetry in preparations of multifrequency coordination. A topological dynamic based on phase attraction, rather than a mode-lock attractor, is proposed as a basis for human coordination under multifrequency constraints.

Acknowledgements

This work could not have self-organized without the patience, generosity, and physical and intellectual motivation from many heterarchical sub-groups. I am deeply indebted. There are many friends whom I will not mention. Instead, I attest that in the dimmer hours of frustration and fatigue, fond memories brought inspiration, rejuvenation and laughter. John and David never disappointed and often impressed. As a student, that was a fortunate experience. Feeling like the bread of an inverted sandwich (the good bits on either side), I was blessed with not one, but two truly brilliant colleagues in Richard Carson and Romeo Chua. Oh lord! The meticulous scrutiny and attention to detail that Richard brought to our environment was inspirational, while Romeo's laser vision kept us on track. The talents and enthusiasm of Cliff Storlund are sprinkled liberally throughout this work. Future events are often the most telling of the past. Rich, Rome, Dave, Steph, Cliff- despite great plans for escape, I await many more adventures under the scientific sun. Special thanks to Professor Turvey and Julie for unrelated and unusual quality. As always, my parents Marvin and Debbie were unconditionally supportive. Finally, I am grateful to my dear friends Laurie and Rae-Anne. Power within and happy endings.

Table of Contents

List of Figures

List of Tables

1 A Research Strategy for Human Coordination

1.1 Introduction

> *The coordination of a movement is the process of mastering the redundant degrees of freedom of the moving organ, in other words, its conversion to a controllable system.*
>
> (Nicholas Bernstein, 1967, p. 127)

Bernstein's degrees-of-freedom problem is now well known. The task of constraining virtually any combination of the nearly 10^3 muscles which bring about energetic changes through one or more of approximately 10^2 joints to produce coordinated movement cannot be managed by a central *coordinator* which prescribes all the relevant parameters for the units themselves. This is notwithstanding the fact that observational units reduce beyond the individual muscles, through the composition of motor units, and culminate at the cellular level in the order of 10^{14} units. The application of forces via muscular contractions causes movement of biomechanical linkages about the joints. Turvey (1990) provides a conservative estimate of 100 *mechanical* degrees of freedom, each characterized in state space by position and velocity, yielding minimally, 200 dimensions. Yet, humans and animals alike demonstrate the ability to effortlessly recruit previously quiescent degrees of freedom and simultaneously annihilate those degrees of freedom which are no longer relevant for the task or boundary conditions imposed. Robotic devices, on the other hand, are not quite as fortunate.

The perspective of movement regulation put forth herein argues that it is not necessary, nor is it logical, to conceive of a general purpose device whose function is that of mapping arbitrary inputs to arbitrary outputs for such a vast array of controllable units, such as those inherent to human motor systems. Instead, a number of arguments are presented which suggest a more parsimonious view of the brain, and nervous system in general. A view of the central nervous system as a special purpose device is considered (e.g., Runeson, 1977). The guiding principles of organization apodted herein are not from external organization, but rather, from self-organization whereby units are constrained mutually and functionally for the particular task at hand. From this perspective it is fortunate that overt behaviour provides a window into the degrees-of-freedom problem. As has been argued, all movement originates from very many degrees of freedom at the microscopic level of observation. However, a persistent feature of movement coordination is indeterminacy- the elements in coordination can be constrained in a variety of ways to reach identical end states (e.g., Hinton, 1984; Jordan, 1989; Kay, 1988; Kelso et al., 1981; Turvey, 1990). Kay (1988) summarizes the argument that indeterminacy arises as the motor system is assembled into the form of a dynamical system. Any number or variety of movement dimensions can be called upon to achieve the movement goal, but these are constrained by the actor into the form of coordinative structures or synergies (e.g., Kelso et al., 1979, 1983; but see Marteniuk et al., 1984 for an alternative viewpoint on the coordination of discrete bimanual movements). The point argued by Kay (1988) is that a reduction in the degrees of freedom is observed. This feature is only possible in a dynamical system which is nonconservative i.e., in which energy *flow* is maintained. A simple example of such a system is a damped mass-spring system. Energy is lost through the force of friction (damping). Not coincidentally, the behaviour of this nonconservative system is characterized by an attractor. That is, after its transient state through which energy is lost, the system rests at a stationary point i.e., a zero-dimensional point attractor, which resembles the preferred state regardless of the arbitrary nature of its initial conditions (inputs). Contrast this with a conservative system where, for instance, is an *undamped* mass spring maintains the original two degrees of freedom from the continuous exchange of inertia and elasticity.

Kay (1988) identifies another level of constraint which arises at the level of the dynamical system itself, that is, how the system evolves over *time*. In the case of rhythmic movement, the system dynamics are identified at the level of behaviour itself and give rise to complex patterns such as multistability, multiple patterns, and flexibility, to name a few. Moreover, these behaviours which dynamically are very rich, can be described in very few dimensions. Thus, as degrees-of freedom are compressed, surface simplicity emerges in the patterns themselves. It has been argued that within the pattern formation process itself lie the laws of coordination (e.g., Jeka & Kelso, 1989). Pattern formation assumes no priority at the level of behaviour per se. However, it is apparent that the level of behaviour yields a compression, reduction, annihilation, and/or spontaneous recruitment of the observable degrees-of-freedom (e.g., Kelso et al., 1993). Indeed, pattern formation extends across many levels of description (e.g., Kelso et al., 1991; Kelso et al., 1992), which vary in their accessibility to the student of coordination and motor control. It is our good fortune that the pattern formation process extends to the level of overt behaviour. The temptation therefore, is to exploit movement behaviour as the relevant level of analysis not only for coordination, but as an accessible window into the principles of organization for nervous systems in general.

The present focus is on interlimb coordination taken at the observable level of coordination itself. Movement behaviour is examined through *acts* of coordination (i.e., stable, reproducible, and perhaps complex behaviours, which express nonconservatively a compression of degrees of freedom), and as a *product* of coordination (individual elements constrained mutually within a dynamical system). Five features of interlimb coordination are identified:

1. Coordinated limb movements entrain one another.

2. Stability and loss-of-stability (quintessential features of dynamical systems) prescribe interlimb coordination dynamics.

3. Symmetry is not a ubiquitous feature of bimanual coordination[1].

4. Temporal fluctuations in rhythmic movement provide a means for addressing the structure of the underlying neural architecture (and the so-called central pattern generator).

5. The pattern formation process extends beyond the physical constraints of an organism.

The remainder of this introduction is devoted to the theoretical foundation of the five features listed above. Predictions are then extended from theory and examined in an experimental context. The chosen, and recurrent, paradigm is that of multifrequency coordination. The rationale for this pardigm is made clear in subsequent discussions. Multifrequency coordination is characterized by two rhythmic units which initially maintain a fixed, but non unitary relation in frequency. It was expected that such experimental paradigms would reveal behaviour rich enough for a novel examination of features (1) and (2). With respect to human performance in general, the constraints imposed by multifrequency coordination were expected to limit performance characteristics in a manner that has intrigued movement scientists for a century (e.g., Welch, 1898; Woodworth, 1899). The emergent performance phenomena are addressed with a particular regard for the asymmetries in movement as they pertain to coordination (feature 3). The paradigm is then extended to provide examinations of asymmetries which may be ascribed to neural substrate (feature 4), and finally, to the role of either limb considered as an element in a person-environment relation (feature 5).

1.2 The entrainment of coupled oscillators

In The Geometry of Biological Time, Winfree (1972) provides an extensive review of a vast array of periodic processes in living systems. Not surprisingly, rhythmicities

---

[1] All references to asymmetries pertain to right-handed populations unless stated otherwise.

identified in physiological processes bear close resemblance to analogues from (nonlinear) dynamical systems. The basis of physiological processes such as respiration, circadian and menstruation cycles, and cardiac movement stem from a commonality- nonlinear oscillations. It has been proposed therefore that a theory of nonlinear oscillations can provide an explanation of cooperative phenomena (Winfree, 1972; Beek 1989).

Although the rhythmicity underlying physiological processes has been given due consideration, the study of rhythmic movement has not. The reasons underlying the paucity of dynamical analyses of rhythmic movement are due in large part to the domination of the artifactual-machine perspective (e.g., Adams, 1971; Schmidt, 1975) which predominated post-WWII movement research. Abernethy & Sparrow (1992) and Meijer & Roth (1988) provide reviews of the perspective in light of recent developments from the dynamics perspective. Traditionally, the artifactual-machine perspective envisaged movement regulation as an engineering problem i.e., how to effectively control the behaviour of a multivariable system (e.g., Bellman, 1961). In this sense, systems are "cursed" with excessive degrees-of-freedom, and as such, the problem set forth for students of motor control was ambitious indeed. Although a considerable theoretical foundation was constructed, the approach was marred by two important shortcomings. First, all control is prescriptive. The view of the skeletomuscular system as a controlled variable, and the nervous system as the controlling device, provides little explanatory power (see Stein, 1982, and accompanying commentaries). The coherency of coordinated movements is attributed to the coherency of an external controller which itself is not explained (e.g., Kugler et al., 1980) i.e., the original degrees-of-freedom problem is merely shifted to another level. Second, a potentially large mismatch in the energy scales between control at the microscopic (neural) level and the controlled at the macroscopic (behavioural) level arises. Successful biological systems, and biological motion in general, are characterized by considerable energy flow commensurability (Morowitz, 1968), an impossible feature within an allonomic system, but at least possible within an autonomous framework whereby control resides "inside" the system as a natural consequence of self-organization (Kelso & Kay, 1987). In order to re-trace the lineage of movement science from an autonomous perspective we revert back about half a century to the studies of a German physiologist on the fin movements of the *Labrus* which, not surprisingly at the time, went largely unnoticed.

Erich von Holst (1937/1973) was able to classify an extensive range of coordination into two types: absolute coordination in which the units remain constant in phase and frequency, and relative coordination, in which the full state space of coordination is visited while stable phase and frequency relations persist. von Holst determined that each of these types of coordination were characterized by unique tendencies which prevail in either, but remain persistent in both. Relative coordination revealed what von Holst termed the *maintenance tendency*: each rhythmic unit strives to maintain its own characteristic frequency. In absolute coordination however therewas a prevalent expression of the *magnet effect*- the entrainment of one rhythmic unit to the characteristic frequency of the other. von Holst identified the magnet effect as a cooperative balance in coordination. However, both tendencies would persist in latent form, although one would prevail such that each were observable in intermittent fashion. In a series of experiments nearly fifty years later, Kugler & Turvey (1987) revealed that the persistence and latent competition between the maintenance tendency and magnet effect was a feature of human coordination when the limbs were involved in rhythmic oscillations of hand-held pendula. The pendula could be varied in terms of their characteristic frequency. Essentially, the phenomena identified by von Holst were also ubiquitous features of human coordination. The studies of Kugler & Turvey (1987) were instrumental in determining also the tendency toward mutual entrainment of the limbs in absolute coordination- the formation of cooperative virtual systems which mutually entrain to the global, physical demands of the weighted pendula. This was a more cooperative view of von Holst's magnet effect, and helped build a foundation toward a theory of human coordination dynamics.

1.3 Instability: A Precursor to Self-Organization

The problem for the student of motor control is to obtain an appropriate level of description such that the task-relevant degrees-of-freedom can be identified (Kay, 1988). It is not often the case that these may be identified *a priori*. Rather, they have to be identified, and their dynamics determined, through stability analyses. In order to deal with complex systems such as the brain, adequate variables must be determined which describe the system properties. In all cases a macroscopic description allows an enormous compression of information (Haken, 1988). A further means of delineation derives from behaviour which exhibits sudden jumps or state transitions (e.g., Haken et al., 1985; Kugler et al., 1980). Transitions, by definition, identify a qualitative shift from one pattern to another. Probing the system about regions of pre- and post-transition behaviour permits the identification of the essential dimensions of the patterns themselves (Jeka & Kelso, 1989). The dimensions constitute the collective variables or order parameters which describe fully the stable state space of the system. The order parameter expresses the most relevant properties of the system which tend to be few in number, especially around the region of transition, whereby a marked reduction in degrees-of-freedom are observed. Therefore, regions of transition are a logical entry point where description of the system may proceed from the potential to the essential (Carson, 1993).

The seminal application of the state transition methodology to the study of human movement regulation was conducted by Scott Kelso in examinations of rhythmic oscillations of the fingers (Kelso, 1981) and hands (Kelso, 1984). When paced by an auditory metronome subjects would begin cycling in an out-of-phase pattern (homologous muscles active asynchronously). When the frequency of oscillation was scaled upward in a regular manner, a sudden jump from out-of-phase to in-phase (homologous muscles active synchronously) was observed. The new pattern would remain stable regardless of whether or not frequency was maintained, increased, or decreased. However, when prepared in-phase, no shift in pattern would emerge under frequency scaling. Under the contention that the phase relation between the limbs (i.e., relative phase, Φ) was the relevant order parameter for coordination, a series of experiments (Haken et al., 1985; Kelso et al., 1986; Schöner & Kelso, 1988 a; Scholz and Kelso, 1989) examined the properties of Φ. The signature features of a true order parameter were discovered in extant preparations of bimanual coordination. These are encapsulated by: *modality* (two or more stable states) in the presence of *inaccessibility* (an inability to maintain states other than the modal states), *state transitions* (as above), *enhancement of fluctuations* (instability preceding transition), and *critical slowing down* (a longer return to stability when perturbed near the region of transition). Haken et al (1985) presented a model (HKB) of human coordination which characterized the relative phase dynamics as a product of the nonlinear coupling of essentially autonomous, nonlinear limit-cycle oscillators. Adopting Haken's principles of synergetics (Haken, 1977, 1983) the HKB model of Φ was derived in the form of a potential function such that,

$$\frac{d\Phi}{dt} = -\frac{dV}{d\Phi} \qquad (1)$$

where V is the so called potential function: an overdamped landscape through which a particle (Φ) can move. Under the assumptions of periodicity,

$$V(\Phi + 2\pi) = V(\Phi) \qquad (2)$$

and symmetry,

$$V(\Phi) = V(-\Phi) \qquad (3)$$

V may be written as a superimposition of two cosine functions,

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

which return stable solutions at $\Phi = 0,\pi$ i.e., in-phase and anti-phase.

The principles of synergetics suggest that the ratio of b/a from (4) represents the relevant control parameter (frequency of oscillation), a nonspecific variable which under regular scaling will produce a sudden shift in the pattern of Φ. Figure 1.1 illustrates the potential filed. If the ratio of b/a is scaled toward zero, the minima in the potential about $(\pi,-\pi)$ disintegrate. If the behaviour of Φ is taken as the position of a particle within the potential we can intuit how with a small amount of noise (realistic for any real system of which the living is certainly a class) a shift in Φ from π to 0 will occur. The new pattern is not prescribed *a priori.* It emerges as a feature of self-organization- a product, and inevitable consequence of the system dynamics.

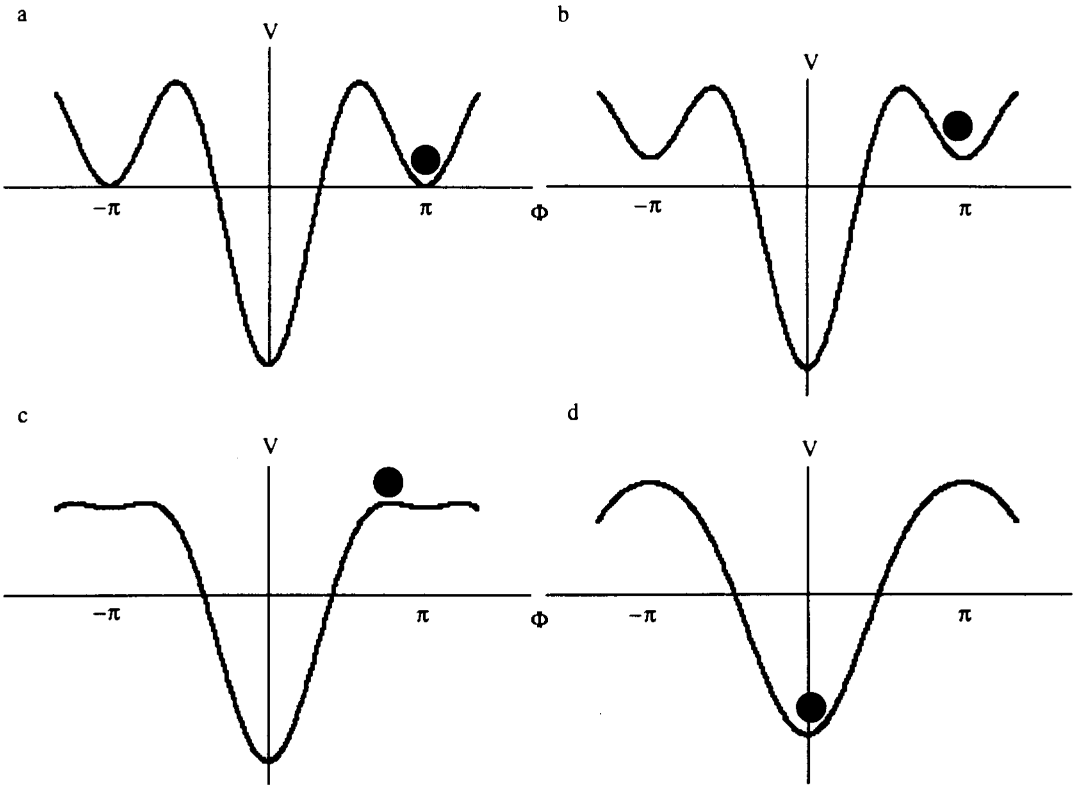


Fig. 1.1. Potential fields of bimanual coordination. Relative phase is modelled as a particle moving through a viscous potential landscape. Figures a through d depict the potential landscape deformations which occur through the scaling of oscillation frequency i.e., a reduction of b/a from eq'n (4) in text. a) Bistability: b/a = 1.000. b) Bistability: b/a = 0.750. c) Transition: b/a= 0.330. d) Monostability: b/a= 0.125. (Adapted from Haken et al., 1985).

The behaviour as identified in the HKB model, and observed experimentally, identify an anomoly within the conception of a "motor program" under the information processing perspective. Under this approach, the invokation of neurons, may be considered analagous to computer programs which steer individual motions. Motor programs are fixed in the sense that all movements are prescribed- they do not allow for fluctuations. The system as described in Figure 1.1c produces consistently reproducible fluctuations (critical fluctuations which precede nonequilibrium phase transitions) as a natural consequence of system dynamics.

There have been independent, but similar, examinations of biological coordination (e.g., swimming patterns of the lamprey) which adopt Φ as a suitable collective variable (e.g., Rand et al., 1988; Schmidt et al., 1993 b), although there has been some contention as to whether or not the dynamical models put forth are suitable characterizations of human coordination around the region of transition specifically. This issue is expanded in later sections in the consideration of the model of Rand et al. (1988). Of particular interest to the present work is the feature of loss-of-stability as an index of intrinsic system dynamics. For example, an in-phase preparation is said to be more stable intrinsically than an anti-phase preparation. The concept of an attractor is again useful. The stable patterns of relative phase are mapped onto attractors in the dynamical model. Relative phase is essentially dimensionless in this respect since it is characterized by point attractors corresponding to 0 and π. The system is characterized by zero degrees of freedom since it equilibrates to $\Phi = 0$ eventually i.e., whether stability is lost through the implementation of a control parameter regime or not.

Loss-of-stability however, is also a prevalent feature of systems where the individual rhythmic units are not prepared in absolute coordination per se (i.e., 1:1 frequency , anti-phase), but rather, when prepared at disparate frequencies. Under multifrequency constraints, the system is said to be mode-locked in frequency although relative phase is essentially a continuously changing (i..e, unstable) variable. How do the intrinsic dynamics of bimanual coordination as described by the HKB model encapsulate the stability and loss-of-stability in multifrequency regimes? This research question is motivated by the known decrements which arise in performance when the limbs are prepared under multifrequency constraints in tapping (e.g., Deutsch, 1983; Peters & Schwartz, 1989; Summers et al.,

1993) or, in the loss of stability in continuous rhythmic movement (e.g., Beek, 1989; DeGuzman & Kelso, 1991; Peper et al., 1991). For example, preparations in certain frequency relations of a higher order can lead to bifurcations (transitions) to lower-order relations. Are these transition phenomena an expression of the intrinsic dynamics, as identified by Haken et al. (1985)? What features of coordination rationalize the loss of stability at higher order frequency relations? Consideration of these questions with regard for the performance of bimanual tasks (e.g., Carson, 1993; Marteniuk et al., 1984; Peters, 1990) suggests that the well-documented asymmetries between limb systems may contribute to the loss-of-stability in multifrequency coordination (e.g., Peters & Schwartz, 1989).

1.4 Symmetry is Not a Ubiquitous Feature of Human Coordination

The expression of asymmetries in bimanual coordination from the dynamical systems perspective has been examined in preliminary studies within our laboratory (e.g., Byblow et al., 1994; Carson et al., 1994) and subsequently, has expanded to broader characterizations of the role of symmetry in human movement regulation (Byblow et al., in press; Carson et al., submitted a-c; and Riek et al., in press). A consistent finding throughout these examinations was that in extant preparations of absolute (1:1) bimanual coordination, asymmetries were expressed at the level of the relative phase dynamics. Focusing attention to the level of the collective variable for the present discussion (recall that generally, the dynamics perspective applies *across* levels of description), a specific characteristic of the region of transition deserves notice.Specifically, the transition pathways were delineated on the basis of asymmetries. Generally, transition pathways were isodirectional in nature whereby the left (non dominant) hand affected transitions more than the right. Therefore, although the pattern of relative phase between the limbs clearly expressed a spontaneous jump from anti-phase to in-phase, the distribution of transition directions was not symmetrical, as predicted by the HKB model.

The HKB model can in fact be modified to incorporate broken symmetry (e.g., Kelso et al., 1990; Kelso & Jeka, 1992) through the inclusion of a symmetry breaking term. Consider,

$$\frac{d\Phi}{dt} = \delta\omega - a\sin\Phi - 2b\sin\Phi \qquad (5)$$

where $\delta\omega$ is the symmetry breaking term expressed as the difference or ratio (depending on the derivation) of the eigenfrequencies (characteristic frequencies) of the component oscillators. The symmetry breaking term forces the system toward isodirectional transitions, but also, toward fixed point drift. As the name implies, the stable "fixed points" of relative phase (i.e., about in-phase and anti-phase) drift away from 0 and π respectively under frequency scaling. The phenomenon of fixed point drift however has not been observed in "natural" preparations of human bimanual coordination (Byblow et al., 1994; Byblow et al. ,in press; Carson et al., 1994). It is our contention that models of broken symmetry are best suited to systems which clearly differ in eigenfrequency between the component oscillators such as those provided in examinations of whole body coordination (Kelso & Jeka, 1992) or, in bimanual coordination where the limbs are attached to weighted pendula which can be explicitly altered in eigenfrequency (e.g., Kugler & Turvey, 1987).

In order to account for isodirectional transitions in the absence of fixed point drift, it was surmised that asymmetries may be manifest within the coupling functions (strengths) between the oscillators themselves. Adopting the nomenclature of Rand et al's (1988) average phase difference model (RCH), relative phase is depicted,

$$\frac{d\Phi}{dt} = \delta\omega - K\sin\Phi \qquad (6)$$

or,

$$\Phi = \arcsin \frac{\omega_l - \omega_r}{k_{lr} + k_{rl}} \tag{7}$$

where ω_l and ω_r represent the eigenfrequencies of the left and right oscillators respectively, $\delta\omega$ their difference, k_{rl} the influence (coupling strength) of the left oscillator on the right, k_{lr} the converse, and K the sum of coupling forces.

Phase and frequency locking are predicted to occur about $\Phi = 0$ and $\Phi = \pi$ if $\delta\omega$ is sufficiently small relative to K. These features have persisted across the several examinations so far discussed, and thus characterize stable patterns of coordination in general. If we consider that k_{lr} and k_{rl} are inversely proportional to oscillation frequency (ω_v), then from the data of Sternad et al. (1992), the coupling expressions of the RCH model are expanded,

$$k_{rl} = G_l \frac{\omega_l}{\omega_v} \tag{8}$$

$$k_{lr} = G_r \frac{\omega_r}{\omega_v} \tag{9}$$

where G_l and G_r are constants of proportionality expressing for each hand the degree to which the respective coupling strengths scale in magnitude with frequency of oscillation (Carson, 1993). Isodirectional transitions in Φ would be an inevitable consequence if an inequality was present such that,

$$G_l > G_r. \tag{10}$$

The inequality (10) results in a depression of k_{lr} under scaling of ω_v which is greater than that of k_{rl}. The rationale for the proportionality constants stem from consistent expressions of manual asymmetries (Peters, 1977, 1987, 1990) which state that the maximal rates of responding are higher for the right hand than those of the left, whereas the preferred frequencies do not differ between the hands (Byblow et al., 1994; Carson, 1993).

It is apparent then, that the expression of asymmetries is a product of the cooperativity between the limbs (or coupling, K) rather than an expression of the forces of competition (or difference, $\delta\omega$) between them. In the language of von Holst, the inherent dynamics of bimanual coordination may be considered as the asymmetrical forces of cooperation brought about by the *magnet effect,* rather than the competiton stemming from the underlying *maintenance tendency.* Are expressions of asymmetries consistent in multifrequency coordination i.e., ubiquitous to bimanual coordination in general? By definition, multifrequency coordination imposes broken symmetry with respect to the oscillation frequencies. If asymmetries persist, will they remain a feature of cooperativity as prescribed by the intrinsic dynamics or, will features of symmetry breaking emerge?

A final consideration of asymmetries in bimanual coordination specifically, stems from the perspective of attention, and limitations of attention. Peters (1987; 1990) has provided compelling arguments which suggest that the variability associated with particular examples of bimanual performance reflect an inherent preference of right-handed individuals in directing attention toward their dominant versus their non dominant hand. This phenomenon has been argued as a basis for performance asymmetries in bimanual coordination, and thus, the attention hypothesis is given due consideration in the bimanual paradigms of Experiment 1 (section 2).

1.5 Temporal Variability: A Window into Neural Components

The tendency for the psychologist to approach behaviour with the intention of explaining variability away has probably been misguided (Wing, 1992). Variability is a signature feature of all living systems and can be observed in many physiological and psychological processes. Movement regulation is no exception, and the edited volume Variability and Motor Control (Newell & Corcos, Eds., 1993) provides many convincing arguments. The experimental work of Wing and his colleagues (e..g, Wing & Kristofersson, 1973; Wing, 1980; Wing et al., 1989; Vorberg & Wing, in press) has dealt explicitly with the variability of timing in human movement as an interesting feature in its own right. Wing and Kristofersson (1973) speculated that two sources of variability contribute to the variance between repetitive responses (e.g., repetitive tapping). One contribution is ascribed to a timekeeper which is effective in maintaining the temporal patterning of responses over a wide range of target intervals (Stevens, 1886). The other contribution, as posited by Wing and Kristofersson (1973), reflects the neural transmission delay between the triggering of the motor command (via the timekeeper) and the observable events at the periphery (the response). Schematically, the model is presented in Figure 1.2 for a hypothetical series of rhythmic cycles of movement.

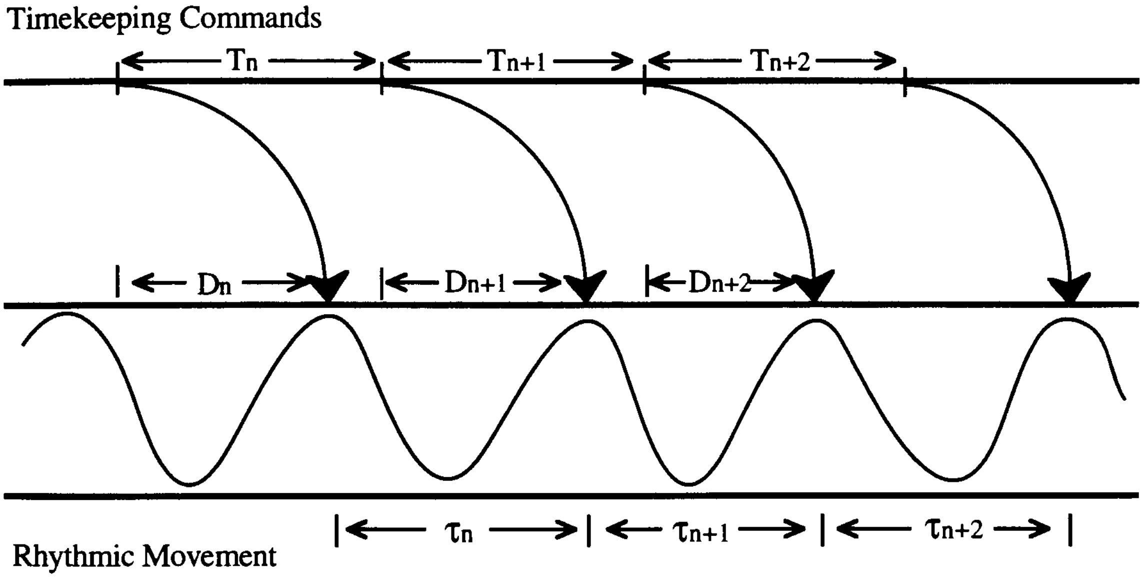


Fig. 1.2. The two process model of response timing (Wing & Kristofersson, 1973). Timekeeping commands (T) trigger responses (in this case rhythmic movement) of period τ which are subject to intervening neuromuscular delays (D).

The assumptions and formulation of the model are presented in their entirety in a later section. For the present discussion it is useful to summarize only the theoretical motivation for the two-process model. These derive from the original works of Bernstein (1967) and Lashley (1951) on the serial order of human action. The model recognizes that the completion of each movement in a sequence (for example via feedback) is neither a necessary nor desirable stage in the generation of the next element in the sequence (Vorberg & Wing, in press).

Evidence for this position extends logically to the domain of rhythmicity in biology, and the conceptualization of the neural circuitry which underlies stable rhythmicity. Grillner (1975) describes the neural networks underlying locomotion in vertebrates as ascribable to a single circuit, namely a central pattern generator (CPG). Under this view, the CPG was considered responsible for the phase relations between muscles within a movement cycle and, for generating the inter-cycle phasing of the movements. More recently, Lennard (1985) conceptualized the role of the CPG as ascribable to the former only, whereas the function of inter-cycle timekeeping remained separate. In examinations of human subjects, Ivry & Keele (1989) implicate the role of timekeeping to the cerebellum i.e., a level above that of the so-called CPG's which are said to govern locomotion. Examinations of temporal variability in human rhythmic movement suggest that the intracycle phasing component *only* may be conceptually closer to the CPG, and linked functionally, to the delay component of the two-process model (Turvey et al., 1989). From compartmentalized analyses of the two process model, these authors linked the variability in the *delay* component to disparity in the characteristic frequencies of the wrist-pendulum systems. In another study (Turvey et al., 1986), variability ascribed to the *timekeeping* functions as partitioned by the model, were dependent upon the relative phase, Φ, between the wrist-pendula . These findings are expanded in greater detail in later sections. At present they serve to note the influence of parameters in the dynamical model which may subserve the functional organization of neural substrate.

The intended goals in adopting analyses derived from the two process model of Wing & Kristofersson (1973) to the rhythmic domain (Turvey et al., 1986) were to examine the expression of asymmetries at a level ascribable to timekeeping and pattern generation functions. In examinations of alternate tapping, Wing et al. (1989) did not implicate either hand as more or less variable at this level. Our previous examinations of bimanual coordination with particular regard to asymmetries (e.g, Carson et al., 1994) were positive in the identification of asymmetries within the dynamics of Φ, as well as at the level of limit-cycle dynamics. As such the two-process model was extended to the rhythmic domain to examine asymmetries, and the functional organization of multifrequency coordination in general. Finally, it was questioned whether or not the two-process model, which is explicitly dependent upon temporal variability in movement, would be sensitive to measures of stability in the parameter space which characterizes bimanual coordination?

1.6 Coordination Dynamics of Perception-Action Coupling

The coupling of perception and action is a pervasisve feature of human behaviour (MacKay, 1987). The phenomenon is not hard to imagine. For example consider the temporal coupling between a perceptual rhythm and ongoing motor activities. Lashley (1951) examined such a coupling for various actions of subjects as they listened to the music of a band. Step, gesture, and even breath, became entrained to the rhythm of the band. Allen (1972) also provided striking evidence for perception-action coupling. Subjects were instructed to tap to the rhythm of an ordinary spoken sentence. Subjects were not only able to respond to this request, but did so consistently at the intra-personal and inter-personal levels. It has been speculated that the same timing mechanisms might underlie perception and action despite the apparent asymmetries between them (e.g., MacKay, 1987). The argument is put forth herein that perhaps the same *pattern formation process* prescribes coordination patterns between perception and action as it does within the interlimb coordinations discussed thus far.

A convincing example of perception-action coupling is provided from treatments of between-person coordination. The mutual interaction of two individuals can be such that they appear to act as single organism (Asch, 1952). Schmidt et al. (1990) examined the extent of interactions between the synchronous movements of two persons. The coordination dynamics between persons were qualitatively similar to those of within-person (e.g., interlimb) coordination. When two subjects performed rhythmic oscillations of the legs the relative phase, Φ, between the limbs (one of each subject) would exhibit stability patterns identical to within person coordination when looking at one another. Predominantly, transitions occured from anti-phase to in-phase (defined spatially) and were preceded by critical fluctuations indicating a loss of stability of the anti-phase pattern i.e., as predicted from the annihilation of the attractor at anti-phase in the HKB model (e.g., Figure 1.1). Hysterisis was also maintained. Transitions were not observed however, when subjects did not look at each other. The experiment was paramount in demonstrating the identity between the major features of the order parameter dynamics in coordinations between visual-perceptual systems and coordinations within a single haptic-perceptual system. In quantifiable dynamical terms, the anatomical and optical connectives between rhythmic movements are identical (Turvey, 1990), and thus, as alluded to by Asch (1952), two nervous systems may be shown to interact in a manner similar to one.

Byblow et al. (in press) extended the examination of informational interactions pioneered by Schmidt et al. (1990) and subsequently by Wimmers et al. (1992), in a paradigm of person-environment coordination. In a manner identical to the visual perceptual coupling of between-person coordination, it was anticipated that human movement would entrain to a regular rhythmic environmental stimulus (e.g., a visually displayed oscillator). Thus, person-environment coordination would assume the same dynamical form as interlimb coordination, and between-person coordination. A paradigm of unimanual coordination was employed whereby subjects coordinated rhythmic forearm movement with a periodic visual stimulus. When prepared anti-phase (i.e., movement in the opposite direction of the stimulus) a phase transition to in-phase would occur or, a complete loss of stability in Φ would be observed (i.e., phase wandering) under the scaling of frequency. In-phase preparations however would not exhibit transitions although phase wandering was again evident at high frequencies (albeit stability was maintained longer when prepared in-phase). The complete loss in stability of Φ implicates the importance, and relative magnitude of coupling in the maintenance of within person coordination. Secondly, phase wandering in person-environment coordination implicates the feature of broken symmetry in dynamical models for regimes which entrain oscillators of independent characteristic frequencies. More importantly however was the virtue of shared dynamics of within-person coordination and person-environment coordination. Byblow et al. (in press) identified differential stability between the limb-display collectives formed with either the dominant limb (more stable) or non dominant limb (less stable). Thus, asymmetries were manifest at the level of the collective variable in person-environment coordination analagous to the asymmetries of interlimb coordination observed in Carson et al. (1993).

Stability and instability of Φ is preserved outside the realm of within-person coordination. It is suggested however that the person-environment paradigm opens an exciting new window into coordination in general, namely by allowing the movement system to enter or maintain, at least briefly, previously "inaccessible" regions of Φ space. The phase of the perceived stimulus may be controlled experimentally. Theoretically, examinations of inaccessible regions are possible if the following two conditions are met. First, single limb rhythmicities must possess dynamics reminiscent of limit-cycle oscillators, and hence maintain a sense of autonomy. This feature of human rhythmic movement has received consistent support across a variety of movement classes (e.g., Kelso et al., 1981). If stable limit-cycle behaviour is present then environmental perturbations must compete with the (previously) stable state dynamics. Second, the dynamics of within-person coordination (and arguably, between-person coordination) must be alterable by willful intent. It has been shown that intention can be modelled in the same topological form as Φ (Scholz & Kelso, 1989), and thus, impinge upon the inherent coordination dynamics. It is possible in the physical and dynamical sense to preempt or prevent the emergence of transitions of the type order-->order, by mapping intentional dynamics onto the inherent dynamics. Thus, it was anticipated that transitions of the type order-->disorder were similarly corruptable. The perturbation of an environmental stimulus to a non-harmonic frequency relation with respect to the limb allowed a number of questions, generic to coordination, to be addressed. Namely,

a) Is there a preferred relation in frequency of limb to environmental stimulus in multifrequency coordination? That is, does the stability portrait of Φ reflect the assignment of limb to the dominant (faster, or "driving" frequency) versus the slower (driven) assignment within the limb-stimulus relation?

Or,

b) Is the preference of limb-stimulus relation dependent on whether the dominant versus non dominant limb is comprised within the collective?

Finally,

c) Is the expression of creativity through the dominant limb (e.g., Guiard, 1989) a feature of flexibility reflected in Φ space, or more specifically, those regions which are not consistently accessible to interlimb coordination?

A paradigm of person-environment coordination was constructed within the above context with a particular regard for inherent asymmetries in an attempt to probe the underlying dynamics of perception and action coupling in general.

1.7 Summary

Four experiments are reported. Each examined multifrequency coordination in a paragdigm of rhythmic movement. Experiments 1 and 4 examine extensively the features outlined in sections 1.2, 1.3 and 1.4. Namely, a quantification of the intrinsic dynamics of multifrequency regimes are sought with a particular emphasis on stability and the identification of performance asymmetries[2]. Experiment 2 examines explicitly the predictions put forth in section 1.5, which encompass the partitioning of temporal variability of rhythmic movement into respective timekeeping and delay sources. Performance asymmetries are examined from this perspective as well as at the level of collective variable dynamics. Experiment 3 addresses the predictions of section 1.6 in a paradigm of person-environment coordination. Inherent dynamics are examined in coordinations which arise through the coupling of perception and action, and are contrasted to those of interlimb coordination. The ubiquity of asymmetries, and the nature of coupling are discussed within and between regimes. Finally, the essential features of multifrequency coordination dynamics are summarized in section 6 in which the major predictions of section 1 are evaluated.

---

[2] Section 2 (Experiment 1) is reported in entirety in, Performance asymmetries in multifrequency coordination. Byblow, W.D. & Goodman, D., *Human Movement Science* (in press).

2. Experiment 1

Performance Asymmetries in Multifrequency Coordination

2.1 Introduction

Nearly a century ago Welch (1898) reported an experiment in which subjects exerted a steady tracking force with one hand while exerting pressure rhythmically with the other. When the rhythmic task was assigned to the left hand there was considerably greater interference in the ability of the right hand to exert a steady force than in the converse arrangement. We refer to such a phenomenon as a *performance asymmetry*. Since then, the temporal and spatial coupling of the two hands has proven a ubiquitous feature of bimanual coordination (e.g., Kelso et al., 1979), although many current treatments of coordination with respect to their dynamics remain unspecific with respect to the role of asymmetries (e.g., Haken et al., 1985). The identification of constraints underlying the coupling between the limbs in general remains elusive and thus, considerable and diverse research attention continues to be directed toward understanding bimanual coordination (e.g., Peper et al., 1991; Peters, 1985; Schöner et al., 1986; Sternad et al., 1992; Summers et al., 1993; Swinnen & Walter, 1991). Similar to Welch (1898), Peters (1985) observed performance asymmetries in the tapping of a 2:1 rhythm. Peters noted consistently poorer performance (e.g., slower tapping rates, increased variability) when subjects were required to tap with the left hand at twice the frequency of the right hand than vice versa. In the studies noted, asymmetries arise in task performance based on the assignment given to each hand in the accomplishment of the global task, although the global task demands are not expected to differ between assignments. In our opinion these phenomena suggest that any (new) theory of bimanual performance must account for asymmetries, as symmetry in general is unlikely to prove a ubiquitous feature of human coordination (Carson, 1993; Carson et al., 1994).

As a working hypothesis to account for performance asymmetries, Peters (1985) suggested that the intervening variable may be attention. That is, in bimanual conditions, subjects exhibited an attentional bias toward the right hand. Also, when the hands moved at different rates (e.g., 2:1 tapping), subjects were more likely to direct attention toward the faster moving hand (Peters & Schwartz, 1989). In combination these aspects reveal the paradoxical condition that confronts the subject when the left hand assumes the faster rate in the 2:1 tapping task. Specifically, is attention directed toward (demanded by) the dominant hand or the faster moving limb? The supposition is that the conflict of attention, or of attentional direction, subserves the greater overall variability commonly observed within the "left-hand-fast" system. Admittedly, Peters cautions the reader, and questions the appropriateness of the term *attention* in this context, but presents the argument in support of focused attention toward the component parts of temporal sequences, both in the perception and production phases, under predefined task arrangements (e.g., Peters, 1990).

2.1.1 Attention and Performance: A Dynamics Perspective

It is our contention that in the realm of bimanual coordination, intuiting the role of attention as an intervening variable or limiting factor in performance, does not necessarily address phenomena at a level consistent with patterns observed at the macroscopic level of behaviour and thus, cannot provide a suitable characterization of its essential elements. The implicit assumptions underlying attentional accounts of bimanual coordination phenomena are clearly incongruent with current theoretical perspectives of coordination whose common ground stress pattern formation in open dissipative systems (e.g.,Haken et al., 1985; Kugler & Turvey, 1987; Schmidt et al., 1993 b; Schöner & Kelso, 1988 a). This perspective owes considerable debt to the German physiologist, von Holst (1937/1973), who demonstrated that in many fish and invertebrate nervous systems interactions which give rise to the synchrony of limb movements arise through cooperative and competitive tendencies of the respective elements. As a result, order is an emergent feature of interactions of component elements which demonstrate lawful regularities (Turvey, 1990). Spatiotemporal patterns emerge spontaneously (i.e., self-organize) under the scaling of *control parameters* (which remain unspecific with respect to the prescribed patterns themselves).

Haken's synergetics (e.g., Haken, 1977, 1983, 1988) has since become the most widely cited basis of nonlinear dynamics applications in natural systems which focus on self-organization - a desirable feature in any complex system since the governing principles may be described in very few dimensions. The suggestion has been put forth that the elements of bimanual coordination are assembled under the principles of self-organization. Although the dynamics underlying the limbs themselves reveal patterns reminiscent of (potentially high-dimensional) autonomous limit-cycle oscillators (e.g., Kay et al., 1991; Kugler & Turvey, 1987), it is at the level of the spatiotemporal parameter, *relative phase* (the phase relation of one limb with respect to the other), that the system exhibits low-dimensional behaviour (e.g., Haken et al., 1985; Turvey, 1990). At the collective level of relative phase, spontaneous shifts in patterns emerge: an essential and signature feature of the synergetic approach. Qualitative changes in system behaviour, such as *phase transitions*, have been observed in extant paradigms of rhythmic human movement (e.g., Kelso, 1981, 1984). In fact, across a variety of species and scales of observation, similar patterns emerge across levels of observation (e.g., overt behaviour, neural firing rates, biochemical reactions), all of which emanate from fundamentally distinct material or metabolic substrates. For example, a recent examination of neuromagnetic field patterns in the human brain suggest that the linkage between events at the microscopic (e.g., neuronal) level, and the macroscopic (behavioural) level is by virtue of shared dynamics (Kelso et al., 1992).

The spontaneous emergence of behavioural patterns arise not in the presence of volition or prescription by independent pattern generators, but rather as a consequence of the underlying dynamics. The oft-cited example of phase transitions in human behaviour is that from an asymmetric (anti-phase) mode of coordination (i.e., non-homologous muscle groups are active synchronously) to that of symmetric (in-phase) coordination (synchronous activation of homologous muscles) under the scaling of oscillation frequency (a control parameter). Transitions in limb-limb relative phase have been encountered across paradigms of absolute coordination within persons (e.g., Kelso & Scholz, 1985), and between persons (Schmidt et al., 1990). As such, patterns at the macroscopic level of behaviour may emerge through linkages which are physical (e.g., neuromuscular), as well as informational (e.g., through visual perception) (Byblow et al., 1994, and Schmidt et al., 1990, provide recent treatments of informational interactions).

The conception of information is highly specific within the dynamical realm. Perceptual information is viewed as relevant only in terms of the behaviour it modifies. More explicitly, "information is viewed as *meaningful* and *specific* to the extent that it contributes to the collective dynamics attracting the system toward an (environmentally-specified, memorized, intended) behavioral pattern" (Schöner & Kelso, 1988 b, p. 77). Thus, behavioral patterns may also encapsulate external influences superimposed upon the intrinsic dynamics of the bimanual system. For example, a control parameter signal in the form of external information (e.g., an auditory pacing metronome), can be shown to possess dynamics which impinge upon the limit-cycle dynamics and collective variable dynamics relevant to coordination itself (Beek, 1989; Byblow et al., 1994). These *incidental dynamics* enter at specific regions of the limit-cycle termed *inherent anchors* (normally points of maximal excursion) which themselves exhibit diminished variability on the limit-cycle due to inherent (biomechanical/neuroanatomical) constraints (Beek & Bingham, 1991). For example, in rhythmic rotations of the forearm, both pronation and supination endpoints describe regions of diminished amplitude variability on the limit-cycle. However, on the occurrence of phase transitions, the resultant synchronization pattern of the limbs with the external pacing signal is often prescribed to the pronation endpoint, as it is inherently the more stable anchor (Byblow et al.,1994). Thus, information may be represented as both an inherent and an incidental dynamical resource.

An additional factor which should be regarded in treatments of bimanual coordination is that of *manual asymmetries*. There is an increasing body of literature which supports the fundamental difference in the stability of the left and right component oscillators themselves (Byblow et al., 1994; Carson, 1993; Carson et al., 1994; Kay et al., 1991). However, there remain few descriptions of phenomena such as performance asymmetries at the level of the collective. One strategy which has seen limited success has been the inclusion of a symmetry breaking term in the equation of motion which models the collective variable dynamics under conditions in which the component oscillators differ in eigenfrequency (e.g., Kelso et al., 1990, Schmidt, Shaw & Turvey, 1993). Although the inclusion of a symmetry breaking term adequately modifies the system dynamics, manual asymmetries may not be dissociable on the basis of (meaningful) eigenfrequency difference. Rather, in the language of coupled oscillator theory (e.g., Rand et al., 1988), asymmetries can be treated as a consequence of differential coupling of the limbs on one another (see Carson et al., 1994). This view differs from models of symmetry breaking, where specifically *fixed point drift* of (stable) relative phase is predicted (i.e., offset from perfect in-phase or anti-phase as a function of eigenfrequency difference). It is our understanding that this feature has not yet been observed under natural preparations (i.e., when limbs or pendula are unweighted), although other features of broken symmetry such as isodirectional transitions, have been observed. To account for these features, we (Byblow et al., 1994) have proposed a force-flow model of coordination which can account for the cooperative and competitive tendencies accruing from forces of asymmetry, and inherent and incidental anchoring.

2.1.2 Multifrequency Coordination

The present investigation extends on existing knowledge of bimanual coordination by focusing on multifrequency coordination and observed performance asymmetries. The focus lies primarily on issues related to stability, and whether or not patterns of behaviour at the level of relative phase correspond, or map onto, those which underlie 1:1 coordination. Bifurcations (transitions) through mode-locked states of descending order were predicted (e.g., Beek et al., 1992; DeGuzman & Kelso, 1991; Peper et al., 1991). As such, transition phenomena serve as an index of stability of bimanual systems defined by hand and task assignment i.e., left-hand-fast versus right-hand-fast. Another feature related to stability is that of *phase attraction* i.e., the tendency for relative phase to dwell near, but not in, stable regions of phase space (Kelso et al., 1991). Regions of phase attraction act as "local wells" which capture the system temporarily in the attractor states defined by the intrinsic dynamics i.e., in-phase and anti-phase. However, multifrequency coordination is characterized by *relative coordination* through which all phase relationships are encountered according to a statistical function of broad bandwidth (von Holst, 1937/1973). By living near, but not in, the "ghost of mode-locked states" (Kelso & Ding, 1993), a system is afforded flexibility and anticipatory qualities. Our prediction for the multifrequency regime was that of decreasing attraction to the phase relation corresponding to anti-phase coordination as frequency was scaled beyond a critical bound i.e., beyond the frequency at which phase transitions from anti-phase to in-phase emerge in the 1:1 regime (e.g., Kelso et al., 1991). With respect to performance asymmetries, we anticipated that the assignment of hand to frequency may be characterized by phase attraction and thus, reflect the relative stability of the respective bimanual preparations. Of further interest was whether or not stable patterns emerge within multifrequency coordination which extend beyond in-phase and anti-phase. For example, do landmark events such as movement reversals of the faster moving limb reflect coordination tendencies (e.g., Swinnen & Walter, 1991) and, are these an expression of performance asymmetries defined by hand and frequency assignment?

We extend the conception of information as described above in an attempt to characterize the role of attention in the active production of a multifrequency rhythm. In consideration of Peters (1985), two (inherent) constraints were expected to influence performance in the *absence* of external information: a pre-disposition toward attending to the right hand, and a tendency to direct attention toward the faster moving hand (e.g., Peters, 1985). One prediction was that the superimposition of external information on these constraints would impinge upon the system dynamics in a manner analogous to the view of focused attention toward, or away from, the predisposed limb. This was examined via the implementation of two control parameter regimes which were identical in frequency (the chosen control parameter), but predicted to be orthogonal with respect to the limit-cycle dynamics.

Our goal was to characterize the stability of low-order (2:1) multifrequency coordination with special reference to performance asymmetries, and the forces underlying their emergence. Two hypotheses were advanced. First, the intrinsic dynamics of the two possible hand/frequency assignments in 2:1 coordination were expected to differ from one another at the level of the collective variable. Second, in a manner analogous to that of focused or directed attention, the variation of external information coincident with landmark events of either hand was expected to influence the observed coordination dynamics.

2.2. Methods

2.2.1 Subjects

Subjects were recruited on a volunteer basis. Self-professed right-handed subjects were screened initially for their ability to actively produce 2:1 coordination in a self-paced condition. Four male subjects (age 26-48) who demonstrated an ability to maintain 2:1 coordination during the initial screening and were accepted for further testing. Subjects 1, 3, and 4 indicated that they had been exposed to some degree of musical training. Subject 2 reported no history of musical training.

2.2.2 Apparatus

Custom built manipulanda were used to record pronation and supination of the forearm. Linear potentiometers (Bourns Instruments, Model # 3540, 0.25% linearity) located coaxially with the center of rotation of each manipulandum (length 18 cm, diameter 2 cm) allowed for the continuous transduction of angular displacement. Output voltage signals from each potentiometer and metronome pulses were sampled at 250 Hz by an 8-channel A/D converter and stored to disk after each trial. The manipulanda were mounted on a table in front of the seated subject . The height of the seat was adjusted so that when each subject grasped the manipulanda their elbows were flexed at 90 degrees. Subjects' upper arms were secured with a wide velcro belt, ensuring that movements were restricted to pronation/supination of the forearm. The hands were occluded from vision and subjects were provided a small target in their central visual field on which to fixate.

2.2.3 Self-Paced Trials

Subjects performed rhythmic oscillations in two modes of coordination: 1:1 and 2:1. In the 1:1 regime two patterns of coordination were studied, in-phase and anti-phase. In the in-phase mode, pronation (supination) of one forearm was coincident with pronation (supination) of the other forearm. In the anti-phase mode, pronation (supination) of one forearm was coincident with supination (pronation) of the other forearm. In multifrequency coordination two conditions were examined: <u>1:2</u> where the left limb cycled at half the frequency of the right; and <u>2:1</u> where the right limb cycled at half the frequency of the left. Emphasis was placed upon the adoption of a comfortable frequency and amplitude such that the movements "could be performed all day" if necessary.

2.2.4 Frequency-Scaled Trials

2.2.4.1 1:1 Coordination

The beat of an auditory metronome (50 ms, 500 Hz square wave) was used to pace subjects under frequency-scaling conditions. In 1:1 coordination, subjects were required to produce one full cycle of their movement for each beat of an auditory metronome while maintaining the prescribed mode of coordination (in-phase or anti-phase). The frequency of the metronome was increased from an initial frequency ranging from 1.0 - 1.4 Hz, depending on the subject and condition, to a frequency of 3.00 - 3.40 Hz. Metronome frequency was incremented in discrete steps of 0.2 Hz, resulting in 10 plateaus, each of approximately 4.5 second duration. In the in-phase condition (IP) subjects were asked to match the beat of the metronome with the pronation movement endpoint of the two limbs. In the anti-phase conditions, subjects synchronized with the beat of the metronome with either leftward movements i.e., left-hand supination and right-hand pronation (AL), or rightward movements (AR).

2.2.4.2 Multifrequency Coordination

Two metronome conditions, identical with respect to required frequency of oscillation, were chosen for scaling the multifrequency conditions. The instructions for synchronization were altered, but not the required frequency of oscillation. In one condition subjects were asked to synchronize with the beat of the metronome on the pronation endpoint of the slower moving hand. This was denoted as the full-information (FI) condition. The second metronome condition was denoted as half-information (HI), where subjects synchronized with the beat of the metronome with every pronation endpoint of the slower moving hand, and every other pronation endpoint of the faster moving hand. Attentional bias was expected toward the faster moving hand in the FI condition where the pulses were coincident consistently with a unitary movement endpoint (i.e., pronation). In the HI condition, attentional bias was expected toward the slower moving hand which was synchronized on pronation, but on every cycle, as opposed to every other cycle.

2.2.5 Protocol

Thirty experimental trials were performed in each condition, in each of three sessions run over successive days. Self-paced trials were of 20 second duration, whereas metronome-paced trials were of 45 second duration. In the first session, subjects were acquainted with the apparatus before practice and collection trials in self-paced (IP), and metronome-paced (IP, AL, and AR) conditions. After a brief rest period, subjects performed 5 self-paced trials in each of the multifrequency conditions. The second session began with self-paced trials in both regimes, but consisted primarily of metronome-paced trials in the FI condition (20 trials), and concluded with five scaled trials in the 1:1 regime. The third session was identical to the second with the exception that scaled trials for the multifrequency conditions were presented in the HI format.

Subjects were instructed to maintain the pattern of coordination and frequency ratio in which they were prepared while maintaining stringently the oscillation frequency of the metronome. In the event that a spontaneous change in pattern or frequency relation between the limbs was detected, subjects were asked not to intervene, but rather to maintain the new pattern at the tempo of the prevailing metronome frequency.

2.2.6 Experimental Variables and Analyses

The mean frequency of oscillation was calculated for each limb over a 15 s interval within self-paced trials. The stability of mean preferred frequency was monitored between hands, conditions, and sessions. Also, mean-adjusted variability of preferred frequency was measured as coefficient of variation.

Continuous time series were converted to an estimate of continuous phase through implementation of the algorithm,

$$\Phi_j = \tan^{-1}[(dX/dt)/X] \qquad (1)$$

where Φ_j is the phase of the individual oscillator j, X is the normalized position of the oscillator rescaled to the interval -1,1 for each movement cycle, and dX/dt is the normalized instantaneous velocity (Scholz & Kelso, 1989). This procedure was deemed appropriate for the present data, as a reduction in movement amplitude was often observed in conjunction with increasing frequency of oscillation (e.g., Beek & Beek, 1988) From these estimates of continuous phase, the collective variable relative phase was determined by,

$$\Phi = \Phi_R - \Phi_L. \qquad (2)$$

Transitional behaviour was examined through measures of time-to-transition in the AL and AR conditions. Subsequently, the stability of time-to-transition was measured over sessions thus providing a measure of stability both before and after exposure to conditions of multifrequency coordination. In multifrequency coordination, the continuous estimate of Φ was a continuously increasing (or decreasing) function i.e., the phase differences between the limbs escalated toward infinity with time since the movement cycles of either limb were defined by different periods. The continuous estimate of Φ was partitioned for the determination of phase attraction. Converting relative phase to the interval [0,0.5], the expected mean phase was 0.25 if indeed the coordination patterns remain perfectly relative. Significant deviation away from the expected value suggested bias toward in-phase (0.0) or anti-phase (0.5). Phase attraction was measured as a proportion of time spent i.e., dwell time, in regions centered about in-phase (0.0-0.167), anti-phase (0.333-0.5), and intermediate phase (0.167-0.333).

Adopting the algorithm of Kelso et al. (1991), discrete relative phase was calculated as

$$\Phi_D = 2\pi tn/Tn, \tag{3}$$

where Tn is any "peak-to-peak" period of one oscillator and tn is the time from this event to a peak onset in the concurrent oscillator. The coherency of the measure Φ_D was examined over the task-defined conditions of multifrequency coordination. It was possible to define alternate time scales with discrete estimates of relative phase (e.g., full cycles, half cycles) in order to capture the dynamics specific to multifrequency coordination. Two estimates of discrete relative phase, denoted Φ_{D1} and Φ_{D2}, were derived. For Φ_{D1} the region between maximal pronation and supination, and vice versa, of the slower moving forearm was normalized to the same interval of phase space (360 degrees) as peak-to-peak displacement of the faster moving limb. Φ_{D1} was expected to lie at 0 (360) degrees under multifrequency conditions. The second estimate,Φ_{D2}, was derived to determine the tendency for coordination between movement reversals of the faster limb, with respect to pronation and supination endpoints of the slower limb. Although perfect 2:1 coordination would return a value of 180 degrees for Φ_{D2}, a priori there was no reason to suspect that Φ_{D2} would not return an estimate consistently offset from 180 degrees.

Variability of Φ_{D1} and Φ_{D2} reflected the stability of coordination under their respective constraints. In consideration of the phase-plane model, variability of relative phase was best represented as a measure of uniformity derived from the decomposition of the respective relative phase angles into sine and cosine components (Burgess-Limerick et al., 1992). The mean of a population of angles represented the angle between the origin and the sum of all vectors. The magnitude of the mean resultant vector determined the uniformity, which was expressed in the interval [0,1] (Mardia, 1972). Under this procedure, variability was not contaminated by abrupt steps between 0 and 360 degrees. The Rayleigh Test of Uniformity was used to determine a confidence interval for the respective mean resultant vector based on a given number of observations (Mardia, 1972, Appendix 2.5, pp. 300).

Phase transitions were examined using a partially interactive procedure which allowed the experimenter to view relative phase profiles via a graphical interface. Details of the procedure and estimates of reliability and validity are reported elsewhere (Byblow et al., 1992). The procedure reported time-to-transition, the interval from trial initiation to the onset of transition.

2.3 Results

2.3.1 Self-Paced Conditions

1:1 Regime

A one-way ANOVA revealed that mean cycle-to-cycle frequencies were stable over sessions in the IP condition ($F_{2,6}=1.274$, $p>0.05$). Also, coefficients of variation of mean preferred frequency were not found to differ between left and right hands ($F_{1,15}<1.0$). Thus, both mean and variability of preferred frequency were consistent across limbs, and stable throughout sessions. Mean relative phase data were analyzed for individual subjects to determine if the observed means differed from the expected value of 0.00. No significant effects were realized in these analyses suggesting that subjects were successful in conforming to the task-defined phase pattern (in-phase) and frequency ratio (1:1).

Multifrequency Regime

Mean preferred frequencies for both fast-moving hand (right-1:2, left-2:1), and slow-moving hand (left-1:2,right-2:1) were analyzed individually for subjects in a one-way ANOVA. In the analyses of the slow-moving hand, there were no effects of hand. Analysis of the faster moving hand replicated these results except for subject 4 who exhibited a faster pace in the right hand i.e., 1:2 pattern ($F_{1,12}=5.001$, $p<0.05$). Coefficients of variation were analyzed in an identical design in order to assess differences in variability of movement frequency in the respective task assignments. There were no significant effects of pattern or hand observed for coefficients of variation.

Estimates of mean relative phase revealed that in both the 1:2 and 2:1 conditions, all subjects exhibited a significant bias toward in-phase coordination (Table 2.1). The initial analyses of phase were expanded upon in compartmentalized analyses of phase attraction. Proportions of time spent in each region were calculated over a 15 second block within each trial. The proportion scores were converted using an arcsin/square-root transformation. The effect of pattern was examined for each subject at regions centered about in-phase, anti-phase, and intermediate phase, respectively. Time spent within the in-phase region did not differ between patterns for any subject ($p > 0.1$), nor were consistent directions observed between pattern means. Subject 3 exhibited significantly greater attraction toward anti-phase coordination in the 2:1 pattern ($p<0.01$), and also in time spent in intermediate phase relations, wherein the greater proportion was observed in the 1:2 pattern ($p<0.05$).

Table 2.1 Translated Mean Relative Phase of Self-Paced Trials in Multifrequency Coordination (t values represent deviation from the Expected Value = 0.25)

Pattern	1:2		2:1	
Subject	Phase	$t_{(6)}$	Phase	$t_{(6)}$
1	0.223	5.729**	0.211	9.546**
2	0.234	3.267*	0.230	2.898*
3	0.221	10.954**	0.226	4.250**
4	0.239	3.361*	0.234	4.260**

* $p<0.05$ ** $p<0.01$

2.3.2 Frequency-Scaling: 1:1 Coordination

Discrete estimates of relative phase captured tendencies of 1:1 coordination at "peaks" and "valleys" of the movement cycles. Differences in variability of relative phase were assessed in measures of uniformity in the interval $[0,1]$ and transformed to the interval $[0,\infty]$. Uniformity scores were analyzed individually for subjects in an anti-phase mode (AL, AR) x pre-transitional plateau design . As illustrated in Figure 2.1, there were main effects of frequency plateau for all subjects such that variability increased over plateaus as transitions approached. In all cases, variability in the final plateau preceding the transition plateau was of equal or greater magnitude than earlier frequency plateaus. Tukey's HSD comparisons revealed that for S2 and S4 the plateau immediately adjacent to the transition plateau was significantly more variable than all preceding plateaus ($p < 0.01$). There were no effects of anti-phase mode, nor did mode interact with plateau.

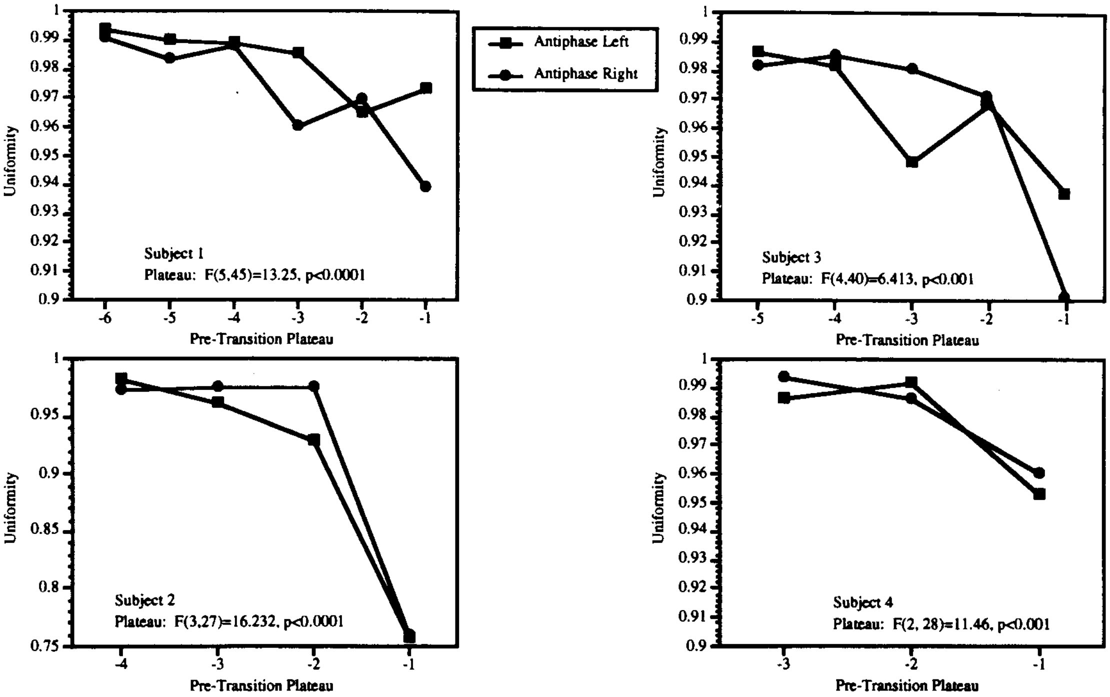


Fig. 2.1. Uniformity measures for AL and AR conditions over pre-transition frequency plateaus.

Phase Transitions

Subjects exhibited state transitions to in-phase coordination from both anti-phase preparations. Time-to-transition was determined for trials in which transitions were evident. These data were collapsed over AL and AR conditions within a one-way ANOVA over sessions for individual subjects. The session means and relevant statistics are reported in Table 2.2. Time-to-transition increased significantly upon exposure to multifrequency regimes for S3, whereas S1 and S2 exhibited means in the same direction, but not to a statistically significant degree.

Table 2.2 Time-to-Transition in 1:1 Coordination: Pre- and Post-Exposure to Multifrequency Regimes

	Time-to-Transition (sec)		ANOVA Results		
Subject	Pre	Post	dF	F	prob.
1	33.80	37.87	1,9	3.50	<0.09
2	25.08	32.70	1,9	4.46	<0.06
3	27.04	33.71	1,11	9.55	<0.01
4	22.57	22.26	1,14	<1.0	

2.3.3 Frequency Scaling: Multifrequency Regime

Phase attraction was measured as proportion of time spent in each phase region for each frequency plateau. Within subject ANOVA's were performed for each pre-defined region separately in a pattern (1:2,2:1) by information (FI,HI) by pre-transitional plateau design. Results indicated that for S2, S3, and S4, attraction toward in-phase increased as oscillation frequency increased ($F_{2,70}$=3.207, $p < 0.05$; $F_{4,144} = 8.231$, $p < 0.0001$; $F_{8,288}$=3.576, $p < 0.001$, respectively), and for S3 and S4, there was a corresponding decrease in time spent in anti-phase regions ($F_{4,144} = 9.721$, $p < 0.0001$; $F_{8,288}$=10.193, $p < 0.0001$). The overall means, denoted as proportion of time spent in each region of phase space, are illustrated in Figure 2.2.

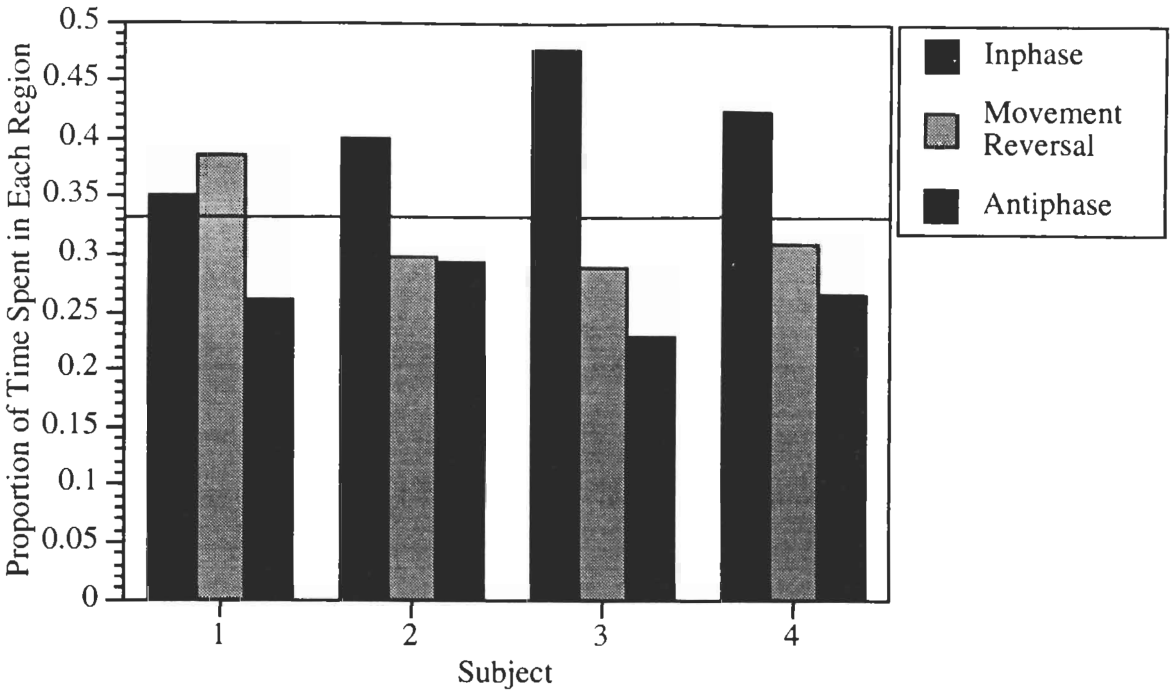


Fig. 2.2. Proportion of time spent in regions of phase space. The horizontal line represents expected values for ideal relative coordination.

Subjects 1, 3 and 4 exhibited greater attraction to in-phase when the 2:1 pattern was adopted ($F_{1,29}$=18.608, $p < 0.001$; $F_{1,36}$=61.54, $p < 0.0001$; $F_{1,36} = 6.568$, $p < 0.02$), whereas the pattern means for S2 did not differ significantly ($F_{1,35} < 1.0$). Phase attraction pathways of S4 are illustrated in Figure 2.3. With respect to information, S1, S3 and S4 demonstrated a significantly greater attraction to in-phase in the HI condition ($F_{1,29}$=28.712, $p < 0.0001$; $F_{1,36}$=39.367, $p < 0.0001$; $F_{1,36} = 7.078$, $p < 0.02$, respectively). No significant difference was observed between the information means of S2 ($F_{1,35}$= 1.568, $p > 0.2$). The data of S3 (Figure 2.4) revealed a significant interaction of pattern and information ($F_{1,36}$=15.811, $p < 0.0005$). Tukey's HSD comparisons suggested that attraction toward the in-phase region was significantly greater in the 2:1/HI condition than in the other three conditions ($p < 0.01$).

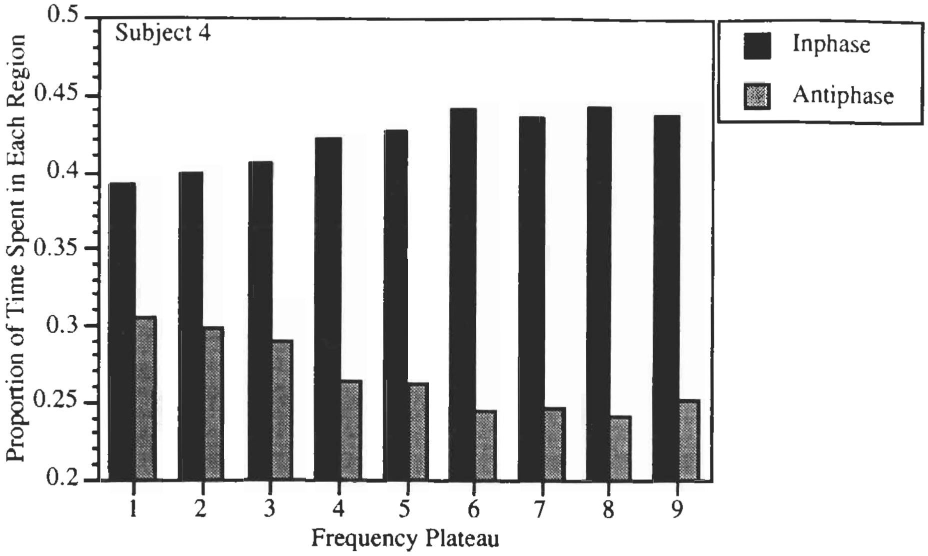


Fig. 2.3. Subject 4- Phase attraction measured as the proportion of time spent within in-phase and anti-phase regions of phase space over pre-transition frequency plateaus.

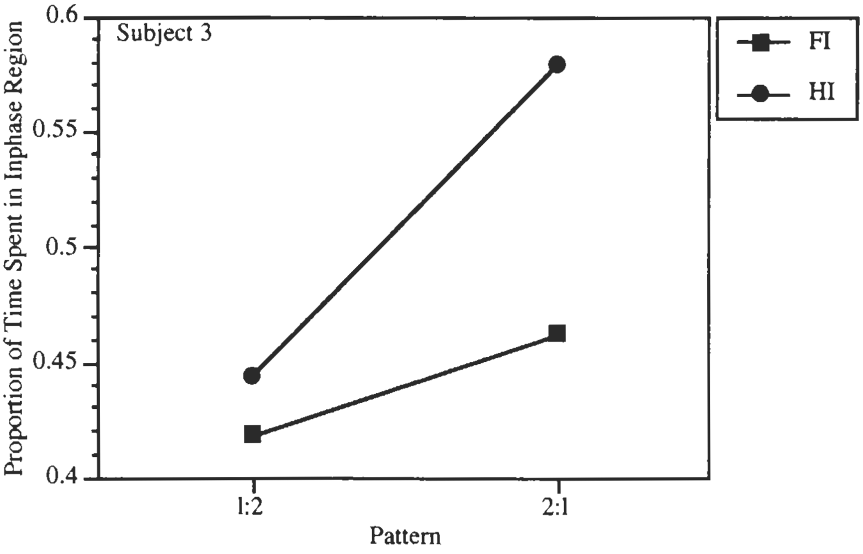


Fig. 2.4. Subject 3- Proportion of time spent in-phase for pattern and information conditions.

Transformed measures of uniformity were analyzed in an information x pattern x pre-transitional plateaus ANOVA for each subject. The same statistically significant effects were observed for measures of uniformity derived from both Φ_{D1} and Φ_{D2} estimates of relative phase i.e., both measures were adequate characterizations of the coordination tendencies in the 2:1 regime. The estimate Φ_{D1} is reported in detail. The data of S4 are reported fully since they represent nearly the complete range of plateau frequencies. (Bifurcations to 1:1 in-phase coordination were observed occasionally at only the final frequency plateau for this subject). The results of these analyses are summarized in Table 2.3.

Table 2.3 Summary of Uniformity Analyses derived from Discrete Estimates of Relative Phase

	Subject							
	1		2		3		4	
	Estimate							
Effect	Φ_{D1}	Φ_{D2}	Φ_{D1}	Φ_{D2}	Φ_{D1}	Φ_{D2}	Φ_{D1}	Φ_{D2}
Information	x	x	*	*	*	**	x	x
Pattern	x	x	**	**	**	**	**	**
IP	x	x	x	x	x	x	x	x
Frequency	*	x	**	**	**	**	**	**
IF	x	x	x	*	x	x	x	x
PF	**	x	x	x	**	x	**	*
IPF	x	x	x	x	x	x	x	x

x- $p > 0.05$ *- $p < 0.05$ **- $p < 0.01$

The main effect of pattern was significant ($F_{1,36}=37.19$, $p < 0.0001$) with greater uniformity in the 1:2 assignment. The mean uniformity scores, reported in Table 2.4, were 0.955 and 0.902 for 1:2 and 2:1 respectively. These means fell above the critical value ($\alpha = 0.1$) of the Rayleigh test of uniformity (Mardia, 1972) for the range $[5 < n < 13]$. The main effect of frequency ($F_{8,288}= 26.333$, $p < 0.0001$) revealed increasing variability with successive plateaus. This effect is illustrated in Figure 2.5. There was a significant interaction of pattern and frequency ($F_{8,288}=3.977$, $p < 0.0005$) suggesting a progressively greater increase in variability for the 2:1 pattern as frequency was scaled (Figure 2.6).

Table 2.4 Rayleigh Test of Uniformity for Means of Multifrequency Pattern for all Subjects

	1:2		Pattern	2:1	
	Φ_{D1}	Φ_{D2}	Estimate	Φ_{D1}	Φ_{D2}
Subject					
1 [8]	0.963**	0.961**		0.945**	0.943**
2 [6]	0.859*	0.895*		0.659†	0.650†
3 [8]	0.951**	0.961**		0.565†	0.573†
4 [12]	0.959**	0.963**		0.917**	0.914**

†- $\alpha = 0.1$ *- $\alpha = 0.01$ **- $\alpha = 0.001$
-square parentheses indicate mean number of observations based on available pre-transitional data

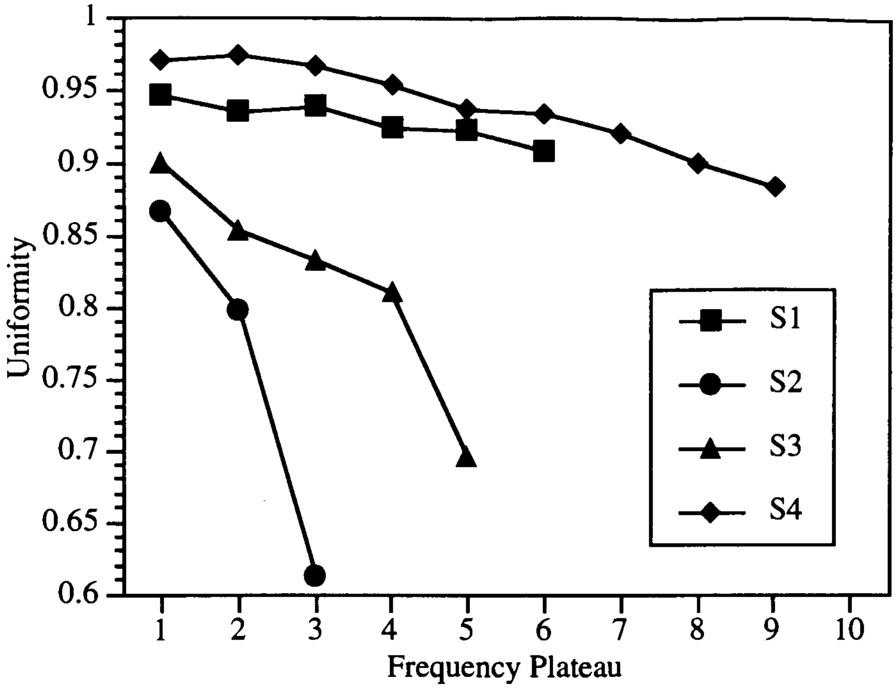


Fig. 2.5. Main effects of frequency plateau for measures of uniformity for all subjects.

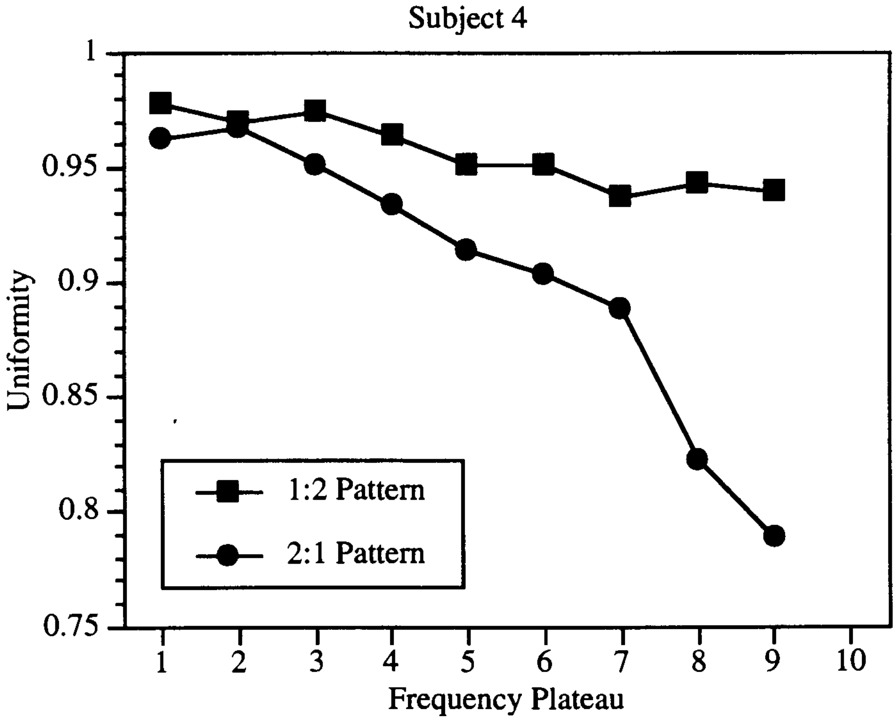


Fig. 2.6. Pattern by frequency plateau interactions of uniformity for S4 and S1.

The data of subjects 1, 2 and 3 compare well to those of S4 (Table 2.4). Subjects 2 and 3 replicated the main effect of pattern. Although this effect did not reach statistical significance for S1, the interaction of pattern x frequency (Figure 2.6) was present for the analysis derived from Φ_{D1} measures and, similar to S4, suggested a greater influence of pattern at higher frequencies. All subjects exhibited a significant main effect of frequency in the expected direction (Figure 2.5). Analyses of measures derived from Φ_{D2} replicated this effect for all subjects except S1, although again the means of this subject were in the expected direction. There was a significant main effect of information for S2 and S3 ($F_{1,16}=4.635$, $p < 0.05$; $F_{1,36}=5.417$, $p < 0.05$) with greater uniformity observed in the HI conditions.

2.3.4 Bifurcations to 1:1 Coordination

Bifurcations from multifrequency coordination to 1:1 coordination were commonly observed, but to a varying degree in different subjects and conditions (Table 2.5). In all observed cases of bifurcations, two effects were prevalent. First, an in-phase pattern of limb-limb coordination was achieved. Second, all bifurcations were manifest by way of the slow hand increasing in tempo to that of the fast hand. Overall, there was a greater tendency toward bifurcations when initially prepared 2:1. With respect to external information, there was a greater tendency for bifurcations in the FI conditions. Bifurcations were observed with S1 in both the HI and FI conditions for 2:1 preparations, but not for 1:2 preparations. Subjects 2 and 3 demonstrated bifurcations in all pattern and information conditions but again, to varying degrees. Finally, S4 did not exhibit bifurcations away from multifrequency coordination in any of the experimental conditions.

Table 2.5 Mean Time-to-Transition and Frequency Count (Trials) of Bifurcations from Multifrequency to 1:1 Coordination

	1:2		Pattern	2:1	
	FI	HI	Information	FI	HI
Subject					
1	----	----		29.01 (6)	37.85 (6)
2	15.96 (9)	32.17 (3)		16.03 (7)	33.43 (4)
3	28.68 (1)	34.64 (5)		26.87 (7)	34.71 (2)
4	----	----		----	----
Totals	(10)	(8)		(20)	(12)

2.3.5 Summary of Results

a. Self-paced conditions did not implicate either limb as inherently more or less stable regardless of hand or frequency assignment. In the analyses of the faster moving hand, a tendency was noted for the right hand to adopt a higher mean frequency, although a corresponding decrease in variability was not observed in coefficients of variation. Both multifrequency patterns revealed a consistent bias toward in-phase coordination, although phase attraction did not differ between patterns.

b. There was considerable evidence for phase attraction toward the in-phase region in the multifrequency conditions, and attraction to this region increased as frequency was scaled. These effects were accompanied by a corresponding decrease in time within the anti-phase region. In-phase attraction was more persistent in the 2:1 assignment than the 1:2 assignment. Finally, there was limited evidence to suggest that the reduction of available information (HI) was reflected in tendencies toward in-phase attraction.

c. Uniformity analyses confirmed the validity of both derivations of discrete relative phase as adequate characterizations of the coordination tendencies in the multifrequency regime. A consistent effect of pattern was observed in uniformity measures derived from discrete relative phase whereby greater uniformity i.e., less variability, was exhibited in 1:2 assignment. Greater variability resulted from the frequency scaling mediated via external pacing. The interaction of pattern and frequency of oscillation reflected a greater degree of instability in the 2:1 assignment.

d. Bifurcations from multifrequency coordination to 1:1 coordination were more commonly observed when prepared in the 2:1 assignment, as well as under the full information condition. Transition data suggested that the low-order (2:1) multifrequency rhythm may be more stable than anti-phase preparations of 1:1 coordination.

e. Critical fluctuations were evident in anti-phase preparations of 1:1 coordination. All subjects demonstrated a decrease in uniformity (increase in variability) in the region preceding transition. There was limited evidence that time-to-transition from anti-phase to in-phase coordination increased after exposure to the multifrequency regime.

2.4. Discussion

2.4.1 Inherent Dynamics

The inherent dynamics of bimanual coordination observed in extant paradigms of bimanual coordination (e.g., Haken et al., 1985) were manifest in the present data, characterized by bistability (in-phase and anti-phase) below a certain critical frequency, and monostability above that frequency (in-phase only). However, the notion that performance asymmetries arise between the respective hand/frequency assignments of multifrequency coordination was also supported and comports well to previous research efforts undertaken in dissimilar paradigms (e.g., Peters, 1985). Greater variability was expressed in the 2:1 hand and frequency assignment (i.e., left-hand-fast), and the disparity in variability of relative phase between 1:2 and 2:1 assignments increased with frequency scaling. That is, the 2:1 assignment was more sensitive to scaling of the control parameter. Phase attraction was characterized by a bias toward in-phase (and away from anti-phase) regions of phase space. These phenomena were more pronounced in the 2:1 assignment under both self-paced, and frequency-scaled regimes. In essence, these findings characterize performance asymmetries by the measured stability at the level of the collective variable arising from the respective hand and frequency assignments. The predominant implication is that performance asymmetries reflect the inherent dynamics of unique bimanual systems contingent upon assignments of task with hand.

2.4.2 Incidental Dynamics

The "information hypothesis" was not consistently supported. The availability of external information was expected to alter the observed dynamics through isomorphism with either the fast hand (FI) or the slow hand (HI). One expectation was that measured stability would increase under conditions in which subjects were biased toward the fast hand (e.g., Peters and Schwartz, 1989). Further it was suspected that subjects would exhibit a predisposition toward attending to the dominant hand (Peters, 1985). Thus , optimal performance and stability was expected in the 1:2 FI condition, and poorest performance in the 2:1 HI condition, assuming hand speed predominates hand preference. The remaining pattern and information conditions were expected to express intermediate levels of stability. The phase attraction data (e.g., Figure 2.4) provided only limited evidence for these predictions. For a single subject, the 2:1 pattern under the HI protocol expressed a greater bias toward the in-phase region. This supports the supposition that the dynamics arising from external information map onto the respective intrinsic dynamics of bimanual systems defined under hand and frequency assignment. The most stable pattern was 1:2 under FI and HI protocols in that order, although these means did not differ significantly.

The effect of the external pacing regime on phase attraction was most evident in the larger data sets of S1, S3 and S4 (i.e., where there were a larger number of pre-transition frequency plateaus). Increased attraction to the in-phase region under the HI protocol suggested that the limited availability of pacing information imposed greater internal timing constraints. The larger relative attraction to in-phase versus anti-phase is a well-noted feature of the bistable attractor landscape underlying the intrinsic dynamics (e.g., Haken et al., 1985), and was most evident when less information was mapped onto the system.

Measures of uniformity revealed a tendency for diminished variability of relative phase in the HI conditions. Given these data, it was not surprising that bifurcations to 1:1 (in-phase) coordination were exhibited most often in the 2:1 FI condition. Intuitively, one might initially expect a compression of variability in relative phase and longer time-to-transition in the FI condition arising from fewer internal timing demands. However, the data of the 1:2 pattern assignment do not support this interpretation. The HI condition revealed compressed variability of relative phase and prolonged time-to-transition with respect to the FI condition. These findings were obtained primarily with S2 and S3. Table 2.4 and Figure 2.5 support the notion that overall, these subjects exhibited the greatest amount of variability. Since order of presentation (of external pacing regimes) was not controlled in this investigation, the main effect of information for these subjects may best be interpreted as a learning effect. It is our contention that the coordination dynamics corresponding to the required frequency ratio may have evolved over the time course of the experiment (e.g., Schmidt et al., 1992). As such, the stability of multifrequency coordination, indexed by increasing uniformity, increased over exposure i.e., information conditions.

2.4.3 Bifurcation Pathways

Bifurcations observed from multifrequency to 1:1 coordination were completely isodirectional. Examination of bifurcation pathways revealed that in all instances the slow hand adopted the kinematic pattern of the fast hand in the formation of an in-phase (1:1) coordination pattern. Thus, the left hand adopted a new frequency and synchronization pattern in the 1:2 assignment, and the right hand initiated bifurcations in the 2:1 assignment. Isodirectional state transitions are common in paradigms of bimanual coordination which directly control synchronization patterns of hand and metronome (e.g., Byblow et al., 1994). Isodirectional tendencies rationalize manual asymmetries, as well as characterizing influences of anchoring i.e., regions of compressed movement variability, which arise from incidental and inherent dynamical resources. As such, these "forces" superimpose in a meaningful and predictable manner with respect to transition pathways. In the present investigation, pathways were dominated by hand/frequency assignment, such that influences arising from forces of manual asymmetries and anchoring, remained latent with respect to qualitative change in behavioural patterns i.e., which hand altered its initially prepared state. With respect to time-to-transition, one might expect quicker overall transitions when prepared initially 2:1 versus 1:2, in accordance with evidence for greater overall stability for the 1:2 assignment. The data of Table 5 do not support this position however. Our interpretation of these data is that in the 2:1 assignment, the right hand must alter its kinematics with respect to the initial preparation, a condition to which right-handers are not predisposed (e.g., Carson et al., 1994). On the other hand, bifurcations from the 1:2 pattern are expected to occur later due to the inherent stability of this assignment, yet may be accelerated since the non-dominant hand is that which alters its kinematics. This interpretation is supported by the data of Table 5, in which no obvious distinctions were revealed in time-to-transition between patterns for subjects who exhibited bifurcations in both preparations. However, it must be stressed that the overall occurrence of bifurcations from multifrequency to 1:1 coordination was higher when initially prepared 2:1 versus 1:2, and thus, the data comport to the stability hypothesis at a qualitative level.

All subjects exhibited transitions from anti-phase to in-phase coordination when prepared under 1:1 mode-locked conditions. However, not all subjects exhibited transitions from 1:2 to 1:1 coordination, under equivalent frequency scaling parameters. In terms of stability, it is apparent that the intrinsic dynamics corresponding to in-phase and anti-phase coordination reflect a stronger influence on system behaviour than those forces which accrue from the so-called Farey-tree dynamics (i.e., the tendency to bifurcate from higher-order to lower-order frequency ratios) (e.g., Peper et al., 1991). Instabilities emerged in anti-phase preparations of 1:1 coordination at lower oscillation frequencies than in multifrequency preparations (most notably, 1:2 assignments). Thus, stable multifrequency coordination was preserved at and beyond transition frequencies in 1:1 coordination. This comports with the suggestion that absolute coordination (characteristic of the 1:1 regime) may indeed be the exception rather than the rule for coordinated behaviour (e.g, Kelso et al., 1991). A system which "lives" rigidly within a mode-locked state as characterized by anti-phase coordination possesses less flexibility, and hence less stability, than a system which explores the full region of phase space (from in-phase to anti-phase), in spite of the complexity of higher-order rhythms.

2.4.4 Models of Bimanual Coordination

The present data stress the need for inclusion of asymmetries within dynamical models of bimanual coordination (e.g., Carson, 1993), although not in the form of symmetry breaking (e.g., Kelso & Jeka, 1992; Schmidt et al., 1993 b) which dictate that component oscillators differ in eigenfrequency. Neither self-paced nor frequency-scaled conditions in the present 1:1 treatments revealed fixed point drift of relative phase as would be predicted by models of symmetry breaking. At the level of limit-cycles, our data suggest nondiscernible differences in amplitude/frequency characteristics of the left versus right limb under self-paced conditions in both 1:1 and multifrequency regimes.

With respect to multifrequency coordination specifically, we suggest that models which incorporate phase attraction as a parameter be pursued (e.g., DeGuzman & Kelso, 1991). Clearly, phase attraction dynamics were a predominant force guiding the observed behaviour within the present experimental protocol. The phase-attractive circle map framework as proposed by DeGuzman & Kelso (1991) may be modified within its local parameter space to account for asymmetries such as those observed between 1:2 versus 2:1 regimes. Essentially a discretized version of the Haken et al. (1985) model, the phase-attractive circle map describes the evolution of phase over iterations such that,

$$\Phi_{n+1} = \Phi_n + \Omega - K/2\pi(1 + A\cos 2\pi\Phi_n)\sin 2\pi\Phi_n \qquad (4)$$

The map relies on two parameters, A and K, where A expresses the bistability of relative phase (i.e., the relative importance of the intrinsic dynamics which account for phase attraction), and K is a nonlinear coupling parameter. For any frequency ratio Ω, there may exist a (finite) set of possible functions relating K to A which yield stable multifrequency coordination, and subsequently, a finite set of solutions in K-Ω space (known as Arnold tongues). The width of Arnold tongues reflect the stability of frequency lockings. This dynamical feature rationalizes why low-integer ratios, characterized by wider tongues, are more commonly observed in biological systems, and why bifurcations occur from high-order to low-order ratios (Kelso et al., 1991). We propose that the observed differences in stability between the assignments of 2:1 (1:2) coordination examined here can be regarded as a difference in the prescribed function relating K to A between the respective assignments. Specifically, it appears that the right-hand-fast assignment possesses dynamics which reflect a greater influence of the underlying intrinsic dynamics (a larger A) for any given K, resulting in wider Arnold tongues, and hence greater stability. Under this interpretation, the 2:1 assignment moves from bistability to monostability earlier than the 1:2 assignment. The shift toward a monostable dynamic creates inflexibility and subsequent loss of stability of the existing frequency ratio, whereby the system seeks out a more stable (i.e., lower order) pattern.

2.5. Conclusion

Performance asymmetries in multifrequency bimanual coordination reflect qualitative and quantitative differences characterized by the intrinsic dynamics specific to assignments of task with hand. Current models of human coordination (e.g., Carson et al., 1994; DeGuzman & Kelso, 1991) have been proposed, and those which assume symmetry between the components rejected. However, attention as a hypothetical construct remains ill-defined within the dynamical framework. Partial success was achieved in the characterization of attentional bias within the language of dynamical systems, although further explorations will serve to address attention, and asymmetries, at the level of analysis relevant for human coordination.

3. Experiment 2

Temporal Variability in Multifrequency Coordination

3.1. Introduction

The focus of this study is directed toward the role of timekeeping in rhythmic movement, and particularly in rhythmic units which maintain multifrequency relations. Timing and stability are said to be essential features of bimanual coordination (Schöner & Kelso, 1988 a). Within the dynamics framework, stability and more importantly, loss-of-stability in bimanual coordination has been examined in many paradigms of rhythmicity (e.g., Byblow et al., 1994; Byblow et al. ,in press; Haken et al., 1985; Kelso, 1981, 1984; Kelso & Scholz, 1985; Schmidt et al., 1990), although few attempts have been made toward the characterization of multifrequency coordination specifically (Experiment 1; DeGuzman & Kelso, 1991; Swinnen & Walter, 1993). The present study follows from Experiment 1 in the characterization of the multifrequency coordination, and the role of performance asymmetries when the limbs are assigned nonidentical roles in frequency- a necessary constraint of multifrequency relations. An examination of temporal variability in multifrequency coordination is provided which is sensitive to: a) the inherent dynamics of multifrequency bimanual coordination, and b) the neural architecture (e.g., central timekeepers, or pattern generators) deemed responsible for the timing of movements observable at the level of overt behaviour.

The adopted strategy owes greatly to Wing & Kristofersson (1973), where it was shown that in a repetitive tapping task, the inter-tap variability could be partitioned such that independent components of the neural substrate could be identified if certain boundary conditions in the data were met. One component was that of a timekeeper responsible for the inter-tap (or inter-cycle) phasing of the unit. The other component was responsible for the implementation of the movement itself i.e., the intra-cycle component associated with delays in the motor system (see Figure 1.2).

3.1.1 Derivation of the Two-Process Model (Wing & Kristofersson, 1973)

The central tenet of the two component model of response timing in repetitive (or rhythmic) movement is that temporally abutting cycles will be negatively correlated. In other words, a period of long duration will be followed by a shorter than average period, and so on. To see how this prediction arises we must consider that at a regular interval T, a timekeeper is assumed to emit a pulse that initiates a response at the implementation (motor) level. Following a short delay, the overt behaviour is measured. Thus, the period of interval j, τ_j, of a rhythmic movement can be viewed as the sum of the timekeeper interval T_j, plus the difference of motor delays D_{j-1} and D_j which initiate and terminate the interval respectively. Therefore,

$$\tau_j = T_j + D_j - D_{j-1} \tag{1}$$

Assuming T and D are independent random variables with associate variances, it follows that,

$$\sigma^2{}_\tau = \sigma^2{}_T + 2\sigma^2{}_D \tag{2}$$

Although $\sigma^2{}_\tau$ can be obtained directly from the data series, $\sigma^2{}_T$ and $\sigma^2{}_D$ must be derived from the covariance estimate of successive cycle periods. We note that the variance estimate (2) is simply the lag 0 covariance,

$$\mathrm{cov}(\tau_j,\tau_j) = \Sigma(\tau_j-\tau)^2/N \tag{3}$$

where τ is the mean period. The assumption of independence between T and D reveal that the lag 1 covariance structure reduces to a measure of motor delay variance:

$$\mathrm{cov}(\tau_j,\tau_{j-1}) = -\sigma^2{}_D \tag{4}$$

where,

$$\mathrm{cov}(\tau_j,\tau_{j-1})= \Sigma(\tau_j-\tau)(\tau_{j-1}-\tau)/N-1 \tag{5}$$

The covariance structure of all lag $k > 1$ however, reduce to expected values of zero. Thus, correlations of lag $k > 1$ are also expected to be zero since,

$$\mathrm{cor}(\tau_j,\tau_{j-k}) = \mathrm{cov}(\tau_j,\tau_{j-k})/\sigma^2_\tau \tag{6}$$

The lag 1 autocorrelation therefore is most easily expressed as the ratio of (2) to (4),

$$\mathrm{cor}(\tau_j,\tau_{j-1})= -1/(2+\sigma^2_T/\sigma^2_D) \tag{7}$$

Thus , the lag 1 autocorrelation is predicted to be negative, and bounded by the values 0 (large σ^2_T relative to σ^2_D), and -0.5 (large σ^2_D relative to σ^2_T).

From (4) and (7) it is important to recognize that the negative lag 1 dependence does not implicate a fed-back influence from one cycle to the next, but rather, an inevitable consequence of the inherent motor delays. Therefore, a long motor delay at cycle j-1 induces a long j-1 cycle period and subsequently, a short j cycle period. As the covariances reveal, it is assumed that each clock output is independent from every other as is each motor delay. Since clock and motor sources are also independent of each other, the system is essentially open-loop.

A number of important features regarding temporal variability have been discovered in treatments of unimanual and bimanual repetitive movement. From the seminal data of Wing and his colleagues(cf. Wing, 1980) it has been shown that under certain boundary conditions in unimanual tapping, timekeeper variability increases proportional to inter-response interval, whereas variability associated with motor delays remains relatively stable. Thus, the inherent variability associated with longer response intervals is prescribed to variability in timekeeping which are presumed to arise from higher cortical structures such as the cerebellum (Ivry & Keele, 1989). In contrast, the phasing of relations between muscles within a cycle, as prescribed by the so-called central pattern generators of rhythmicity/locomotion, is captured in the motor variance conforming to the suggestion that timing and pattern generation functions remain independent. The intracycle pattern generator may be conceptualized as an overdamped oscillator driven by (entrained with) the timekeeping network (e.g., Lennard, 1985; Turvey et al., 1989).

3.1.2 Sources of Clock Variability

Turvey and colleagues extended the two component model of Wing & Kristofersson (1973) to the domain of rhythmic movement in analyses of in-phase and anti-phase coordinations (Turvey et al., 1986), and for rhythmic units which differed in their characteristic periods in absolute coordination (Turvey, et al., 1989). In the former study, the authors noted that variability in absolute coordination varied as a function of relative phase, Φ, such that period variability was greater for anti-phase versus in-phase coordinations. Specifically, the greater variability anti-phase was prescribed to the clocking process. The contention put forth (Turvey et. al., 1993) is that the modal task space attractor acts implicitly as a timekeeping function with greater stability when $\Phi = 0$ than when $\Phi = 180$. Further, the model of Haken et al. (1985) suggests that the relative strength of the attractor corresponding to anti-phase is weaker than that corresponding to in-phase for any stable oscillation frequency, a finding which has received considerable experimental support (e.g., Byblow, et al., in press; Scholz et al., 1987).

A feature also related to timekeeping was evident in the findings of the Turvey et al. (1989). In their study of absolute coordination, the temporal variability of the limbs in rhythmic coordination were characterized by a *single* timekeeping function i.e., correlations between right and left clock variance estimates were significant and positive. This was suggested to reflect not the coupling of two local clocking mechanisms, but the formation of a globally defined clock as a feature of cooperativity as the formation of a unitary process. Of interest in the present investigation is the role of timekeeping when the limbs are prepared in a continuously variable phase relation i.e., characteristic of multifrequency coordination. In this regime coordination is driven by phase attraction i.e., synchronization at anti-phase and in-phase regions of phase (e.g., Experiment 1). At issue is whether or not:

a) structures of timekeeping underlie the basis of performance asymmetries between assignments of dominant (non dominant) hand to dominant (non dominant) frequency;

b) phase attraction to anti-phase, which is known to relate inversely to frequency of oscillation, maps one-to-one with clock variance;

c) a unitary clocking process emerges despite the maintenance of disparate frequencies.

Prediction a) follows from Experiment 1 by addressing the role of frequency relations between the respective oscillators which exhibit reciprocal forcing (i.e., coupling) in bimanual regimes (e.g. DeGuzman & Kelso, 1991). In the present study, the terminology of driver and driven relations will be adopted to describe the forcing of the faster (driving or dominant) limb on the slower (driven) limb. Prediction b) was also implicated in defining the emergent coordination patterns of Experiment 1. Prediction c) is novel to the present regime.

3.1.3 Sources of Motor Variability

Using the oft-cited wrist-pendulum paradigm of Kugler & Turvey (1987), the data of Turvey et al. (1989) revealed that by increasing the disparity between the characteristic periods of the pendula swung in an alternate mode of coordination, an associated increase in motor delay variance was observed in the absence of an associated increase in timekeeping variability. However, the above study did not (attempt to) assess the difference of manipulating the characteristic period of the left versus right wrist-pendulum system (only the right was manipulated). In an investigation by Wing et al. (1989), variability in timing was examined in alternate tapping i.e., a discrete movement correlate of anti-phase rhythmic coordination. An important aspect of the latter data with respect to asymmetries was that motor-delay variances were equal between left and right hands. These data agree with the suggestion that asymmetries, while expressed in the dynamics of relative phase in tasks of bimanual coordination (e.g., Byblow et al., 1994), may not be manifest at the level of the limbs themselves. Thus asymmetries may not persist within associated motor delays, or within state dynamics at the level of limit-cycles (e.g., Experiment 1) for example, when the prescribed frequencies are essentially below the maximal rates of responding.

In the present investigation of rhythmic movement, it was predicted that motor variances would not differ between left and right limbs in unimanual preparations. However, in multifrequency coordination, performance asymmetries were anticipated between assignments of frequency to hand i.e., 1:2 versus 2:1. If such asymmetries are expressed at the implementation level in bimanual preparations, which are absent in unimanual preparations, and these vary over bimanual assignments, this would support the notion of differential bi-directional coupling forces in the inherent dynamics of the respective assignments. Nondifferent motor variances between unimanual and bimanual assignments in general lend support to the notion that the forces of coupling in bimanual coordination arise solely between the respective timing (inter-cycle phasing) networks (e.g., Yaminishi et al., 1980) of the oscillators themselves.

3.1.4 The Role of Information in Temporal Variability

Wing et al. (1989) demonstrated informally an effect of feedback in timing variability. Their observations revealed that the withdrawal of auditory information increased the variability of associated response intervals. This suggestion has important implications for the two-process model in general if in fact the information provided via auditory demarcations of response serve the system in a fed-back manner. An alternative to the feedback interpretation is that the external information serves to anchor the state variables of the limit-cycle dynamics. This effect has been observed experimentally in compressions of variability in amplitude (position) under a variety of rhythmic movement protocols (Beek, 1989; Byblow et al., 1994), and agrees with the suggestion that information subserves stability as an inherent, and incidental, dynamical resource (Beek & Bingham, 1991).

The two-process model provides a means for assessing whether or not temporal variability is compressed in a manner which supports an interpretation of autonomy (i.e., open-loop) versus non-autonomous (closed-loop) whereby the assumptions of the two-process model are violated. The present experiment was designed specifically to contrast conditions of external information (present or absent) in self-paced and frequency scaled regimes to examine these issues.

3.2. Methods

3.2.1 Subjects

Four right-handed male subjects (ages 22, 24, 35, 42) participated on a volunteer basis.

3.2.2 Apparatus

The class of movement considered was that of finger flexion and extension i.e., the rhythmic analogue of repetitive finger tapping. The subject was seated in a comfortable position (fully adjustable) with arms extended forward and rested in an upright (pronated) position. The hands were positioned beneath a small lever (8cm length, 4mm diameter) which was secured to the second metacarpal via adhesive tape such that the axis of rotation was proximal to the carpometacarpal joint permitting finger flexion and extension. As in

Experiment 1, potentiometers transduced angular displacements. The sampling frequency of all series was 250 Hz. The remainder of data acquisition procedures were equivalent to experiment 1. An auditory metronome (50 msec) was once again generated via computer control.

3.2.3 Protocol.

The experiment extended over 9 sessions of approximately 45 minutes each. Sessions included 36 trials of 60 second duration, entailing approximately 16,000 cycles of movement per subject. In the first six sessions, unimanual conditions were imposed in order to examine baseline estimates of temporal variability (and respective components) at of the respective oscillations.in isolation. Bimanual (multifrequency) conditions were performed over the final three sessions. Subjects were asked to initiate flexion and extension of the finger under self-paced conditions or in synchronization (flexion) with the metronome. Subjects indicated when synchronization was achieved at which time data collection was initiated. In all cases subjects were instructed to maintain the original frequency of oscillation for the duration of the trial.

Unimanual Oscillations

Hand was alternated between trials. As in the traditional induction/continuation paradigm (Wing & Kristofersson, 1973) the subject produced movements in synchronization with the metronome for 30 seconds (induction) after which time the metronome was removed while the movement was maintained for another 30 seconds (continuation). Trials were blocked in groups of 10 where the continuation phase provided either: a) no external information, or b) an auditory signal (50 msec) which signified the flexion excursion (i.e., feedback). In the case of the latter, there was a one cycle interval between induction and continuation phases so that the subject was aware when the source of auditory information had changed from the metronome (induction) to movement information (continuation). The order of the information blocking was balanced across subjects.

In self-paced conditions, auditory information which signified the flexion excursion was present for the first half of the trial (self-paced analogue of the continuation condition "b" above), after which time it was removed such that the remainder of the trial was completed in the absence of an auditory signal (self-paced analogue of the continuation condition "a" above).

Multifrequency Bimanual Coordination

Assignments of limb to frequency (left-fast versus right-fast) were alternated between trials. Subjects were instructed to synchronize flexion of the faster oscillating finger with the metronome while maintaining a 2:1 pattern between the fingers. Information during continuation was blocked in groups of 12 trials for the session. Self-paced conditions were completed under the same information protocol of unimanual conditions.

3.2.4 Design

All subjects completed all conditions in unimanual and multifrequency sessions. The factors of side (left, right), information (present, absent), and frequency (0.7, 1.0, 1.4, 2.0, 2.8 Hz) were investigated under paced (inducted) conditions. Frequency was not a factor in the self-paced conditions. In multifrequency conditions the factors of assignment (left-fast , right-fast), information (present, absent), and frequency (0.7-1.4, 1.0-2.0, 1.4-2.8 Hz) were examined.

3.2.5 Data Treatment and Analyses

In-house algorithms were developed in order to partition period variances as outlined in Section 1.2. Lag 1 correlations, and clock and motor variances were computed. From these data group-averaged procedures were used to plot the correlation and variance estimates against period (frequency). Regression equations were used to determine the slope of the correlation, clock, and motor functions (Ivry & Corcos, 1993). Contrasts were derived between unimanual conditions and the respective limb in bimanual conditions.

Measures of relative phase were determined via discrete estimation as outlined in Experiment 1. Particularly, an algorithm was derived such that stability at prescribed frequency ratios and assignments (e.g., 1:2, 2:1) returned stable relative phase values. A fine-grained analysis of relative phase was garnered through measures of uniformity i.e., a measure inversely proportional to variability. Uniformity measures in the range $[0,1]$ were transformed to the interval $[0,\infty]$ (Mardia, 1972).

Phase attraction was determined for multifrequency conditions from pseudo-continuous relative phase estimation i.e., relative phase estimates interpolated between the sampling interval. Relative phase series' were transformed into the range 0 (in-phase) to 0.5 (anti-phase) and partitioned into three regions about in-phase (0.0-0.17), anti-phase (0.33- 0.5), and intermediate phase (0.17-0.33). An arcsin transformation was used to treat the proportion data. Phase attraction was expressed as a ratio of in-phase to anti-phase and this ratio was used in subsequent analyses. The contention put forth is that the ratio expresses the relative importance of the stable intrinsic dynamics, in-phase and anti-phase, in a single measure.

3.3. Results

3.3.1 Lag 1 Correlations

Lag 1 correlations were determined in self-paced and induction-continuation protocols under both unimanual and bimanual regimes. Although there were violations to the two-process model, the lag 1 correlations were in the theoretically predicted range of -0.5 - 0.0

in a majority of the trials[3]. Figure 3.1 shows the degree of conformity in unimanual conditions in the induction-continuation protocol. The area between the horizontal bars represents the theoretically predicted range. In multifrequency assignments, Figure 3.2 illustrates the lag 1 correlations of left versus right limbs under self paced conditions collapsed over information conditions. The areas between the horizontal and vertical bars represents the theoretically predicted range. The horizontal region represents the driver in the multifrequency relation, the vertical region, the driven. The disparity in degree of conformity between driver (low) and driven (high) is evident. Lag 1 correlations were regressed for driver on driven. As evident if Figure 3.2, the r^2 values revealed no correlation (both $r^2<0.03$) for the 1:2 and 2:1 assignments.

---

[3] The two process model also predicts that autocorrelations of lag $k>1$ will be zero. The autocorrelations for lag $k=2,3$ were determined. Few occurences of nonzero correlations were found for lag 2,3 correlations in the absence of lag 1 violations. As with violations for lag 1 correlations, data which expressed violations at lag $k>1$ were discarded from further analyses.

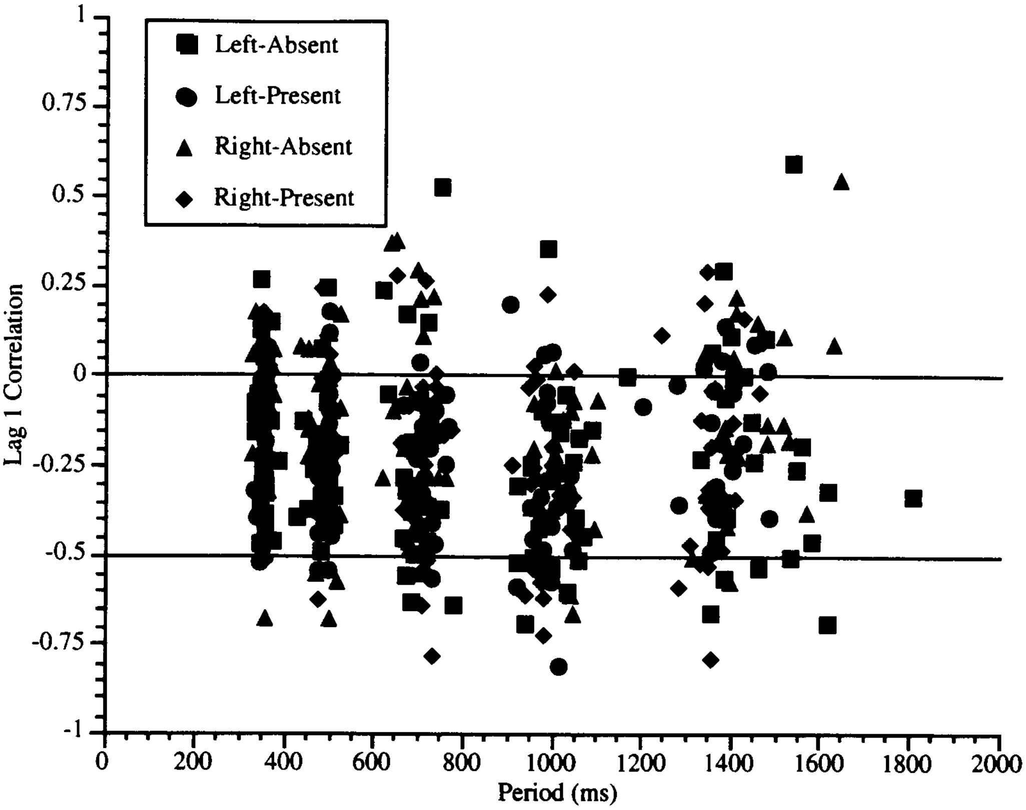


Fig. 3.1 Lag1 autocorrelations versus period of externally paced unimanual movements under the two infomation protocols. The region between horizontal lines represents the theoretically predicted range of the two process model which accounted for 71% of the data.

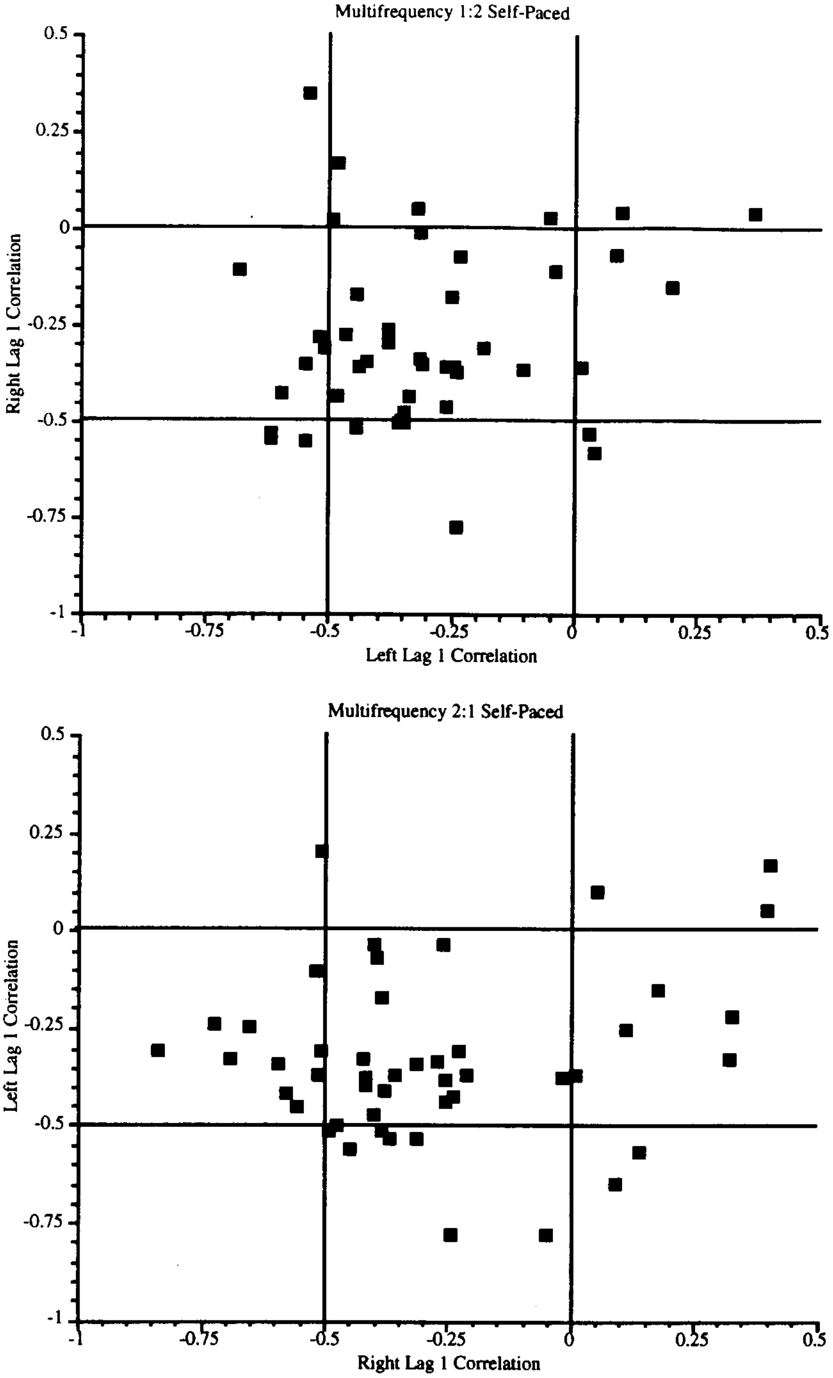


Fig. 3.2 Lag 1 autocorrelations of driver versus driven limb in self-paced multifrequency bimanual preparations averaged over information conditions.

3.3.2 Relative Phase

In order to determine the relative stability of each multifrequency assignment, discrete estimates of relative phase were derived, and measures of uniformity determined. Uniformity measures were assessed against the critical values of the Rayleigh Test of Uniformity (Mardia, 1972, p. 300) for numbers of observations in the range of 30 (0.7-1.4 Hz), 40 (1.0-2.0 Hz), and 55 (1.4-2.8 Hz). The Rayleigh test indicates whether directional data are sufficiently uniform to derive measures of central tendency and dispersion. All conditions satisfied the criterion of uniformity at or below an α-level of 0.05 except at the lowest movement frequency in the 2:1 assignment ,where α was between 0.1 and 0.05. The data were accepted as uniform and analyzed in a 2 assignment by 2 information by 3 frequency between ANOVA (trials as subjects) of multifrequency conditions The 1:2 assignment was significantly more stable in relative phase than the 2:1 assignment ($F_{1,273}=147.90$, $p<0.0001$). The grand means (transformed) were 1.50 and 0.88 for 1:2 and 2:1 respectively. The effect of information was also significant with greater overall stability when information was present coincident with movement endpoints ($F_{1,273}=4.640$, $p<0.05$). There were no effects of frequency nor were there any interactions (all $p> 0.2$). Separate analyses were performed on data from self-paced regimes in a 2 assignment by 2 information design. The analysis revealed that overall measures of uniformity were higher in the 1:2 assignment ($F_{1,184}=99.901$, $p<0.0001$). The grand means (transformed) were 1.464 in 1:2 assignment, and 0.819 in the 2:1 assignment. There was no effect of information in the self-paced regime.

3.3.3 Clock and Motor Analyses

3.3.3.1. Self-Paced

Clock and motor variances (SD) from unimanual preparations were regressed against mean period in independent regression analyses over hand (left, right) and information (present, absent). The regression coefficients were all significant ($p<0.01$). Coefficients of determination are presented with coefficient (slope) and intercept data in Table 3.1. Evident from these data are positive coefficients (increasing variance with increasing period) for both motor and clock variances, and intercepts which regress toward zero. Contrasts of hand, hand over information, and information over hand, revealed no significant differences (all p>0.1) for t-tests of the period coefficients (i.e., slopes) regressed against clock and motor variances.

Table 3.1 Unimanual Self-Paced: Regressions of Clock and Motor SD on Period and Contrasts between Hand and Information

Hand	Left		Right	
Component	Clock	Motor	Clock	Motor
Information				
Present	0.049x - 7.14	0.049x - 9.7	0.036x -3.15	0.029x - 2.42
r^2	0.473 **	0.287 **	0.415 **	0.179 *
t_{hand}	1.10	1.12		
dF	64			
Absent	0.046x - 0.56	0.078x - 18.7	0.042x -4.34	0.047x - 10.4
r^2	0.145 *	0.507 **	0.334 **	0.355 **
t_{hand}	0.16	1.67		
dF	60			
t_{info}	0.13	1.56	0.46	1.06
dF	67		57	

* $p < 0.05$, ** $p < 0.01$

3.3.3.2 Induction-Continuation: Unimanual

Independent regressions of motor and clock SD against period were determined for data acquired in the continuation phase of the pacing protocol (Figure 3.3). The regression data are shown in Table 3.2 for all trials which conformed to the two-process model. All regressions were significant and positive. In identical contrasts of the self-paced analyses, independent t-tests determined that the slopes of the regressions did not differ (all p>0.1).

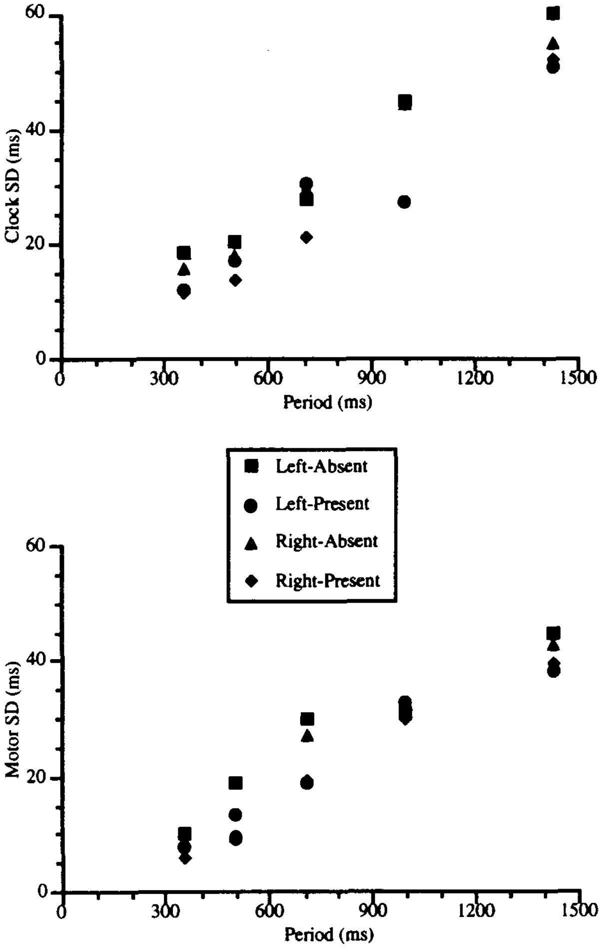


Fig. 3.3 Clock and motor component SD versus period of limbs under unimanual paced conditions.

Table 3.2 Unimanual Metronome Paced: Regressions of Clock and Motor SD on Period and Contrasts between Hand and Information

Hand	Left		Right	
Component	Clock	Motor	Clock	Motor
Information				
Present	0.040x + 1.85	0.030x + 3.03	0.041x - 0.02	0.034x - 3.04
r^2	0.433 **	0.341 **	0.485 **	0.416 **
t_{hand}	0.15	0.71		
dF	150			
Absent	0.035x + 0.03	0.032x - 3.61	0.044x -6.27	0.034x - 6.51
r^2	0.387 **	0.350 **	0.562 **	0.403 **
t_{hand}	1.38	0.29		
dF	165			
t_{info}	0.75	0.40	0.39	0.02
dF	167		148	

* $p < 0.05$, ** $p < 0.01$

3.3.2.3 Induction-Continuation: Bimanual Multifrequency

Independent regressions of period on clock and motor SD were performed for each limb in each assignment. Only trials in which the lag 1 correlations of both limbs fell within the theoretical bounds of the two-process model were included. All regressions but one (2:1, right-motor) were significant and positive. Independent t-tests between clock coefficients and motor coefficients were performed for contrasts of assignment on hand, and of hand in similar role in assignments (Table 3.3). Contrasts of assignment (1:2, 2:1) for each hand revealed that for each hand the slopes of the motor coefficients were steeper when the hand was assigned to the role of driver (both $p< 0.01$). However, when contrasting the hands when assigned similar roles (e.g., left-1:2 versus right-2:1) there were no differences in clock or motor regressions for driver or driven contrasts. The clock and motor SD means are plotted against period in Figure 3.4.

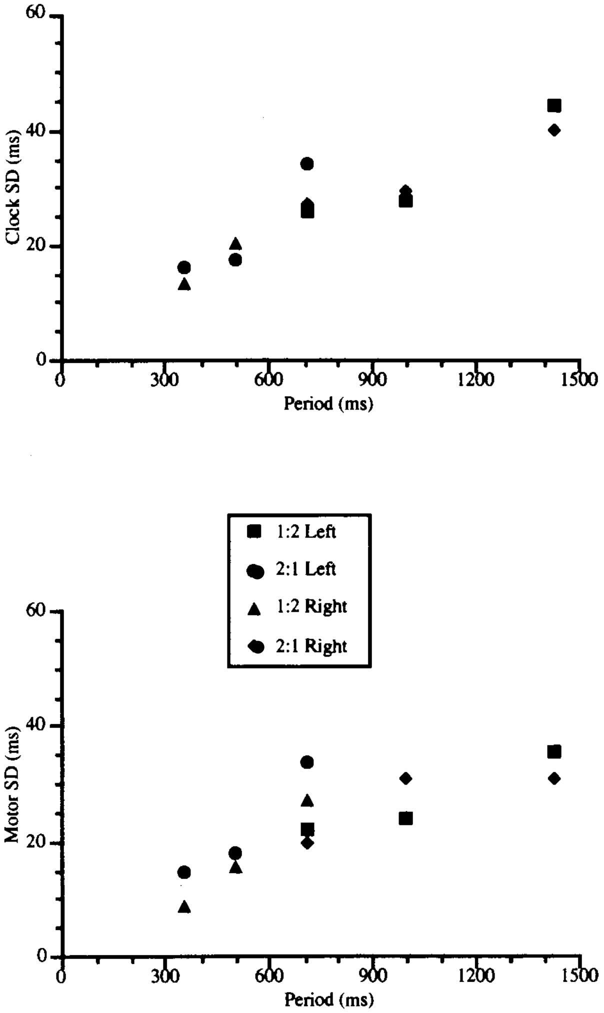


Figure 3.4 Clock and motor component SD versus period of limbs under multifrequency paced conditions.

Table 3.3 Multifrequency Metronome Paced: Regressions of Clock and Motor SD on Period and Contrasts of Assignment for Hand and Hand in Similar Roles in Assignments

Hand	Left		Right	
Component	Clock	Motor	Clock	Motor
Assignment	1:2		2:1	
	0.029x + 3.52	0.021x + 5.26	0.019x + 12.4	0.016x + 9.87
r^2	0.202 **	0.149 **	0.067*	0.050
t_{driven}	0.84	0.46		
dF	133			
Assignment	2:1		1:2	
	0.055x - 5.23	0.061x - 8.90	0.040x - 0.43	0.058x - 12.9
r^2	0.145 **	0.255 **	0.148 **	0.354 **
t_{driver}	0.94	0.23		
dF	207			
t_{assign}	1.49	2.84 **	1.53	3.57 **
dF	164		176	

* $p < 0.05$, ** $p < 0.01$

Separate multiple regressions were performed for the clock and motor variances (SD) of the driven oscillator (left for 1:2, right for 2:1) regressed against five independent variables: the clock variance (SD) and motor variance (SD) of the driver, the period of the driven, and the phase attraction ratio, and the uniformity of relative phase. Only trials in which the lag 1 correlations of both limbs fell within the theoretical bounds of the two-process model were included. The multiple regression coefficients and statistics are provided in Table 3.4. Coefficients of determination were positive and significant ($p<0.05$) for all but one regression (2:1-Clock, $p<0.1$). Under the 1:2 assignment, period was a significant predictor of left clock variance, whereas uniformity approached significance ($p<0.06$) as a predictor of left motor variance. Under the 2:1 assignment, phase attraction was a significant (negative) contributor to right clock and right motor variance. No other independent variables served as significant predictors in the multiple regressions.

Table 3.4 Multifrequency Metronome Paced: Regression Coefficients from Multiple Regressions of Driver Clock SD, Driver Motor SD, Driven Period, Phase Attraction, and Uniformity on Driven Clock (Motor) SD

Assignment	1:2		2:1	
	Regression Coefficients			
Driven Component	Clock	Motor	Clock	Motor
Uniformity	5.13	11.61 †	-7.14	-0.779
Phase Attraction	5.99	6.25	-17.0 *	-21.1 **
Driven Period	0.023 *	0.007	0.053	0.009
Motor SD (Driver)	0.198	0.255	0.386	0.183
Clock SD (Driver)	0.005	0.105	0.213	0.081
r^2	0.274 *	0.281 **	0.175 †	0.200 *

† $p < 0.1$,* $p < 0.05$, ** $p< 0.01$

3.3.2.4 Contrasting Unimanual versus Bimanual Multifrequency Clock and Motor SD

Contrasts of motor and clock SD versus period regressions were determined for each hand between unimanual and multifrequency assignments. Unimanual regressions were re-computed for only those frequencies of the particular multifrequency contrast. Thus, trials in the 0.7-1.4 Hz range were included in the unimanual regressions for contrast with the driven limb in the relation, whereas unimanual trials in the 1.4-2.8 Hz range were contrasted with the driver in multifrequency assignments. Coefficients of determination were significant and positive between period and clock (motor) SD for the new regressions (all $p<0.01$) for all but the right limb in the 1.4-2.8 range ($p>0.1$). It was in this condition in which the only significant contrast was observed whereby the slope of the right motor regression in the 1:2 relation was deemed steeper than the (nonsignificant) slope re-computed for the unimanual case.

3.3.3 Summary of Results

a. Lag 1 correlations fell predominantly between -0.5 and 0.0 conforming to the prerdictions of the Wing & Kristofersson (1973). However, the number of violations increased from unimanual to multifrequency preparations. External information did not implicate a fed-back influence on variability.

b. Variability ascribed to clock and delay sources increased proportionately with period, although the effect of period did not differ in effects on clock and motor delay variability.

c. Neither left nor right limb was implicated as more or less variable in estimates of clock or motor variance. Variability estimates did not differentiate between unimanual and multifrequency preparations for either limb.

d. Uniformity estimates of Φ implicated the 2:1 assignment as inherently less stable than the 1:2 assignment, and an increase of stability of Φ with the presence of external information.

e. There was limited evidence to implicate Φ dynamics in the prediction of clock and motor variance.

3.4. Discussion

3.4.1 Intrinsic Dynamics of Multifrequency Coordination

The relative phase dynamics suggest that multifrequency coordination is characterized by performance asymmetries. As in Experiment 1, greater stability in relative phase was evident for the assignment in which the right (dominant) limb maintained the dominant (driving) frequency. This feature of bimanual coordination has been attributed to the coupling dynamics inherent to the coordination itself (e.g., Experiment 1; Byblow et al., 1994; Carson et al., 1994), rather than that which arises from higher-order constructs such as attention (e.g., Peters, 1985). Specifically, the relative importance of the intrinsic dynamics (attraction to in-phase and anti-phase) varies as a function of the assignment frequency to hand. It has been suggested (e.g, Byblow et al., 1994; Carson, 1993; Carson et al., 1994) that the bi-directional coupling between the limbs varies as a function of limb such that the left is more stringently coupled to the right than vice versa. This feature itself can arise from differences in the individual limbs themselves such as a difference in maximal rates in responding, which subserves the independent scaling of the bi-directional coupling terms (Carson, 1993).

3.4.2 Neural Correlates of Dynamic (In)Stability

In the present study an attempt was made to ascribe fluctuations which arise from the competitive and cooperative forces of coupling to independent components of the neural substrate, namely the timekeeping (clock) and implementation (motor) components as identified in the two-process timing model of Wing & Kristofersson (1973). In large part, the data observed in unimanual and bimanual multifrequency preparations conformed to the predictions of the two process model. In a majority of trials, temporally abutted cycles were correlated in a negative manner and between the theoretically predicted range -0.5 and 0.0. These findings are consistent with those of Turvey et al. (1986, 1989) who originally extended the two process model to the rhythmic domain within paradigm of wrist-pendular oscillations (e.g., Kugler & Turvey, 1987). Our results extend the two-process model to rhythmic finger oscillations of flexion and extension (a tapping analogue in rhythmicity) which share in virtue the dynamics of limit-cycle oscillators (e.g., Kay et al., 1987; Kelso et al., 1981). Asymmetries were not evident at the level of the limit-cycles themselves i.e., between the respective clock and motor variances. With respect to unimanual preparations, these data are consistent with Wing et al. (1989) in that temporal variability did not differ as a function of hand. Clock and motor variance (SD) regressed significantly and positively with period such that variability increased with period. This effect was somewhat surprising since the seminal data of Wing & Kristofersson (1973) demonstrated an increase in clock variance proportional to inter-response interval, but without a corresponding increase in motor delay variance. The present data however extended over a range of higher periods and is suspected to have affected motor variances subsequently. The regressions were consistent in the sense that at all periods, variance attributable to timekeeping was larger than that attributable to implementation (Wing, 1980). Of methodological consideration, the selection of SD as the relevant measure of variance (e.g., Ivry & Corcos, 1993) was confirmed as both clock and motor SD regressed toward zero values (initial analyses of variance revealed large negative intercepts in the 200-300 ms^2 range- an illogical result). Ultimately however, slope analyses (e.g., Killeen & Weiss, 1978) of clock and motor SD against period did not implicate either limb as inherently more or less variable, whether in self-paced regimes or under the induction-continuation protocol. (Figure 3.3).

3.4.3 Timekeeping and Motor Delays in Multifrequency Coordination

The intended goal was to examine whether neural correlates could be identified for difference in stability between assignments in multifrequency coordination leading to performance asymmetries. It is not uncommon for asymmetries to remain latent at the level of the limit-cycles themselves, yet to emerge at the level of relative phase especially below maximal rates of responding (e.g., Experiment 1). The present data comport to this feature of performance asymmetries in the spatiotemporal distinction of relative phase. The prediction that performance asymmetries may be manifest within components ascribed to the timekeeping architecture of the respective limbs in multifrequency assignments was not supported. For example, in analyses of clock regressions, slope did not differ as a function of role in the driver/driven relation. The motor slopes however, differed in both analyses with the slope of the motor SD produced by the driving hand demonstrating a significantly steeper slope. When contrasted with slopes from unimanual preparations at identical frequencies, the differences in motor regressions from above appear more a function of period rather than the role of hand in the multifrequency relation i.e., driver versus driven. In the between-hand contrasts between assignments (i.e., contrasts between hands in identical roles in the relation), neither clock or motor variance was distinguishable as different from the other.

There was no evidence to support the formation of a unitary clocking process under multifrequency regimes. That is the clock variance of one limb was not a significant predictor of clock variance of the other, regardless of assignment. This finding rationalizes a fundamental distinction between absolute 1:1 coordination and multifrequency coordination, namely the degree to which timekeeping resources are demanded, and thus the inherent difficulty of producing higher-order frequency relations (e.g., Deutsch, 1983; DeGuzman & Kelso, 1991). Turvey et al. (1989) demonstrated how wrist-pendulum systems of identical and nonidentical characteristic frequency were governed by a unitary clocking process. Under the constraints of multifrequency coordination, the nervous system is unable to take advantage of a strategy that allows such flexible organization in the maintenance of the intended coordination pattern. This feature also identifies how absolute (1:1) coordination may be more the exception rather than the rule in biological coordination (Kelso et al., 1991). These data suggest that frequency locking at integer ratios above 1:1 is fundamentally distinct from 1:1 frequency-locking. *Absolute coordination*, in the sense of von Holst (1937/1973), is descriptive of the latter (1:1 regime) only. Multifrequency patterns are better described by von Holsts' *relative coordination* in which strict phase and frequency lockings are not maintained, but rather, *phase attraction* between points of synchronization corresponding to in-phase and anti-phase i.e., the stable modes of absolute coordination, which map onto point attractors in the potential landscape, as modelled by Haken et al. (1985).

The final point with respect to the temporal variance in multifrequency coordination is that relative phase dynamics were implicated in timekeeping and motor variance. It was demonstrated from multiple regression analyses that phase attraction was a significant predictor of clock and motor SD in the non preferred (2:1) assignment. From previous examinations (Experiment 1) phase attraction has been implicated in the loss-of-stability of relative phase, a feature which is predominant in the non-preferred assignment (and hence rationalizes performance asymmetries). The present data suggest that the underlying dynamics expressed through phase attraction (in the least stable, 2:1 assignment) contribute significantly to the temporal variability of the driven limb in the relation. Variables such as period, and the clock and motor SD's of the driver however, were not significant predictors of the clock and motor SD's of the driven limb in the multiple regression. However, the influence of relative phase dynamics (uniformity, phase attraction) were not obviously distinguishable between clock and motor components, respectively.

3.4.3 Influence of Information on Temporal Variability

The influence of external information on temporal variability was examined throughout the experiment although it did not factor significantly into the clock and motor analyses. For example, the regressions of clock and motor SD with period in unimanual (Table 3.2) and multifrequency (Table 3.3) preparations did not differ in degree of slope in contrasts between the absence and presence of external auditory information (which demarcated finger flexion). These findings support the assumptions of the two-process model which maintains that negative correlations between adjacent cycles, as observed in the present data, do not represent a fed-back influence, but rather arise as an inevitable result of the inherent delays in the motor system (Wing & Kristofersson, 1973).

At the level of relative phase, there was a significant effect of information such that stability, as assessed in measures of uniformity, was greater when external information was available. This effect is interpreted as an inevitable result of anchoring (e.g., Beek & Bingham, 1988, Byblow et al., 1994; Carson et al., 1994) whereby variability in amplitude is compressed at regions coincident with external information. Uniformity of the spatiotemporal parameter relative phase was sensitive to these compressions. Importantly, since discrete estimates of relative phase are based on the relative location of peak events between the limbs, or between limb and environmental stimuli (Byblow et al., in press), it appears that the relative timing (phasing) of events between the limbs is the relevant determination of multifrequency performance, rather than neural architecture attributed to timekeeping and implementation of the oscillators considered in isolation. This comforms with the data of Rosenblum & Turvey (1988) and Turvey et al. (1989) who did not implicate deviations from preferred phase relations to neural substrate as defined under the two-process protocol. The present data did not implicate neural correlates (e.g., central inter-cycle timekeeping, peripheral intracycle delays) which extended to the stability of frequency relations and hence, relative phase.

3.5. Conclusion

The relevance of the two-process model was limited in the prediction of the temporal variability in multifrequency coordination . Further, conformity to the central predictions of the model diminished from unimanual conditions to multifrequency conditions. However, the trials which did not show violations were similar in their clock and motor variances between preparations. The implication of the diminishing conformity as the model is extended to multifrequency regimes suggests that the relevant timing parameters may extend beyond the two process model. Treatments provided by Wing and his colleagues (e.g., Wing et al., 1989; Vorberg & Wing, in press) attempt extensions into bimanual regimes, although success has been limited. The two-process model was successful in capturing the escalation in temporal variability as a function of movement period. Ultimately however, the two-process model did not provide an adequate characterization of the known performance asymmetries within multifrequency regimes (e.g., Experiment 1; Peters, 1985). It is suggested that models which incorporate the collective variable dynamics (Haken et al., 1985; DeGuzman & Kelso, 1991) are more aptly suited to the characterization of bimanual coordination in general: the essential features of which are stability *and* timing. Future endeavors toward timing models of bimanual coordination which serve to isolate neural correlates might best be directed toward a consideration at the level of collective behaviour rather than at the level of the limbs considered in isolation.

4. Experiment 3

The Coupling of Perception and Action in Multifrequency Coordination

4.1. Introduction

Stability and flexibility are essential features of the movement behaviour in many living organisms yet the relevance of either are not well understood in acts of coordination. Recently, formal stability analyses have been directed toward human movement regulation (e.g., Kelso et al., 1981, Kugler & Turvey, 1987). It has been shown that for many classes of rhythmic limb movements, the coordination of the limbs can be modeled by dynamical equations of motion which map onto attractors in a potential landscape. For example, in acts of bimanual coordination, the limbs reveal stable and unstable relations in their relative phase (e.g., Kelso, 1981; 1984). Relative phase has been identified as an order parameter as it reveals signature features of self-organization (e.g., Haken, 1977) such as modality (two or more stable relations), critical fluctuations, and spontaneous transitions, under the regular scaling of a control parameter such as oscillation frequency (Schöner & Kelso, 1988 a). As demonstrated in Experiment 1, the stability of interlimb preparations are dependent upon the control parameter dynamics (e.g., frequency of oscillation, frequency relation between the limbs, and the degree of phase attraction), as well as inherent features such as performance asymmetries. The latter stresses the importance of the assignment hand to task (e.g., frequency relation) in a bimanual regime which subsequently can be expressed and observed experimentally in measures related to the stability of relative phase. For our purposes, we have determined that collectively, multifrequency bimanual coordination is generally more stable when the right hand assumes the role of driver in the relation (i.e., adopts the dominant frequency) even though the limbs considered individually express limit-cycle dynamics (e.g., Experiment 1) which are well-within their maximal tolerance limits (Carson, 1993; Peters, 1990).

In Experiment 1 the central concepts of stability and more importantly, loss-of-stability were addressed. We turn now to the concept of *flexibility* as reflected through measures of stability. Just as it is important in the dynamical sense to maintain coordination in terms of phase and frequency between the limbs in acts of walking and swimming (for example), it may also be important that the limbs do not become rigidly locked in their frequency relations since the emergence of new patterns is extinguished by rigid mode-locks. Mode-locking suggests that the system has become trapped. The flexibility to live near, but not in a mode-locked region affords the system an ability not only to explore, but also anticipate, stable phase relations (e.g., Kelso et al., 1991). For example, Beek (1989) has identified the necessity of an organization scheme which configures limb movements in regions near mode-locking in the act of juggling.

A unique feature of the dynamics perspective is that it applies across levels of description, and across systems comprised of various metabolic, neurological, material or physical substrate (Kelso et al., 1991). For example, in both within-person and between-person limb coordination the same order parameter dynamics emerge, including stable phase relations in both in-phase and anti-phase 1:1 coordination, critical fluctuations, and the onset of bifurcations to monostability (where only "in-phase" remains stable) (Schmidt et al., 1990). It is remarkable that the same patterns of behaviour emerge in the preparations involving one or two nervous systems. This suggests that the visual coupling of between-person coordination shares the same dynamics as a system assembled through a physical (neuromuscular) substrate . In fact, recent treatments by Byblow et al. (in press) suggest that the relevant coupling function may be purely informational, the extent or magnitude of which vary over a *degree* of substrate. This may arise for example, through the reciprocal versus unilateral coupling in interlimb versus person-environment regimes respectively. The important feature again, is that similarity in the pattern formation process in these seemingly disparate coupled oscillator regimes is by virtue of shared dynamics.

The coupling between the limbs of different subjects therefore, is not unlike that of a single subject moving a limb in concert with an external stimulus. The latter regime has been depicted in detail (Byblow et al., in press, Kelso et al., 1990; Wimmers et al., 1991), and suggests that the coupling of perception and action may be understood as a pattern formation process. The present study is motivated by this general theme. At issue is the generality of performance asymmetries in multifrequency coordination which, as implicated in Experiment 1, arise through the cooperation (or coupling) between respective elements. Transcendence to the domain of perception-action however provides another important possibility, namely to determine the extent to which subjects produce movements in coordination with an external signal. These patterns may define mode-locked behaviour (i.e., a 2:1 frequency ratio), or more importantly, they may define patterns near, but not within rigid mode-locks. (i.e., almost 2:1). The latter is of particular importance since it allows examinations of Φ space which are normally *inaccessible* to interlimb preparations. These regimes may be implemented quite simply by imposing an external signal, such as an auditory metronome, while the subject attempts to maintain an ongoing limb oscillation. Thus both stability (expected mode-locks) and flexibility (expected phase wandering) can be examined by manipulation of stimulus (e.g., metronome) frequency. In contrast, preparing an *interlimb* coordination near a specific mode-lock would be most difficult indeed, although it is possible to explore a variety of frequency lockings (integer and polyrhythmic) using a physically (torque) driven system (DeGuzman & Kelso, 1991). The perception-action system however, may provide an easily accessible window into the order parameter dynamics of coordination, or specifically, *relative* coordination near frequency lockings.

Recent examinations of within-person and between-person coordination have identified stability as an essential feature of coordination in general. From this perspective, coordination in general may best be understood as a pattern formation process (Kelso et al., 1990). However, there are important differences between regimes defined within and between persons, or between two limbs or limb and environmental stimulus. A concise treatment of the former is provided in Schmidt et al. (1990) and Turvey (1990) and focuses on the (shared) coupling dynamics resident of one versus two nervous systems. The present study addresses the coupling dynamics of the latter. Specifically, the collective behaviour between an overt limb movement and an external oscillatory stimulus is considered, and contrasted to similar preparations in frequency, and frequency ratio, of interlimb regimes. In the latter it is suggested that reciprocal forcing is present between the two oscillators (Byblow et al., 1994; Carson, 1993; Haken et al, 1985; Rand et al., 1988). In the person-environment regime, only the phase and frequency of the movement is free to vary, and hence the forcing is unilateral. In this sense, the limb is always driven by the display although either the limb frequency or the stimulus frequency may define the dominant (i.e., faster) frequency in the relation. Keeping the former point in mind, the relationship of driver/driven will thus refer to relations in *frequency* rather than *coupling*.

With regard to performance asymmetries in perception-action couples, a number of predictions extend logically from the bimanual regime of Experiment 1. First, it was speculated that the right limb and environmental stimulus may comprise a more stable collective than the left in regions defined as mode-locked. However, if the advantage in stability extends *only* to conditions in which the right hand assumes the dominant frequency, then we might conclude that performance asymmetries arise as a feature of driver/driven relations of a coupled oscillator regime (bimanual, interlimb, or otherwise). If this were the case, the left limb would be expected to exhibit a preference with respect to stability when in the role of *driven* , or slower, oscillator. Second, the limb-display collective comprised of the right limb may express a greater degree of flexibility i.e., an enhanced ability to live near, but not within a rigid mode-lock. This novel prediction of asymmetry conforms to studies of musical performance (Guiard, 1989) which suggest that a role of creativity is assigned preferentially to the dominant limb. In the dynamical sense, an unstable phase relation (relative phase) between the dominant (right) limb and an external signal near an integer frequency relation is indicative of flexibility which is requisite for (relatively) stable patterns near regions of mode-locking (e.g., Kelso et al., 1991). It was not certain a priori whether this prediction extended to the driving/driven frequency relations of a unilaterally forced system.

4.2. Methods

4.2.1 Subjects

Three right-handed subjects (two male, one female, age 28, 23, and 28 years) participated on a volunteer basis.

4.2.2 Apparatus

The class of movement was forearm pronation and supination and identical to that of Experiment 1. In the present case however only unimanual movements were required. A hand held manipulandum with potentiometer, as described in Experiment 1, was utilized. An external signal in the form of an auditory metronome was generated under computer control, and presented via speakers placed in front of the subject. The subject was seated such that the handle was positioned comfortably (laterally) for the assigned hand condition.

4.2.3 Protocol

The experiment extended over three identical sessions, repeated on successive days. Each session was of 90 minute duration, entailing 48 trials of 60 seconds each. Trials were comprised of 30 - 90 cycles of movement, depending on condition, yielding approximately 8500 cycles of movement per subject. Subjects were asked to initiate forearm pronation and supination in concert with a metronome beat. All subjects preferred to synchronize on the pronation endpoint (e.g., Byblow et al., 1994). Subjects were asked to indicate verbally when synchronization was achieved to intitiate the onset of data collection. The induction period then lasted 20 seconds after which time the metronome was extinguished. Five seconds following the offset, another auditory signal was presented. The final metronome frequency was generated for the final 20 second at either exactly, or roughly (+/- 2.5%), half or double the original frequency. In this sense, the predicted frequency relation between limb and signal was either exactly 2:1 or "near" 2:1. For conditions in which the metronome was doubled in frequency we adopt the terminology of the hand frequency as the *driven frequency,* whereas when the metronome frequency was halved the hand is assumed to maintain the *driving* frequency. In all cases the subjects were asked to maintain the original frequency of oscillation (from induction) throughout the trial i.e., without regard for the metronome frequency generated in the latter half of the trial.

4.2.4 Design

Each subject completed all conditions in every session. The factors of hand (left, right), frequency relation (driver, driven), proximity to mode-locking (integer ratio, advanced from predicted locking, or retarded from predicted locking), and frequency (1.0 or 1.5 Hz induction frequency), were randomized over the 48 trials per session. An additional factor of interval was included to demarcate temporal regions of the multifrequency relation. The factors of frequency and interval were included in the design to accommodate within subject and between subject differences in preferred frequency (e.g., Carson et al., 1994).

4.2.5 Data Treatment and Analysis

The data collection and analysis procedures were identical to that of Experiment 1. The dependent measures of interest were those which characterized the extent of mode-locking, namely the frequency ratio between the limb and display, and the relative phase between the limb and display. Frequency ratios were determined with respect to the intended frequency relation. The ratios under investigation were: 1:1 during induction; 1:2/2:1 during intended mode-locking; and non-integer relations near 1:2/2:1 when the metronome was reinstated advanced or retarded with respect to integer locking. The intended frequency ratios across conditions are depicted in Table 4.1.

Table 4.1 Intended Limb-Display Frequency Relations Across Conditions

Limb Frequency	Intended Frequency Relation	Limb & Metronome Inducted (Hz)	Metronome Continuation (Hz)	Intended Frequency Ratio
	Below Mode-Locked	1.0/1.5	1.95/2.93	1.95
Driven	Mode-Locked	1.0/1.5	2.0/3.0	2
	Above Mode-Locked	1.0/1.5	2.05/3.08	2.05
	Below Mode-Locked	1.0/1.5	0.51/0.77	1.95
Driving	Mode-Locked	1.0/1.5	0.5/0.75	2
	Above Mode-Locked	1.0/1.5	0.49/0.73	2.05

It was predicted that the signature features of interlimb coordination would be revealed in patterns of perception-action i.e., at the level of Φ in the limb-metronome phase relation. The limbs themselves revealed essentially stable state dynamics, whereas the metronome was *modeled* as a limit-cycle oscillatory process. Relative phase was calculated for 2:1 frequency relations through discrete estimation techniques as described in Experiment 1. In short, a stable discrete estimate of relative phase was returned for 2:1

mode-locks which synchronized between limb pronation (in-phase) or supination (anti-phase) and metronome onset. Thus, variability of Φ was assumed to relate inversely to stability, and was reflected through measures of uniformity as in Experiment 1. Conversely, uniformity also related proportionally to the degree of flexibility between limb and display when the display was reinstated at a frequency near, but not at, an integer ratio of the inducted limb frequency. As such, indices of uniformity were garnered as measures of stability *and* flexibility. The uniformity estimates of Φ were transformed to the interval $[0,\infty]$ from Mardia (1972). To reiterate, uniformity provides an index of stability of the collective variable in that it provides a measure inversely proportional to variability. In cases of expected mode-locking, uniformity reflects a stable collective. In expected near-mode-locking, higher uniformity reflects a tendency toward unintended mode-locking, or loss of flexible phase relations.

4.3. Results

Data were analyzed in a 2 hand by 2 relation by 2 frequency by 4 interval mixed ANOVA for individual subjects under conditions of expected integer frequency locking. Thus, interval was considered a variable of repeated measure. In analyses of expected near-mode-locking, an additional factor of offset (frequency ratio above or below 2:1) was added.

4.3.1 Limb-Metronome Frequency Ratio

The observed frequency ratios are depicted across conditions in Table 4.2. A number of features are evident in these data. First, subjects were successful in the induction and continuation phases of the trial (frequency ratio of 1.0 with metronome pacing during induction and continuation). Second, although in absolute terms, the ratios do not map precisely onto the intended ratios of Table 4.1, the relative direction of ratio differences across proximity to multifrequency locking was in the intended direction (as highlighted in the mean ratios of all subjects). As such, the statistical analyses consider differences of intended and actual ratios. Negative measures indicate ratios below the intended mode-locking, positive measures above the intended mode-locking. Third, the ratios exhibited between the limb-display collective do not express an obvious difference of left versus right limb conditions. The absence of performance asymmetries at this level are indicative of analyses of frequency. Finally, variability (SD) associated with the respective ratios, in general, appears to be of greater magnitude when the limb assumes the role of the driven oscillator. The effect of relation arises in spite of the congruence of (absolute) oscillation frequency of the limb in both the driver and driven role. This phenomenon is explored in further statistical analyses of frequency ratio measures..

Table 4.2 Mean and SD of Frequency Ratios Across Conditions

Frequency Ratio		S1 Mean	SD	S2 Mean	SD	S3 Mean	SD	All Ss Mean	SD
	Induction	1.000	0.001	0.999	0.001	0.998	0.001	0.999	0.001
	Continuation	1.000	0.005	0.958	0.005	0.979	0.006	0.979	0.005
Hand / Relation	Intended Relation to 2:1	S1 Mean	SD	S2 Mean	SD	S3 Mean	SD	**All Ss Mean**	**SD**
	Below	0.494	0.001	0.454	0.001	0.480	0.001	**0.476**	**0.001**
Left	Equal	0.501	0.001	0.466	0.002	0.484	0.001	**0.484**	**0.001**
	Above	0.516	0.002	0.477	0.001	0.500	0.001	**0.498**	**0.001**
Driving Freq.									
	Below	0.497	0.003	0.452	0.005	0.468	0.003	**0.472**	**0.004**
Right	Equal	0.509	0.003	0.458	0.003	0.489	0.003	**0.485**	**0.003**
	Above	0.511	0.006	0.474	0.004	0.501	0.002	**0.495**	**0.004**
	Below	2.007	0.038	1.956	0.053	1.892	0.010	**1.952**	**0.034**
Left	Equal	2.012	0.030	1.976	0.025	1.943	0.013	**1.977**	**0.023**
	Above	2.056	0.014	1.970	0.027	1.988	0.008	**2.005**	**0.016**
Driven Freq.									
	Below	2.002	0.017	1.925	0.032	1.905	0.009	**1.944**	**0.019**
Right	Equal	2.045	0.023	1.958	0.051	1.916	0.005	**1.973**	**0.026**
	Above	2.065	0.019	1.972	0.025	1.980	0.006	**2.006**	**0.017**

4.3.1.1 Stability: Integer Relations Supporting Mode-Locking

The 2 hand by 2 relation by 2 frequency by 4 interval analyses of frequency ratio difference (intended minus actual) revealed primarily effects of relation and interval. Figure 4.1 illustrates the interaction between relation and interval for S1 & S2 ($F_{3,111}=6.454$, $p<0.001$; $F_{3,114}=17.818$, $p<0.001$). A more stable frequency relation was observed for S1 when the hand assumed the dominant (driver) frequency, but an increasing lag (below mode-lock) when the hand assumed the driven role in the relation. Stability was better reflected over interval for S2 when either hand assumed the role of driver. As well, a reduction in lead was noted under the driven relation with ratios approaching mode-locking over trial progression. A main effect of relation was observed for S3 ($F_{1,38}=11.273$, $p<0.01$) with a tendency for more stable frequency lockings with the limb at the dominant frequency, whereas there was a tendency for advance at the driven. A main effect of frequency and a three way interaction between relation, frequency and interval (both $p<0.05$) confirmed greater tendency for locked frequency relations with the limb at the dominant frequency, and a strong tendency for the limb to remain above mode-locked when maintaining the driven frequency under the 1 Hz pacing protocol.

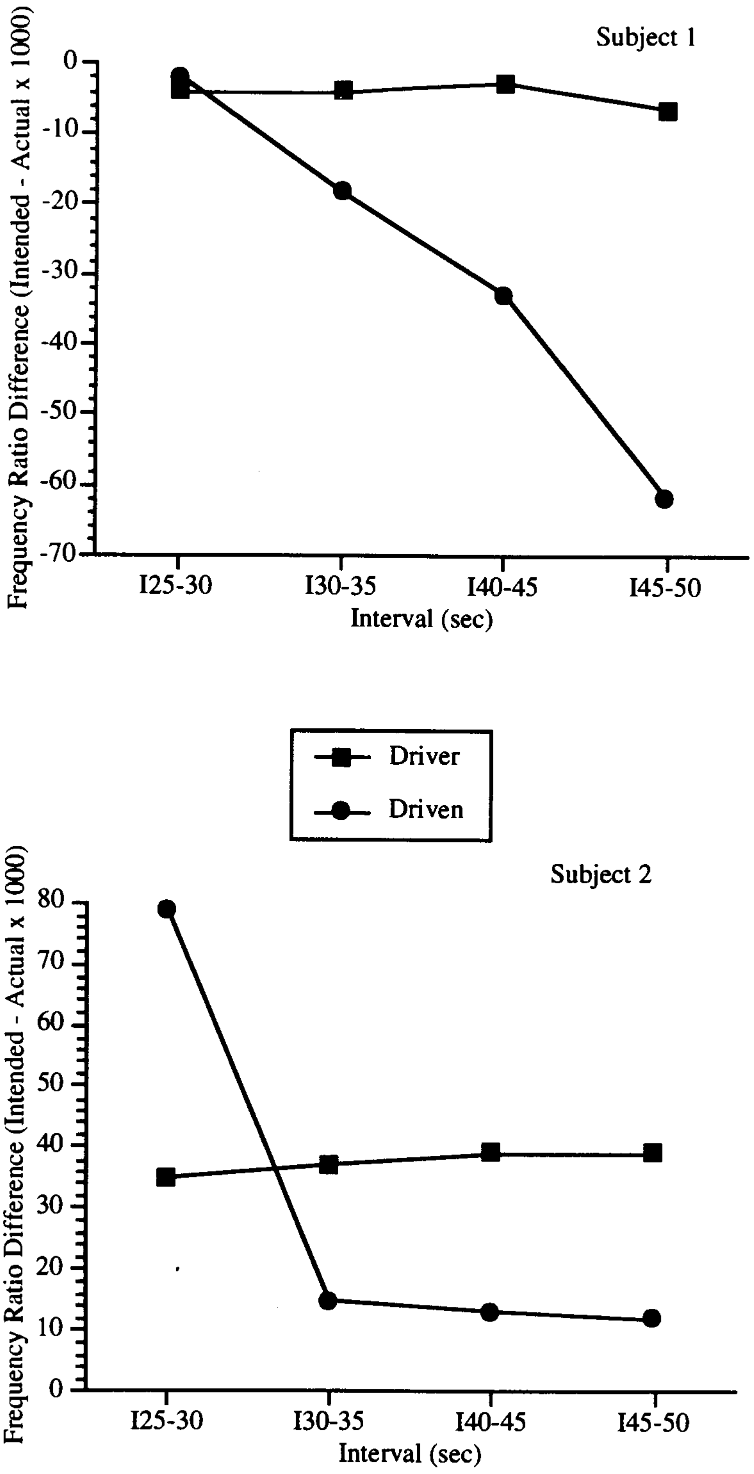


Fig. 4.1. Interactions of relation in frequency and interval in measures of frequency ratio for Subjects 1 & 2.

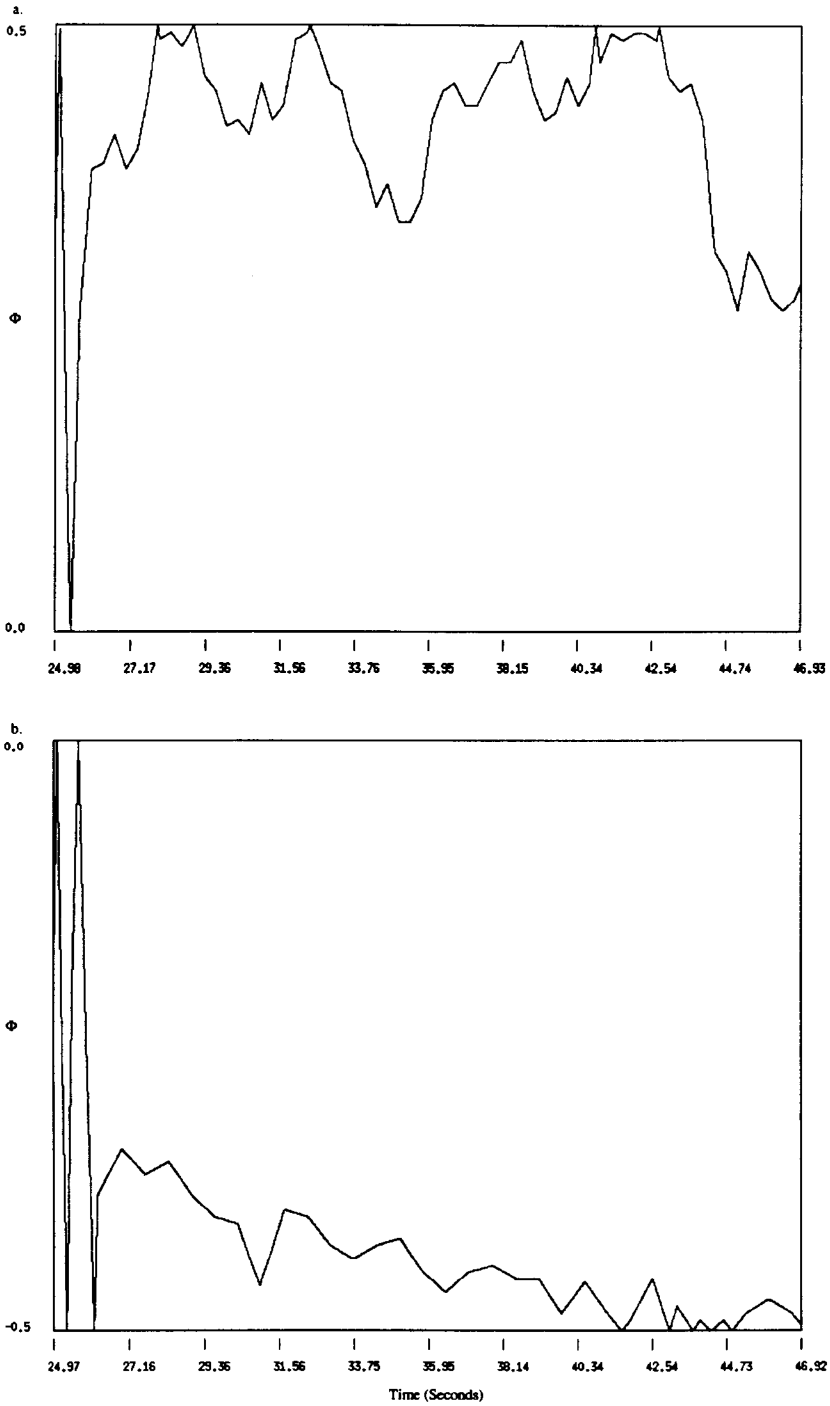
4.3.1.2 Flexibility: Irrational Relations Near Mode-Locking

The 2 hand by 2 relation by 2 offset by 2 frequency by 4 interval analyses again revealed that the dominant effect was that of relation with significant main effects for S1 and S3 ($F_{1,79}$=13.61, $p<0.001$; $F_{1,80}$= 23.11, $p<0.0001$, respectively). Relation by interval interactions were observed for S1 and S2 ($F_{1,79}$= 5.73, $p<0.05$; $F_{1,80}$=15.02, $p<0.001$). There was a greater tendency for mode-locking for S1 when the limb assumed the driving frequency, but lag persisted when at the driven frequency and increased over interval. The same effect of hand at the driving frequency was observed for S3, but a tendency for advance when driven.

Effects of offset (below versus above mode-lock) were observed for S1 and S2 in main effects (both $p<0.01$) and interactions with relations (both $p<0.05$). S1 showed a tendency for the limb to lag when the metronome was returned below 2:1, whereas S3 showed a tendency to lead when the signal returned above 2:1. The interactions confirmed the tendency for lag and lead for S1 and 2 respectively, when the limb assumed the driven frequency role in the limb-display relation.

4.3.2 Limb-Display Relative Phase

Exemplar time series estimates of discrete relative phase (in the multifrequency region) of trials are provided in Figure 4.2. From these series the following features are evident: a & b) stability of Φ in preparations in which mode-locking was expected (a) *and* unexpected (b); c) the phase relation between the limbs would reverse direction i.e., move away from and then return to stable relative phase values (i.e., synchronization at in-phase or anti-phase), despite a regime which dictated an unstable phase relation; d) frequency-lockings at 2:1 appear (stable relative phase) and disappear (unstable relative phase) intermittently. Each of these features are addressed in the discussion section. The overall stability at the level of Φ was depicted in measures of uniformity and subjected to statistical analyses in designs identical to those of frequency ratio.



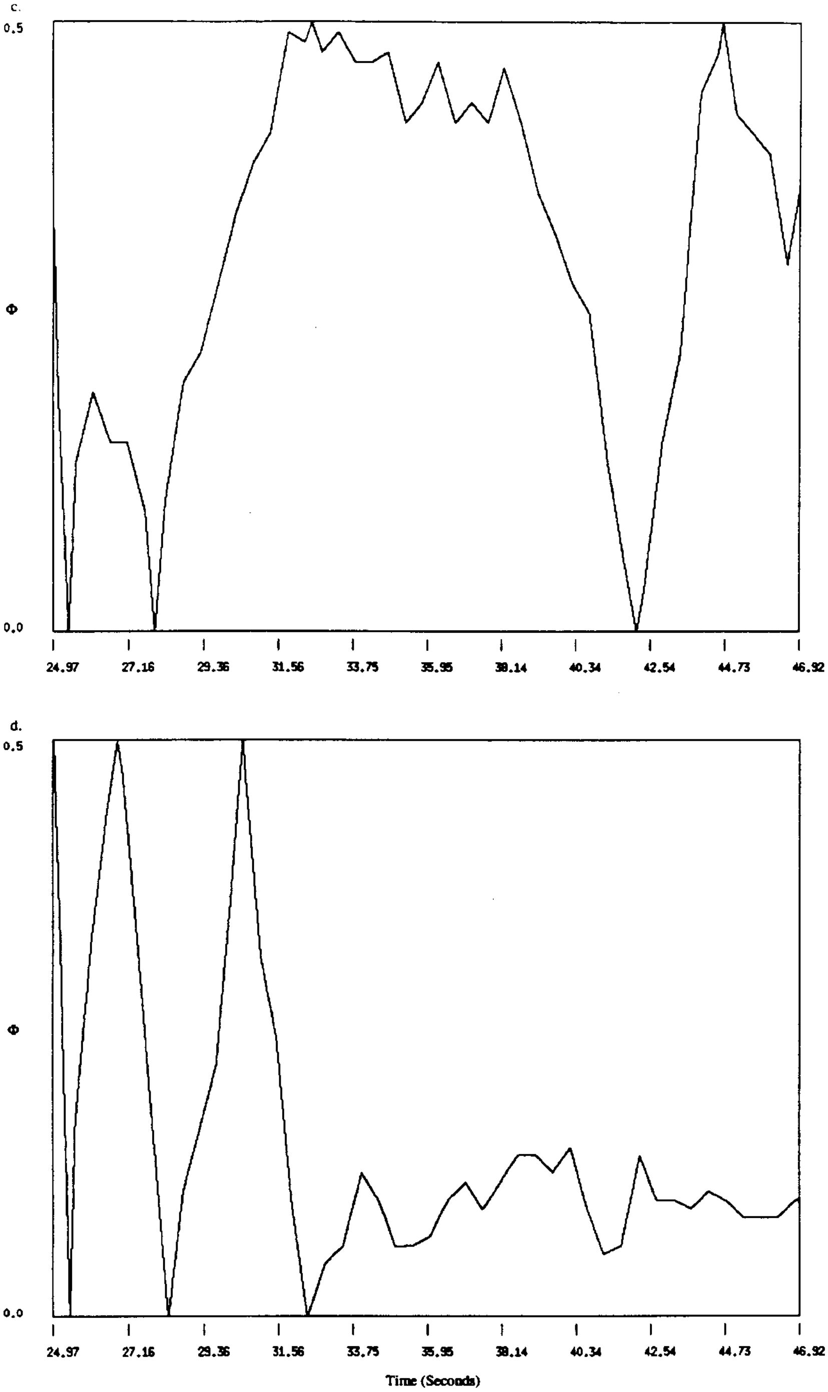


Fig. 4.2. Φ profiles for multifrequency regions of trials of expected mode-locking and near mode-locking. Φ = 0.0, 0.5 are stable points of synchronization for 2:1 (1:2) coordination. See text for details.

4.3.3 Uniformity of Relative Phase

There were no effects which supported the stability hypothesis as it pertained to performance asymmetries in driver/driven relations. That is, no interactions between hand and relation in frequency (driven versus driver) were observed in the uniformity estimates. However, there were consistent effects of relation, as well as a number of unremarkable, although significant, results. Uniformity means are depicted in Table 4.3 for each subject and contrasted across relation in frequency. In all cases, the estimates meet the $\alpha = 0.05$ level ($R = 0.690$, $n=6$)[4] for the Rayleigh test of uniformity (e.g., Mardia, 1972, pp. 300). Apparent in these data is the stability which emerged as a function of relation for each subject. Subjects 1 and 3 demonstrate greater stability when the limb assumes the dominant frequency, whereas subject 2 exhibits greater stability when the limb assumes the driven frequency. Uniformity measures did not differ greatly over conditions of proximity to mode-locking within respective driver/driven relations suggesting that mode-locking between limb and display permeated the conditions of display frequency which were intended to be offset from integer relations i.e., expected near-mode-locked. Statistical analyses of transformed uniformity measures explore these directions in detail.

---

[4] $n=6$ represents the minimum number of cycles in an interval over which an estimate of uniformity was determined.

Table 4.3 Uniformity measures of individual subjects averaged over limb relation to display and intended frequency relation.

Uniformity	Intended Locking	S1	S2	S3
Driving	Mode-Locked	0.959	0.693	0.942
	Near Mode-Locked	0.948	0.739	0.931
Limb Relation				
Driven	Mode-Locked	0.841	0.901	0.732
	Near Mode-Locked	0.862	0.866	0.784

4.3.3.1 Stability: Integer Relations Supporting Mode-Locking

Significant effects of the factor hand were absent with the exception of a hand by interval interaction for S2 ($F_{3,111}=2.759$, $p<0.05$). Subjects 1 and 3 revealed greater uniformity of relative phase with either limb assuming the driving frequency in the limb-metronome relation (S1- $F_{1,37}=13.420$, $p<0.001$; S3- $F_{1,38}=18.900$, $p<0.001$), whereas S2 demonstrated a preference for a driven frequency relation ($F_{1,37}=16.710$, $p<0.001$). Figure 4.3 illustrates how Subjects 1 & 2 demonstrated an interaction of relation and interval (both $p<0.01$) with a notable increase in uniformity under the more stable limb relation (driver and driven for S1 and S2 respectively) as the trial progressed.

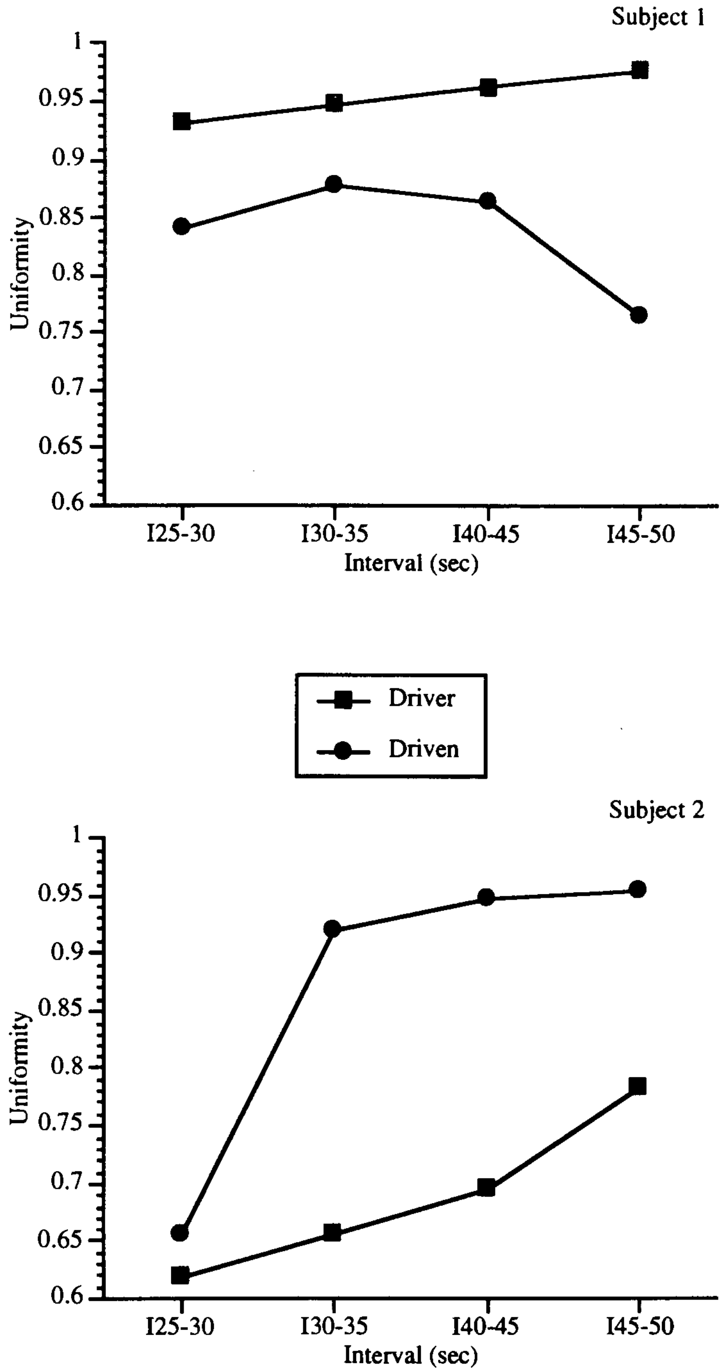


Fig. 4.3. Interactions of relation in frequency and interval in measures of uniformity for Subjects 1 & 2.

4.3.3.2 Flexibility: Irrational Relations Near Mode-Locking

Significant effects with the factor of hand were noted in two subjects in the near mode-locked regime. Greater uniformity in relative phase was evident in limb-display collective of which the left hand was comprised. Subject 3 showed a main effect for hand ($F_{1,80}=4.375$, $p<0.05$), whereas Subject 2 displayed a hand by interval interaction ($F_{3,240}=5.478$, $p<0.01$). Low uniformity measures were evident at early stages with either hand, but the left hand showed a greater increase (tendency for mode-locking) over duration. Again, the effect of relation was significant for all subjects (all $p< 0.001$) and in the direction noted above. All subjects also showed an effect of offset (all $p<0.01$) although the effects were not systematic across subjects. Uniformity of Φ was more stable for S1 and S3 when the display frequency was below that required for an integer lock, whereas S2 demonstrated more stability when the display frequency was accelerated.

4.3.4 Summary of Results

a. Mean frequency ratio depicted successful manipulations of limb-stimulus interactions. ensemble averages reflected ratios in expected and near-mode-locked directions. Subjects expressed a preference in maintaining either the driving *or* driven frequency at an individual level.

b. The limb-display collective was stable in profiles of Φ for conditions of expected and near-mode-locking. Collective behaviour was attracted toward stable regions of Φ.

c. Uniformity estimates reflected a tendency for success in expected stable (mode-locked) and flexible (near-mode-locked) which varied individually in preference for frequency relation. A tendency for unexpected mode-locking was observed with the non dominant limb.

4.4. Discussion

The results indicate that relative phase, rather than frequency ratio, better captured the coordination tendencies between limb and display. As indicated in Tables 4.1 and 4.2, frequency ratios differed from their intended values on an absolute level, however their relative directions over mode-locked and near-mode-locked conditions were in the expected directions. Thus, frequency ratio was a useful tool for determining the effectiveness of the experimental protocol. However, mean frequency ratios were insensitive to features such as intermittent shifts between mode-locking and relative coordination. The overall stability of coordination was thus better served in our estimates of uniformity of relative phase which essentially identified varying, but stable, phase relations between limb and display in all conditions of intended mode-locking. The present discussion is therefore constructed in consideration of the relative phase dynamics.

4.4.1 Asymmetries

A number of features pertinent to multifrequency coordination were revealed in the perception-action regime examined here. There was no evidence that the left limb supported a less stable limb-display collective in the multifrequency regime. These data appear to contrast with those of Byblow et al. (in press) which revealed asymmetries in the limb-display phase relations of 1:1 preparations. However, stability in a multifrequency regime is merely an expression of phase attraction to the stable in-phase and anti-phase relations of 1:1 coordination (e.g., Experiment 1). The present data merely suggest that both limb preparations were effectively mode-locked under ideal frequency relations- an unremarkable finding with respect to asymmetries. However, a novel expression of asymmetries emerged from examinations of flexibility i.e., the ability to live near a rigid (absolute) coordination. The "left" limb-display collective was less effective at maintaining flexible phase and frequency relations. A greater tendency for rigid mode-locking was observed in the collective behaviour of the left versus right system. For two subjects the right limb most often demonstrated the ability to "live" near, but not in, a mode-locked relation to an oscillator coupled via perception to an environmental oscillatory process.

4.4.2 Shared Dynamics of Coupled Oscillator Regimes

A number of features were evident in the relative phase series (e.g., Figure 2) which shed light on the dynamical organization of multifrequency coordination. First, the ability to entrain in phase and frequency to an external signal is evident in the intentional movement system. These stable phase relations may arise in concert with the original, intended movement (a), or in spite of it (b). As such, adjustments in phase and frequency at the level of action arise as a consequence of oscillatory dynamics through entrainment toward stable phase and frequency relations. It is our suspicion, and that of many others, that relative phase is the relevant order parameter for the coordinated limb movements (e.g., Kelso, 1981, 1984; Kugler & Turvey, 1987), as well as for cortical events (e.g., Kelso et al., 1992), and as we suspect here, for the coupling of perception and action (e.g., Byblow et al., in press; Kelso et al., 1990; Wimmers et al., 1992). In the near-mode-locked regimes examined here a resetting of relative phase toward stable regions was typically observed (as in Figure 4.2c) such that synchronization was maintained between the maximal excursions of movement and metronome onset . Thus, adjustments in movement frequency reflected the unilateral coupling forces between stimulus and limb which serve to maintain stability in the order parameter, relative phase. Figure 2d illustrates the intermittent nature of the mode-locking. These data strengthen the position of a flexible, variable coupling term in dynamical models of coordination such as that incorporated into the phase-attractive circle map of DeGuzman & Kelso (1991). This feature of coupling arises as a function of *phase attraction* (toward in-phase or anti-phase) as identified in the original model of Haken et al. (1985) for bimanual coordination, and subsequently, extended to the discrete framework of circle maps by DeGuzman & Kelso (1991). Phase attraction has subsequently been shown to persist experimentally in interlimb regimes (e.g., Experiment 1) as well as in the coupling of perception and action (e.g., Byblow et al., in press). The circle map framework is thus aptly suited to the deterministic generation of collective dynamics for systems which exhibit reciprocal forcing, such as interlimb/within-person regimes, or unilateral forcing as depicted in the present person-environment interactions.

4.4.3. Coordination Dynamics Extend Beyond the Physical

In the circle-map regime (e.g., Glazier & Libchaber, 1988), the stability of a driven oscillator is depicted relative to its phase and frequency relation to a driving oscillator. In multifrequency relations (integer and polyrhythmic) the map describes regions of stability (Arnold tongues) as a function of the number of possible coupling strengths which return stable mode-locks. DeGuzman & Kelso (1991) extended the circle map framework to include the reciprocal forcing between limbs in bimanual coordination. The map was thus endowed with coupling terms which define the relative importance of the intrinsically stable phase relations in-phase and anti-phase. In interlimb coordination (e.g., Experiment 1) it was suggested that the relative parameter space relating coupling (K) to frequency ratio (Ω) may be inherently greater when the right hand assumes the role of driver and the left hand assumes the role of driven. In support of this supposition, the converse arrangement was shown experimentally to be inherently less stable at the level of relative phase. It appears that this expression of performance asymmetries in interlimb coordination is not a generic feature of multifrequency coordinations comprised of a single limb (i.e., either left or right). In the coupling of perception and action between environmental stimulus and rhythmic movement provided here, the right limb did not express a predisposition to the role of driving frequency, nor the left to the driven frequency.

There were however a number of significant features of driver/driven relations with respect to limb and auditory rhythm. There were strong indications which suggested preferred relations between inherent (limb) and external (display) oscillatory processes. A priori there were grounds for implicating either limb to the role of driven in the limb-display relation since only the limb (and not the display) could vary in frequency. However, the prediction of performance asymmetries suggested that the dominant limb might express a preference to a dominant relation in frequency. The present data suggest that although a clear preference is expressed individually, the nature of this preference can differ across subjects. The question remains open as to whether or not these phenomena are an expression of individual difference or psycho-social correlates such as dominant versus submissive roles in between person interactions. Recent examinations in the sociological realm of between-person coordination (Schmidt et al., 1993 a) suggest an interactional synchrony between the limb movements of two individuals, not in an S-R fashion, but as a mutual interaction. It has been suggested that individuals in mutual interaction may act like a single "organism" (Asch, 1952) through a dyadic synergy (Schmidt et. al, 1990). It is well known that coordination in the physical sense can be characterized by cooperative and competitive tendencies (von Holst, 1937/1973). However, similar phenomena also dominate and characterize the social experience (Condon, 1982; LaFrance, 1985). The present study dictates that coordination can occur between an intentional movement system and concurrent oscillatory processes alone, regardless of material, physical or metabolic substrate. That is, our coordinations toward a perceived (or sensed) external oscillatory process, may bear a relation ascribable to dynamical "status", whether or not the external process arises from another (similar) nervous system or not. A more thorough examination of these phenomena might best be examined in between-person regimes, where predictions from the dynamical model can be assessed against correlates from psycho-social or psychological batteries.

5. Experiment 4

Dynamic Stability in Multifrequency Coordination

5.1. Introduction

Embedded in human behaviour are complex levels which will be, or have to be, language-using and thus require "information flows" to elect from the large stream of space-time processes with which they are capable of dealing. They will all *appear* to act intentionally (Iberall, 1993). For example, the movement of the human organism, or of its effector units, through a given distance in a given period of time has often been considered an inevitable result of the representation of movement in an internalized prescription of the movement parameters i.e., a motor program. Is this the language of coordination? As a research strategy, the idea of an *a priori* prescription of movement parameters at a higher level of organization has served little to address the paramount issue in human movement regulation- namely, how does a biological system bring into coordination 10^{14} cellular units in 10^{3} varieties defined over multiple time scales (Bernstein 1967; Turvey, 1990)?

One notion is that cyclical movement might provide a dynamic basis for investigating motor systems (e.g., Morowitz, 1968). For example, Kelso et al. (1981) suggested that a stable limit-cycle organization may come in to play. Indeed, the spatiotemporal organization of the two handed rhythmic movements reduced to low dimensional equations of motion i.e., degrees of freedom were dissipated *a posteriori* i.e., as a consequence of dynamic configuration. Stability and loss of stability as a feature of self-organization (e.g., Kelso, 1981, 1984; Haken et al., 1985) have since been evidenced in human coordination through the entrainment of essentially autonomous oscillatory processes (e.g., Haken et al., 1985; Kugler & Turvey, 1987). The entrainment of multiple limit-cycle oscillatory processes in the regulation of complex systems is a predicted feature of homeokinetic physics (e.g., Yates & Iberall, 1973) which stresses a horizontal reductionism of many interacting time scales through biological escapements.

A number of recent studies (Kay et al., 1991; Kelso et al.; 1981; Sternad et al., 1993) have demonstrated that for a variety of human movement rhythmicities, stable limit-cycle organization is preserved. That is, after delivery of a transient mechanical perturbation, the system returned to a stable limit-cycle orbit in phase (state) space. Limit-cycle attractors are identified if primary kinematic variables such as frequency, amplitude and peak velocity remain unaffected by perturbation. In acts of bimanual coordination a frequent observation is that of a topological organization of the *relative* phasing of the limbs (and their respective cycles). The collective behaviour implies the existence of point attractors corresponding to one or two stable patterns of coordination- in-phase (homologous muscles active in synchrony) at all maintainable oscillation frequencies, or anti-phase (homologous muscles active asynchronously) below critical, individually determined, frequencies (e.g, Cohen, 1971; Kelso, 1981, 1984; Kugler & Turvey, 1987). Since all stable modes of coordination are captured in the low dimensional equations of motion of relative phase (Φ), the order of the system is characterized in a collective manner i.e., at a level above the limit-cycle oscillators themselves. As such Φ is termed an order parameter, or collective variable. The stability of Φ was examined by Scholz & Kelso (1989) through perturbations applied to a single limb when in absolute coordination with its contralateral counterpart. The essential findings were that stable values of Φ were returned following perturbation concomitant with the predicted strength of the respective in-phase and anti-phase attractors. In other words, as frequency increased, the strength of the attractor corresponding to anti-phase diminished such that relaxation times increased. This feature is known as critical slowing down and indexes an inherent loss of stability which precludes spontaneous transition. Spontaneous phase transitions from anti-phase to in-phase coordination are ubiquitous in human coordination and extend across a vast array of movement classes (e.g., Kelso &

Jeka, 1992) dependencies (e.g., Riek et al., in press) and compositions (e.g., Baldissera et al., 1982).

In Experiment 1 it was determined that the inherent dynamics of bimanual coordination in multifrequency regimes i.e., characteristic of relative coordination, were influenced by the same underlying dynamics of extant absolute coordinations. Specifically, an index of phase attraction determined that as oscillation frequency increased, attraction to anti-phase regions in the state space of Φ decreased in a manner analogous to the loss of stability at anti-phase preparations of 1:1 coordination. It was suggested that the loss-of attraction to anti-phase precluded transitions from a multifrequency regime (2:1) to rigid 1:1 frequency lockings in-phase. In other words, the loss of stability corresponding to anti-phase synchronization served to lock the coordination in an inflexible manner, to 1:1 in-phase coordination- the global minimum of the attractor landscape of bimanual coordination, and a ubiquitous entrainment pattern across organisms in locomotion and other rhythmicities. Experiment 1 also served to implicate the assignment of hand to frequency in multifrequency preparations as a template for the inherent dynamics by virtue of asymmetries. In multifrequency preparations of bimanual coordination there is a limb assigned to the role of driver (or dominant frequency), a driven limb (at the slower frequency), and some reciprocal forcing, or coupling, between them. In examinations of 2:1 relations greater stability was observed when the right hand assumed the dominant role in the relation than when the left assumed the dominant frequency. Interestingly, the level of the limit-cycles themselves did not express a clear difference in their state dynamics (at least in frequency, and its variability) which would implicate either limb as inherently more or less stable under the constraints imposed in the multifrequency regime. Therefore, it was within the *collective behaviour* of the system that instability and loss-of-stability were observed (at the level of relative phase), and to a greater extent, in the assignment of left hand at the dominant frequency, thus characterizing performance asymmetries.

The present investigation focused on the stability of relative phase in the multifrequency regime. The signature features of self-organization were examined with special reference to critical slowing down as an index of (in)stability across the respective assignments of frequency to hand in 1:2 (2:1) regimes. Critical slowing down was determined from relaxation time- the time it takes a system to recover from perturbation and relax upon its initial, stable, pre-perturbation state. Relaxation time was measured as the time from offset of perturbation to the point at which the stable organization re-emerges (Winfree, 1972). The return can be measured toward the limit cycle orbit (Kay et al., 1991; Sternad et al., 1993) or to the point of attraction corresponding to the stable pattern of relative phase (Scholz et al., 1989). In consideration of the expression of performance asymmetries in multifrequency coordination which have been observed primarily at the level of relative phase, it was at this level which effort was directed.

In multifrequency coordination, the continuous relative phase of the limbs changes continuously i.e., as a function of their disparate frequencies. However, coordination is likely to occur at localized regions within the global phase space, and thus discrete, stroboscopic estimates of relative phase are suitable characterizations of coordination tendencies (Kelso et al., 1991). In 2:1 coordination for example, synchronization at in-phase, anti-phase , and the point of movement reversals of the faster limb were identified as stable points of synchronization (Swinnen & Walter, 1991; Experiment 1) . As such stable discrete estimates of relative phase were derived from these constraints (Experiment 1). Discrete estimates of relative phase defined under these constraints are stable for multifrequency (2:1) relations, but do not necessarily map onto point attractors corresponding to their specific frequency mode-locks. Rather, relative phase reflects attraction to the intrinsically stable patterns of in-phase and anti-phase.

Relaxation times can be used to predict the strength of an attractor, such as a limit-cycle, by incorporating the function

$\tau_{rel} = Ae^{-\beta t}(\cos\omega t)$ (Sternad et. al., 1993) (1)

The return can be modeled as a logarithm decay function of strength β i.e., the strength of the limit-cycle attractor. The return may have an oscillatory component (hence the cosine term), and when determined at the level of the limit-cycle, is dependent on amplitude (A) and frequency ω.

For the present purposes, relaxation times from the Φ series serve as estimates of phase attraction- longer relaxation times indicative of weaker attraction and vice versa. Scholz and Kelso (1989) demonstrated how relaxation times remained stable across oscillation frequency when prepared in-phase, but increased with frequency when prepared anti-phase: an *a posteriori* consequence of the dynamics imposed by the nonlinear coupling of essentially autonomous oscillators. Thus, frequency acts as a control parameter which guides the coordination landscape from bistability (anti-phase or in-phase) to monostability (in-phase only) (Haken et al., 1985). An increase in relaxation time is indicative of critical slowing down, a consequence of the annihilation of the anti-phase attractor.

The theme of the present study addresses how patterns are defined in biological nervous systems i.e., the language of coordination. Are patterns prescribed by central oscillatory components of the nervous system, such as pattern generators or central timekeepers imbedded in the so-called higher levels of nervous system? There is evidence to suggest that if such processes exist (at presumably lower time and energy scales), they are not independent of the limb dynamics (Kay et al., 1991; Saltzman & Kelso, 1987; Turvey et al., 1986; Experiment 2). It is the intention of this study to examine the role of stability itself as a crucial determinant of coordination patterns, and, if the loss of stability precludes pattern change. The phenomenon of critical slowing down was assessed in the present study in 1:1 and multifrequency regimes with particular regard for asymmetries. If Φ is the essential order parameter for multifrequency coordination, as it is for 1:1 coordination, then relaxation times which differ between 1:2 and 2:1 assignments of hand to frequency would implicate a more stable attractor for one mode-lock versus the other. However, since perturbations may induce transitions from one stable pattern to another (e.g., Scholz & Kelso, 1989), a greater occurrence of perturbation-induced transitions to 1:1 (in-phase) may be expected from 2:1 preparations than 1:2 preparations. Finally, a cursory examination of stable 1:1 coordination patterns is provided in order to determine whether or not the now well known attractor dynamics corresponding to in-phase and anti-phase coordination (e.g., spontaneous transitions, critical slowing down) map onto multifrequency coordination. It was expected that the feature of critical slowing down evident in anti-phase preparations would correspond in frequency to critical slowing down (or perturbation-induced bifurcations) in multifrequency coordination.

5.2. Methods

5.2.1 Subjects

Four males (ages 23, 25, 28, 43 years) were recruited from the university population on a volunteer basis. All were self-professed right-handers and reported no history of neurological impairment.

5.2.2 Apparatus

The apparatus included a table-mounted structure comprised of two hand-held manipulanda which permitted rotations about the wrist in pronation and supination only (provided a firm grip was maintained) from an upright, seated position. Subjects sat comfortably and grasped the handles at 90 degree elbow flexion. A wide (8 cm) Velcro belt secured the arms to the torso just above the elbow. The two handles were forward mounted 40 cm apart and affixed to the shafts of torque motors (Mavilor MT300) which provided square-wave impulses of 80 msec duration to either limb. Perturbations were held constant between limbs and subjects, and were of sufficient intensity to deflect the limb through a 10 - 45 degree range of the trajectory. Affixed to the rear of each motor were linear potentiometers (Bourns Model 3510, 0.1% linearity) which converted angular displacement to voltage. The range of handle motion was restricted mechanically to 315 degrees to prevent over-rotation in the event of malfunction. Occurrences of movements reaching mechanical limits under natural or perturbed influences were negligible. Experimental control was provided via computer control (IBM-PC) which drove the metronome and torque motors via Tecmar LabMaster A/D converter. Analog time series were recovered by a separate IBM-PC via an 8-bit Watscope A-D converter which sampled the potentiometers, motor voltage, and metronome pulses at 250 Hz.

5.2.3 Design

Four patterns of coordination were prescribed as follows: in-phase - maximal excursions at pronation occurring coincident with the metronome beat; anti-phase-synchronization between left pronation and right supination with a counterbalance between left supination (anti-phase left *AL*) and right supination (anti-phase right *AR*) coincident with the metronome; *1:2*- right hand pronation in synchrony with left hand pronation and supination and coincident with the metronome beat; *2:1*- left hand pronation in synchrony with right hand pronation and supination and coincident with the metronome beat.

Under self-paced and frequency scaled regimes, in-phase, anti-phase, 1:2 and 2:1 patterns were examined in individual subject analyses. Contrasts were specified between in-phase and anti-phase (stable intrinsic patterns), 1:2 and 2:1 (performance asymmetries), and the effect of perturbed hand (left versus right) in all preparations. Correspondence between anti-phase and multifrequency patterns was also specified in order to assess phase attractive dynamics and critical behaviour between mode-locks and patterns at consistent frequencies. Perturbations were provided in a decelerative direction to either limb in the pronation phase of movement. Independent analyses of variance were used to determine whether or not there was statistical dependence between patterns (as above), perturbed hand, and oscillation frequency (conditions). For 1:1 analyses, the levels of hand were defined anatomically (left or right), whereas in multifrequency assignments the levels of hand were defined as above, or relational (driver, driven).

5.2.4 Protocol

The experiment extended over two sessions separated by a rest day. In Session 1, subjects completed a frequency scaling protocol in which no perturbations were administered, and then, after a rest period, a self-paced (preferred tempo) protocol in which perturbations were applied to either limb. Frequency-scaling was used in order to determine the mean transition frequency for each subject in each condition. Oscillation frequency was scaled from 1.5 - 3.5 Hz in 0.25 Hz intervals over a 45 second trial. No perturbations were administered- subjects were instructed to maintain the tempo of the metronome in the prescribed pattern of coordination. In the event of spontaneous transitions subjects were instructed not to actively resist or recover the original pattern, but rather, maintain the new pattern at the prescribed tempo. It was expected that transitions would be evident in anti-phase preparations, and also, in multifrequency preparations (2:1 > 1:2, e.g., Experiment 1). Five trials per anti-phase pattern (AL, AR), and 10 trials per multifrequency pattern (1:2, 2:1) were collected in order to determine on a subject by pattern basis the mean transition frequency. Presentation of order of pattern was identical to self-paced conditions. The mean transition data were used to "economize" the perturbation protocol in the subsequent session such that perturbations were presented at frequencies up to and including the mean transition frequency. Frequencies were determined on an individual subject basis and are reported in Table 5.1 (Section 5.3.1).

After a rest period, the self-paced protocol was administered. Subjects were asked to maintain the prescribed pattern of coordination at their most comfortable tempo. Trial duration was 20 seconds. Up to three perturbations were applied in each trial, with a minimum period of 5 seconds separating within-trial perturbations. Perturbations were randomized across hands such that subjects were unaware of the hand which was to be perturbed. Subjects alternated between in-phase and anti-phase in the first of 2 blocks of 12 trials. In the second block subjects alternated between 1:2 and 2:1. In total for the self-paced conditions, subjects performed 6 trials in each pattern with a total of 6 observations (perturbations) per hand per pattern. In the event of perturbation, subjects were instructed to recover/maintain the original pattern of coordination as soon as, or whenever, possible.

In the final session subjects were paced by an auditory metronome at a single frequency for a 20 second trial. One hundred and thirty-six trials were administered. Four pacing frequencies were chosen to encompass a range up to and including the predetermined mean transition frequency for each subject. Similar to the self-paced protocol, one, two or three perturbations were applied per trial. In the first block, subjects alternated between AL and AR conditions for 64 trials. In the second block subjects alternated between 1:2 and 2:1 for another 64 trials. In each block, oscillation frequency, perturbed hand, and number of perturbations were randomized. Eight perturbations per frequency per hand per pattern were administered. Finally, eight metronome-paced trials were performed in-phase at either the maximum or minimum frequency for that subject. A total of five perturbations per frequency per hand were administered in-phase.

5.2.5 Experimental Variables and Analyses

Time-to-transition and phase attraction were determined under the protocols identified in Experiment 1. As in Experiment 1, a continuous estimate of phase was calculated for each limb under the implementation of the algorithm of Scholz & Kelso (1989). However, for multifrequency preparations, a modification was made to the unwrapped phase (i.e., the phase not bound by the interval 0°-360°) of the faster of the two limbs in order to return stable relative phase. For both 1:1 and multifrequency preparations, the calculation of relative phase (Φ) was $\Phi_R - \Phi_L$. Under this protocol it is not unreasonable to predict the recovery of stable Φ for any obtainable multifrequency relation. In the present examination this was accomplished by first obtaining a single landmark point of synchronization between channels. For example, in 1:2 coordination these occurred at pronation-pronation or supination-pronation, for the left-right limbs respectively (assuming a faster moving right limb). From this point, the unwrapped phase of the limb was divided by its frequency coefficient (left phase divided by 1, right phase divided by 2 in the above example).Under this protocol, the algorithm for stable, continuous Φ was accurate as long as subjects maintained a consistent point of synchronization. This is often the case for human coordination and is the basis of discrete estimates of relative phase (e.g., Kelso et al., 1991; Experiment 1). However, in the present analyses a continuous estimate of Φ is required in order to provide an appropriate time-scale resolution in the determination of relaxation time.

Relaxation time was determined using an interactive graphical display technique which automated the calculation of return time, and hence, relaxation time. The interface is depicted in Figure 5.1. The program first calculated the pre-transition mean and SD of Φ from the demarcation of a pre-perturbation window of data as defined by the experimenter. Next, a marker was positioned in the post-perturbation region where Φ was deemed by the experimenter to have returned to stable pre-perturbation levels. Given these pre- and post-perturbation demarcations the program computed relaxation time as follows. The value of Φ was evaluated sample by sample in a backward direction i.e., returning toward the region of perturbation, against a criterion based on the pre-perturbation mean and standard deviation. When the post-perturbation value of Φ was no longer within the prescribed criterion, the sample was identified as a landmark for return time. From this point, the program advanced one cycle period of the perturbed limb in the determination of return time. Thus, Φ would fall inside the criterion SD for one full cycle and return time determined. Relaxation time was calculated as the time from perturbation offset (from the torque channel) to the time of return. As in Scholz and Kelso (1989), this procedure has an inherent conservative bias in the calculation of relaxation time. Faster periods are imbedded with shorter, not longer, period adjustments. The default SD criterion used was 1.0, except for one case where noted.

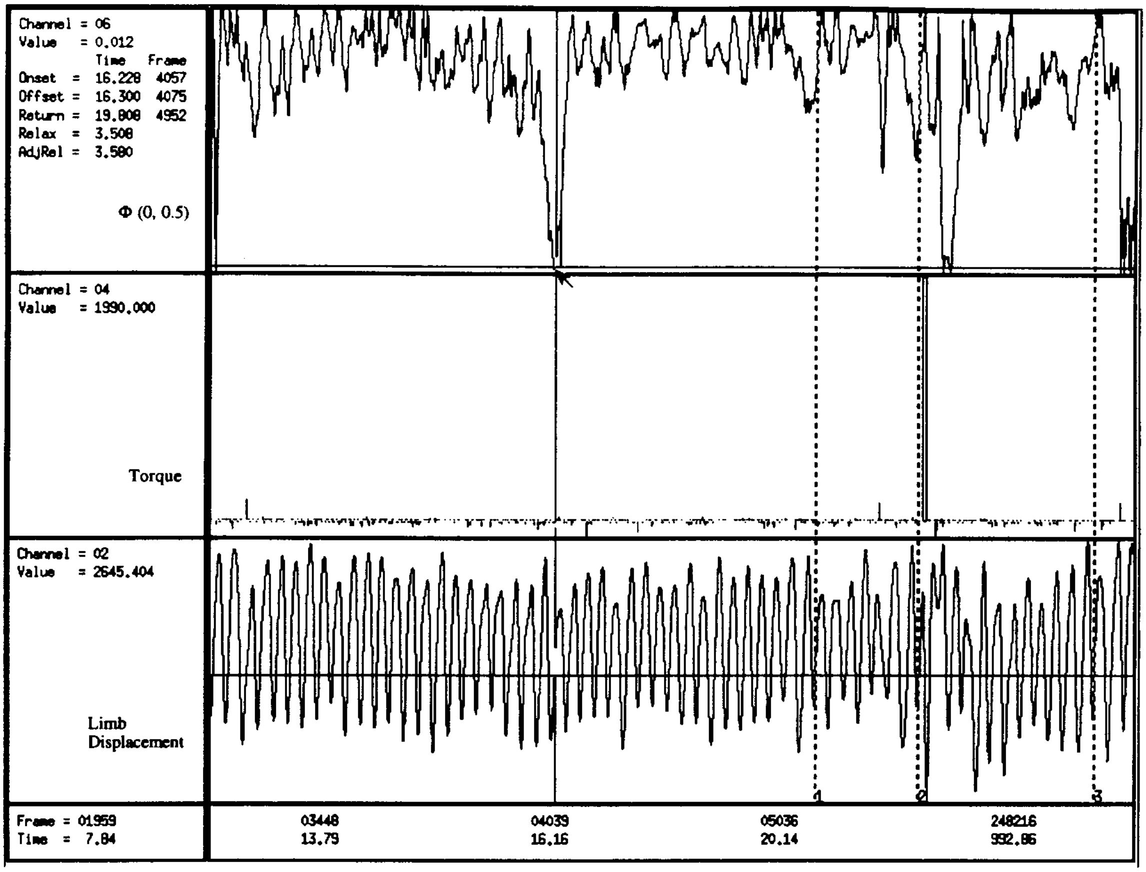


Fig. 5.1 Relaxation time estimation. Preparation was anti-phase ($\Phi = 0.5$) at the critical frequency for the subject. Vertical (dashed) cursors are positioned to preclude torque pulse (middle channel). The arrow demarcates a spontaneous transition. In this case, the magnitude of relaxation time ("Relax") is indicative of critical slowing down.

5.3. Results

5.3.1 Frequency-Scaling Regime: Conformity to Frequency

Conformity to the pacing regime was analyzed in a 2 limb (right-1:2, left-2:1) by 5 plateau design (1.5, 2.0, 2.5, 3.0, 3.5 Hz) Mixed ANOVA for individual subjects. The absolute difference between metronome frequency and limb frequency was the dependent measure in one analysis, standard deviation of frequency the dependent measure in the other. As noted, the frequency of the driver (faster) limb in the multifrequency relation was considered in the analyses i.e., as per instruction. In general, all subjects were successful in maintaining the requirements of the task, although there was evidence for less conformity and greater variability as a function of frequency with each subject (all $p<0.01$). Differences between left limb (2:1) and right limb (1:2) were not consistently expressed. Subject A and B showed significantly less conformity with the left limb ($p<0.01$), whereas Subject C showed less conformity with the right limb at the highest movement frequency ($p<0.01$), and Subject D did not show a difference between limbs. Subject A was more variable in frequency with the left limb, Subject C with the right (3.5 Hz), whereas the other subjects did not show differences between the limbs.

5.3.2 Frequency-Scaling Regime: Transition Event Data

Mean transition times are depicted in Table 5.1 for preparations of 1:1 anti-phase, 1:2, and 2:1 patterns. The following features were evident: post-transition stability was isomorphic i.e., the stable post-transition pattern was always 1:1 in-phase; all anti-phase preparations culminated in transitions to in-phase; transitions were not consistently present in multifrequency preparations; 2:1 preparations affected transitions more than 1:2 (Subject B: *1:2*- 1, *2:1*- 10; Subject C: *1:2*- 0, *2:1*- 1; Subject D: *1:2*- 4, *2:1*- 7); when transitions were evident in both multifrequency preparations (e.g., Subject A) time-to-transition was faster when prepared 2:1 (18.88 sec/2.25Hz) than when prepared 1:2 (30.37 sec/3.0 Hz)

($F_{1,18}$= 15.183, $p<0.01$). In general, the transition data confirm the data of Experiment 1. Based on transition data, critical frequencies were estimated for each subject based on the measured loss of stability of the anti-phase pattern. Oscillation frequencies up to and including the critical frequency were chosen for single-frequency, metronome-paced trials for each subject. These frequencies are depicted in Table 5.1 (d).

Table 5.1 Time-to-Transition for all Subjects (A-D) in Frequency-Scaled Trials

a. **Anti-phase**

	A	B	C	D
	21.58	26.80	18.39	21.84
	15.71	*45.00*	13.21	31.00
	22.23	37.20	12.00	26.47
	10.83	33.08	16.24	32.58
	17.77	27.17	11.84	28.49
	11.26	29.80	23.60	31.96
	25.14	21.62	12.58	28.64
	11.14	34.83	21.12	31.84
	23.10	35.65	24.51	35.92
	6.20	25.32	21.84	31.14
Mean	**16.50**	***31.65***	**17.53**	**29.99**
(Hz)	**2.25**	***3.00***	**2.25**	**3.00**

b. **Multifrequency 1:2**

	A	B	C	D
	38.05	*45.00*	*45.00*	*45.00*
	23.32	*45.00*	*45.00*	*45.00*
	35.49	*45.00*	*45.00*	44.35
	14.45	*45.00*	*45.00*	*45.00*
	30.46	*45.00*	*45.00*	41.12
	39.83	*45.00*	*45.00*	*45.00*
	17.59	*45.00*	*45.00*	44.40
	31.56	*45.00*	*45.00*	*45.00*
	36.80	35.95	*45.00*	*45.00*
	36.10	*45.00*	*45.00*	42.44
Mean	**30.37**	***44.10***	***45.00***	***44.23***
(Hz)	**3.00**	***3.50***	***3.50***	***3.50***

c. **Multifrequency 2:1**

	A	B	C	D
	14.03	35.82	*45.00*	*45.00*
	22.52	35.25	44.32	41.05
	19.26	31.88	*45.00*	36.85
	15.84	30.81	*45.00*	43.63
	18.02	31.23	*45.00*	38.54
	21.76	33.12	*45.00*	43.57
	20.68	30.88	*45.00*	40.97
	18.04	35.78	*45.00*	43.81
	17.55	28.38	*45.00*	*45.00*
	21.06	30.81	*45.00*	*45.00*
Mean	**18.88**	**32.40**	***44.93***	***42.34***
(Hz)	**2.25**	**3.00**	***3.50***	***3.50***

d.

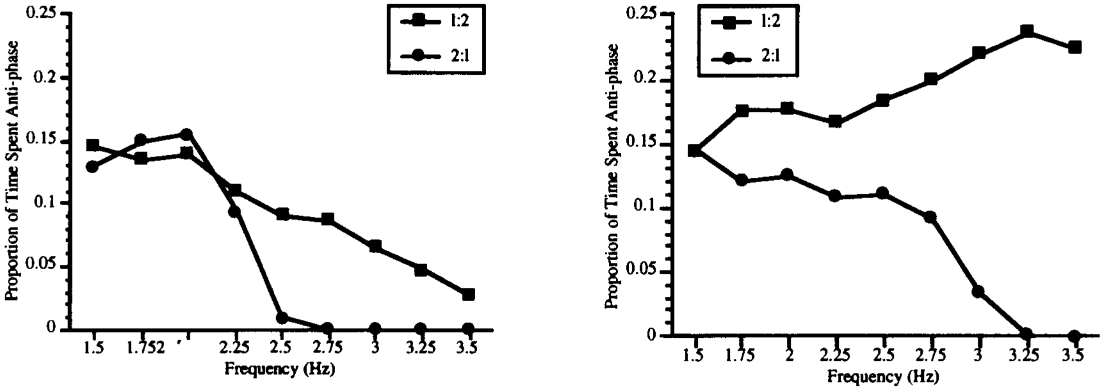
Metronome-Paced Frequencies

A	**B**	**C**	**D**
1.75	**2.25**	**1.75**	**2.25**
2.00	**2.50**	**2.00**	**2.50**
2.25	**2.75**	**2.25**	**2.75**
2.50	**3.00**	**2.50**	**3.00**

a-c. Summary Transition Data for Anti-phase, 1:2, 2:1 preparations respectively.
d. Individually-determined frequencies for metronome paced trials.
(Italics denote transition event "maxima" for trials which did not exhibit stable post-transition means).

5.3.3 Frequency-Scaled: Phase Attraction

Phase attraction was assessed in multifrequency preparations through a 2 pattern (1:2, 2:1) by 9 frequency plateau Mixed ANOVA for individual subjects. The dependent measure was proportion of time spent centered about anti-phase. An arcsin/square-root transformation was used to promote homogeneity of variance in the proportion scores. A main effect of frequency and interaction of pattern with frequency was noted for all subjects (all $p < 0.01$). The consistent result was that of increasing disparity between 1:2 and 2:1 patterns under frequency scaling. Figure 5.2 illustrates the reduction in phase attraction from anti-phase, predominantly 2:1, for Subject A and B. These data support the transition data of Table 5.1, whereby bifurcations to 1:1 in-phase were more common (Subject B), or quicker (Subject A) when prepared 2:1 versus 1:2. As such, a main effect of pattern was also noted in phase attraction for these subjects (both $p < 0.001$).



Subject A

Subject B

Fig. 5.2 Attraction to anti-phase for 1:2 and 2:1 patterns under frequency scaling.

5.3.4 Self-Paced Regime: Frequency Characteristics of Limit-Cycles

Mean preferred frequency and standard deviation of frequency are depicted in Table 5.2 for in-phase, anti-phase, 1:2, and 2:1 self-paced conditions. Preferred frequencies for 1:1 coordination (in-phase and anti-phase) ranged from approximately 1.1-1.5 Hz. Preferred frequencies for multifrequency preparations ranged from approximately 0.7-1.0 Hz for the driven hand, and from 1.6-1.9 Hz for the driver. Thus, the preferred frequency of oscillation of either hand in 1:1 coordination was intermediate to the preferred oscillation frequencies of driven and driver in multifrequency preparations. As evident in Table 5.2, preferred frequencies did not dissociate between in-phase and anti-phase, nor between 1:2 and 2:1. In all preparations, subjects were successful in conforming to the prescribed pattern.

Table 5.2 <u>Preferred Frequencies of Limb Oscillations Across Subjects and Conditions</u>

		1:1 Coordination				**Multifrequency Coordination**			
		In-phase		**Anti-phase**		**1:2**		**2:1**	
Subject		Left	Right	Left	Right	Left	Right	Left	Right
A	Mean	1.41	1.41	1.29	1.28	0.98	1.91	1.94	0.96
	SD	0.14	0.14	0.04	0.05	0.07	0.10	0.03	0.05
B	Mean	1.49	1.48	1.22	1.24	0.88	1.76	1.61	0.82
	SD	0.26	0.25	0.18	0.19	0.05	0.09	0.08	0.03
C	Mean	1.37	1.38	1.20	1.21	0.78	1.54	1.56	0.84
	SD	0.20	0.22	0.14	0.14	0.05	0.09	0.06	0.16
D	Mean	1.17	1.16	1.16	1.16	0.86	1.70	1.85	0.93
	SD	0.05	0.05	0.04	0.04	0.07	0.12	0.07	0.04

5.3.5 Relaxation Times: 1:1 Coordination

The prediction of critical slowing down was assessed through analyses of relaxation time for each subject. Subjects were prepared at a constant frequency and either limb perturbed once, twice or three times per trial. Anti-phase data of each subject were assessed in a 2 perturbed hand (left, right) by 2 synchronization (leftward, rightward) by 4 frequency design. All in-phase data were analyzed in an independent t-test which contrasted the 2 frequencies (lowest and highest from Table 5.1d for each subject. The data are depicted in Figure 5.3.

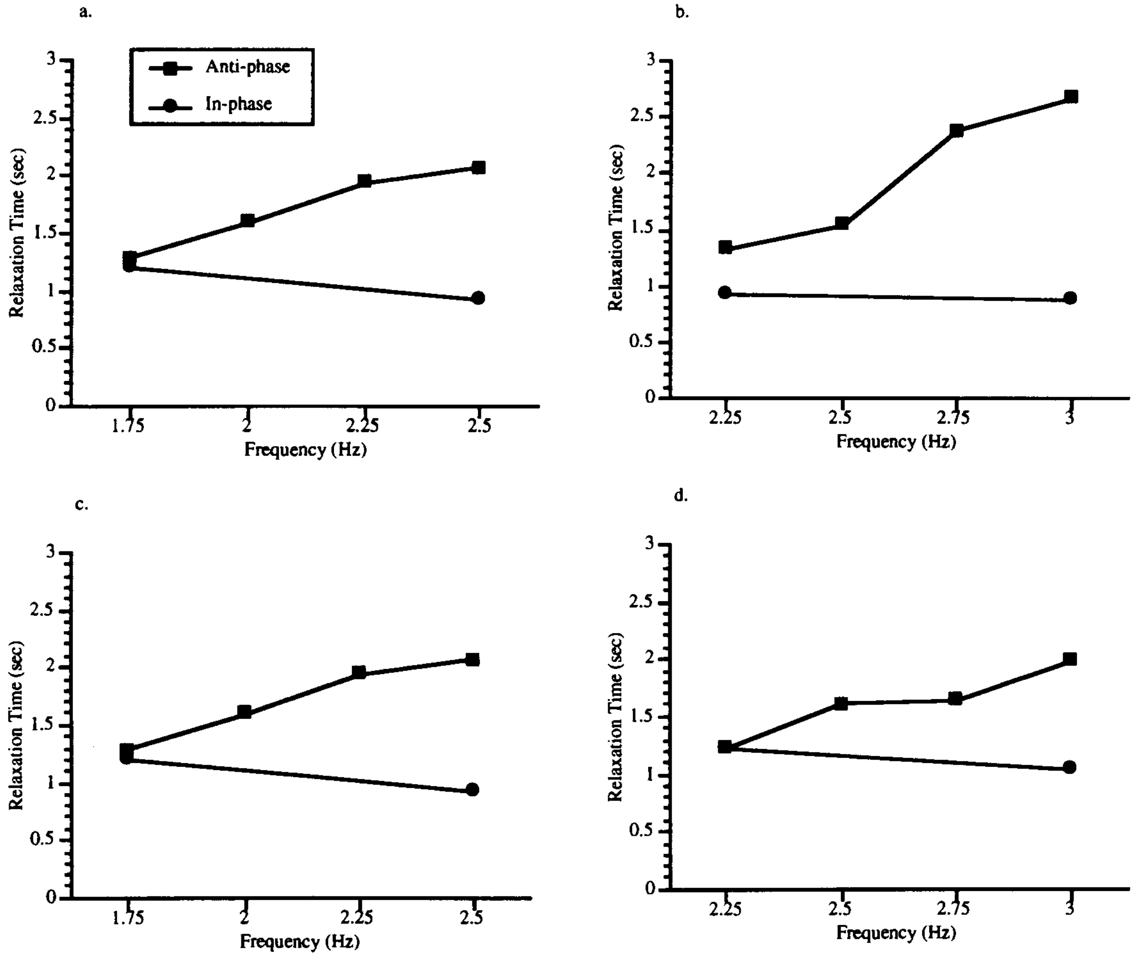


Fig. 5.3 Relaxation times for 1:1 in-phase and anti-phase patterns for Subjects A-D.

The effect of frequency on relaxation time was consistent across subjects for both in-phase and anti-phase conditions. Relaxation time did not differ between frequency conditions when prepared in-phase (A: $F_{1,12}<1.0$; B: $F_{1,9}< 1.0$; C: $F_{1,13}<1.0$; D: $F_{1,6}<1.0$). However, relaxation time increased significantly with frequency when prepared anti-phase (A: $F_{3,100}= 5.066$, $p<0.01$; B: $F_{3,95}=12.705$, $p<0.001$; C: $F_{3,104}= 12.100$, $p<0.001$; $F_{3,94}= 2.978$, $p<0.05$). Tukey's HSD comparisons revealed the following differences: 2.25 and 2.5 Hz significantly slower relaxation times than 1.75 Hz ($p<0.05$) for Subject A; 2.75 and 3.0 Hz significantly slower than 2.25 and 2.5 Hz ($p<0.01$) for Subject B; 2.5 Hz significantly slower than 1.75, 2.0 and 2.25 Hz ($p<0.01$) for Subject C; and 3.0 Hz significantly slower than 2.25 Hz ($p<0.05$) for Subject D.

5.3.6 Relaxation Times: Multifrequency Coordination

There were frequent occurrences of perturbation-induced bifurcations away from stable 1:2/2:1 coordination thus preventing estimation of relaxation time in these instances. Across subjects, there were 44 occurrences when prepared 2:1, 34 occurrences when prepared 1:2. In order to maximize the obtainable data set, the standard deviation criterion was tailored specifically to each subject. A criterion of 1.0 was used for Subject B, C, and D, as in the 1:1 trials. The data of Subject A required a criterion of 0.5 SD in order to obtain a meaningful data set. Finally, the lowest frequency condition from each subject was eliminated from the analyses due to limited relaxation time data (due to abnormally high variability associated with the slower moving limb in the relation).

Data were first analyzed in a 2 pattern (1:2, 2:1) by 3 frequency design for each subject. A main effect of frequency was significant for Subject B ($F_{2,50}=6.018$, $p<0.01$) and approached but failed to reach the criterion for significance for Subject A ($F_{2,52}= 3.025$, $p<0.06$). Subject C reported means in the same direction as A and B, but these means did not differ significantly ($F_{2,50}=1.691$, $p>0.1$). There was no effect of frequency for Subject D ($F<1.0$). The effects of frequency are summarized in Figure 5.4. There were no effects of pattern (all $p>0.1$), nor were there any interactions of pattern with frequency (all $F<1.0$).

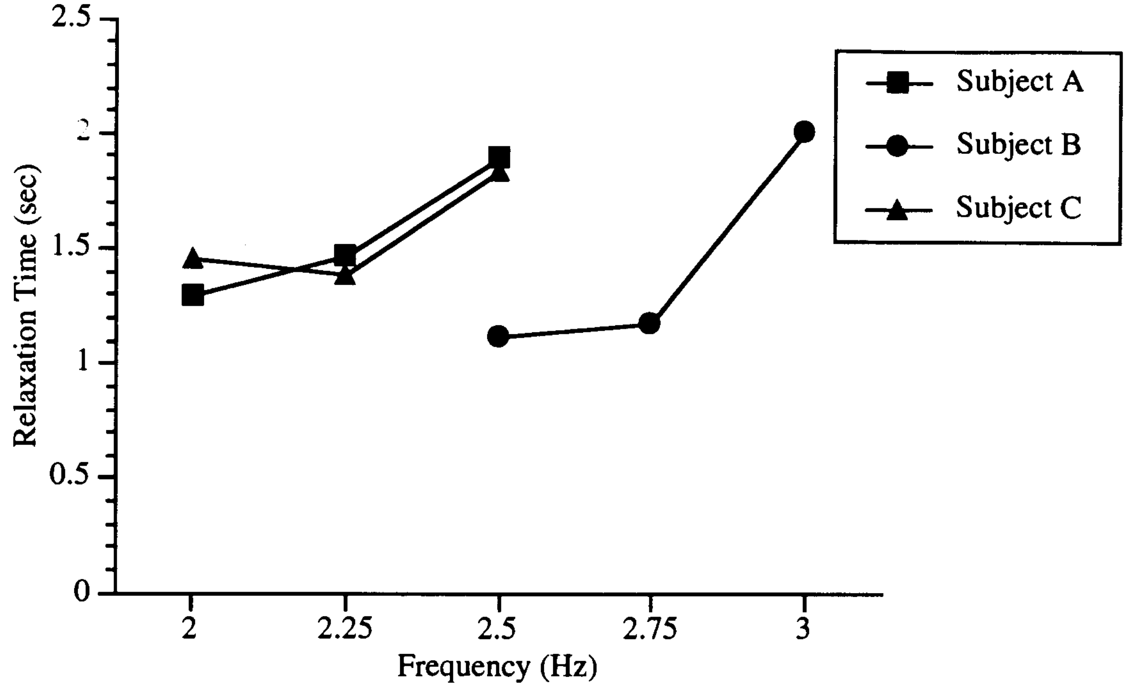


Fig. 5.4 Relaxation times for multifrequency coordination collapsed over pattern (and perturbed hand). Relaxation time differed significantly as a function of frequency for Subject B ($p<0.01$).

Relaxation times were also examined in a 2 perturbed-hand by 2 pattern (1:2, 2:1) by three frequency design for subjects with complete data sets (A, C). The data of Subject B permitted analysis of a 2 "driver perturbed" (left hand perturbations/2:1, right hand perturbations/1:2) by 3 frequency design, whereas the data of Subject D were sufficient for a 2 "driven-perturbed" (left hand perturbations/1:2, right hand perturbations/2:1) design. The above analyses were performed in order to confirm the effect of frequency with a degree of sensitivity to the effect of perturbed hand (which may have biased relaxation time estimates based on limb period). The analyses revealed a significant effect of frequency for two subjects (B: $F_{2,28}=3.480$, $p<0.05$; D: $F_{2,23}=4.358$, $p<0.05$). As in the former analysis, the means of subject A were in the expected direction, but failed to reach significance for frequency ($p<0.08$).

Figure 5.5a illustrates an interaction of perturbed hand with frequency for Subject A ($F_{2,46}=5.740$, $p<0.01$) . Tukey's HSD comparisons revealed that the relaxation times of multifrequency patterns (1:2 and 2:1) increased significantly between 2.25 Hz and 2.5 Hz (the critical frequency for that subject) with left hand perturbations. Subject C revealed a significant effect of hand ($F_{1,44}=5.264$, $p<0.05$) and an interaction of hand and pattern ($F_{1,44}=4.817$, $p<0.05$). These effects are illustrated in Figure 5.5b. Post-hoc comparisons revealed that for the relaxation times for 2:1 preparations, perturbations to the left-hand led to significantly greater relaxation times than perturbations to the right hand ($p<0.05$). There were no effects of pattern or interaction to report for Subject A, no effects or interactions of frequency for Subject C, and finally, no effects of mode, or interactions of mode by frequency, for Subjects B and D (all $p>0.1$).

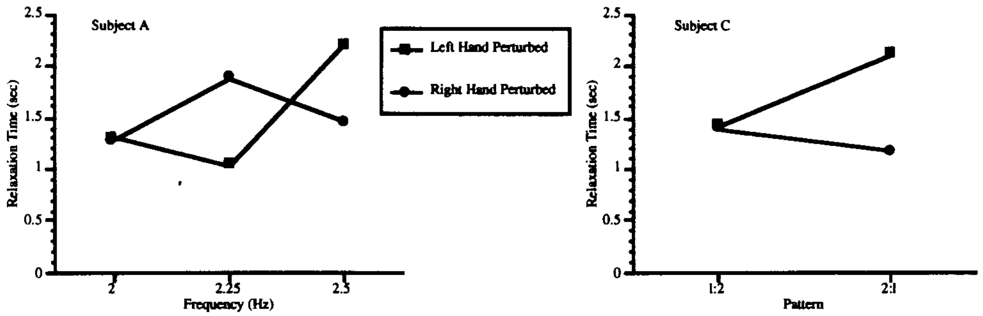


Fig. 5.5. Effects of perturbed hand on relaxation time. a) Relaxation time increases with left hand perturbations between 2.25 and 2.5 Hz for Subject A. b) Relaxation time is greater with left hand versus right hand perturbations when prepared 2:1 for Subject C.

5.3.7 Summary of Results

a. Frequency-scaling regimes identified loss of stability and transition phenomena for preparations of 1:1 anti-phase and multifrequency 1:2 and 2:1 patterns. As in Experiment 1, the 2:1 pattern was identified as less stable than the 1:2 pattern through the onset, and frequency of occurrence, of bifurcations to 1:1 in-phase.

b. In multifrequency preparations, phase attraction was prominent in the loss-of-stability of Φ. As in Experiment 1, attraction to anti-phase regions decreased as a function of frequency, and moreso when prepared 2:1.

c. Relaxation time analyses confirmed the feature of critical slowing down for all subjects in 1:1 coordination. Relaxation times increased with frequency for anti-phase preparations but remained stable for in-phase preparations. Critical behaviour was not dependent on the hand which was perturbed.

d. There was limited evidence for critical slowing down in multifrequency preparations. Asymmetries were not expressed between 2:1 and 1:2 preparations in measures of relaxation time. However, these data implicated a greater effect on the stability of Φ when the left limb was perturbed (Figure 5.4a) , or prepared 2:1 (Figure 5.4b).

5.4 Discussion

The present data support the contention that the language of coordination is not without *stability* in its vocabulary. Patterns of behaviour in biological movement, be they flight, or locomotion, or simple rhythmic movement, maintain a stable, reproducible organization. It is not uncommon to prescribe such patterns to oscillatory processes within the architecture of the central nervous system. Certainly we are not without circuitry which provides oscillatory dynamics (e.g., Stein, 1976; Yaminishi et al., 1979) capable of maintaining stable, reproducible patterns. But what cogent basis is there for the organization of such patterns? What determines the presence or absence of one pattern or another? In the present study, stable patterns of coordination were evident in 1:1 and 2:1 frequency locking of rhythmic movement. However, by probing the (relevant) system parameter i.e., the order parameter Φ, while varying the nonspecific parameter frequency, stability portraits of the patterns revealed an underlying topology of persistent and transient attractors, corresponding to in-phase and anti-phase coordination.

In 1:1 coordination it was evident that pattern change was precluded by loss of stability. Stability was depicted quantitatively in the measure of relaxation time, and loss-of-stability depicted in transition phenomena, spontaneous or induced. As such one can infer, or anticipate, pattern change by the stability portrait of the pattern itself. The observation of the feature of critical slowing down supported the observations of Scholz and Kelso (1989), and supports the model of bimanual coordination based on low dimensional equations of motion as proposed by Haken et al (1985). The emergence of critical behaviour however, was not as readily identified in preparations of multifrequency coordination, although there was evidence for the same underlying dynamics.

Recently, the phenomenon of critical slowing down has been identified in between-person coordination (Schmidt et al., 1990) and person-environment coordination (Wimmers et al., 1991), thus supporting the contention of modality shifts in the stability of human coordination in general. These phenomena identify the virtue of shared dynamics between systems comprised of heterogeneous substrate and forcing. The former is identified by the reciprocal forcing of coupled oscillators in two nervous systems. The latter is idenitifed by the unilateral coupling of a single nervous system to an environmental stimulus. The present study was restricted to the reciprocal forcing between the two hands in bimanual coordination. In such regimes it has been argued that symmetry is not maintained between the limbs, and thus must be accounted for in any dynamical account of bimanual coordination (e.g., Byblow et al., 1994; Carson, 1993; Carson et al., 1994). The effect of asymmetries between the limbs was examined in the current study. First, the phenomenon of performance asymmetries, as identified in Experiments 1-3, as well as in paradigms of rhythmic tapping (e.g., Peters, 1985), were confirmed between 1:2 and 2:1 in preparations in the present wrist rotation regime. Again, when the assignment of frequency to hand was such that the dominant (right) limb maintained the driving frequency in the relation, stability was greater than in the converse arrangement.

The expression of performance asymmetries has been readily observed at the level of relative phase through such measures as time-to-transition, probability of transition, phase attraction, and variability of Φ (Experiment 1). However, the present data were not in consistent support of critical slowing down as a basis for performance asymmetries between respective preparations. It is possible that the chosen frequencies at which the multifrequency preparations were examined were not ideal for such an expression. This however seems unlikely in consideration of the data which speak to phase attraction in the present study, and in the data of Experiment 1. It is more compelling to suggest that relaxation time is not as sensitive a measure of *phase attraction* as it is for *attractor strength*., although the latter may define the former over larger time scales. The present examination of 1:1 coordination supported the contention of an annihilation of an attractor corresponding to the anti-phase pattern. Under the annihilation metaphor the system must simply be perturbed by progressively smaller noise sources in order to effect pattern change (to in-phase). By effectively applying sufficiently small mechanical perturbations, the strength of the existing attractor was deemed to decrease as a function of frequency (as reflected in relaxation time), a quantifiable consequence of the system dynamics as proposed by the HKB model. In mapping these dynamics to other patterns of coordination , it has been suggested that the intrinsic dynamics of in-phase and anti-phase attraction define the stability of higher-order mode-locks. In the parameter space of the sine circle map (e.g., Jackson, 1989) a deterministic generator of all frequency lockings, the dynamics of bimanual coordination can be imposed by the inclusion of a periodic coupling function (DeGuzman & Kelso, 1991). The *phase-attractive* circle map of DeGuzman & Kelso (1991) was proposed as a discrete analog of the HKB model for bimanual coordination,

$$\Phi_{n+1} = \Phi_n + \Omega - K/2\pi(1 + A\cos 2\pi\Phi_n)\sin 2\pi\Phi_n \qquad (2)$$

where iterations of phase Φ_{n+1}, are determined by previous phase Φ_n, the ratio of uncoupled frequencies Ω, and the coupling function, in this case $K/2\pi(1 + A\cos 2\pi\Phi_n)$, which acts as a control parameter for mode-locking. In Experiment 1 it was suggested that the relative importance of the underlying intrinsic dynamics (the parameter A in the map) was greater for the preferred 1:2 assignment, for any given level of coupling K. This would result in a greater area of stable K space for a particular Ω, in this case 0.5, or irrational ratios very near 0.5, depending on the region of K-Ω space. Or, put another way, in the 2:1 assignment, there are fewer coupling strengths K, which yield return stable phase relations at Ω for a given level of A, which relates inversely to the control parameter frequency (e.g., Kelso et al., 1991). It is not unreasonable to suggest that the stability of the mode lock may be defined by phase attraction (as defined by the intrinsically stable modes of in-phase and anti-phase). However, in multifrequency regimes, movement toward or away from anti-phase, as with any other phase relation, is transient. For example, it may be quite difficult to provide a transient perturbation between systems of identical Ω, but of different A, and determine a difference based on relaxation times. The strength of the underlying, transient attractors corresponding to in-phase and anti-phase define the stability of the respective mode-lock at, or near, Ω. Ultimately, the system is less and less likely to be in the very region of Φ space in which a positive effect is possible, given the intrinsic dynamics (attractors) of bimanual coordination.

Clearly, stable rhythmic coordination extends beyond the patterns identified in extant preparations of 1:1 frequency lockings and examples of these were depicted in the present data. However, it is argued that an accurate account of bimanaul coordination must regard *phase attraction* , the feature which permits two coupled biological oscillators to exhibit phase entrainment, as opposed to phase locking, and hence, a feature well noted in human coordination (DeGuzman & Kelso, 1991; Schmidt et al., 1993; Sternad et al., 1992; Turvey et al., 1993). Phase attraction thus endows the system with a feature of flexibility which may give rise to relative coordination (von Holst, 1937/1973) i.e., the ability to escape 1:1 frequency locking and explore the full regions of Φ space. The constraints of multifrequency coordination are such that they permit the system to travel through full regions of Φ space. It is suggested that the phase attractive dynamics corresponding to stable patterns of Φ in 1:1 coordination, permit stability to be maintained through regions of attraction which delineate points of synchronization, and thus, coordination. The phenomenon of phase attraction is such that stable coordination is permitted. Phase attraction thus defines the stability which permits the existence of the patterns themselves, and more importantly, pattern change.

6 General Discussion

The previous sections have provided a dynamical basis, in theory and experiment, for patterns of coordination which emerge under multifrequency constraints. The intention of the present section is to synthesize the major findings from each experiment in the context of the questions and predictions raised in Sections 1.3 to 1.6. The questions are addressed individually with evidence drawn from one or more experiments, as each is considered. The discussion is divided broadly into two sections which focus on issues related to stability and loss-of-stability and, asymmetries in coordination. The initial discussion however, addresses aspects of the data from Experiments 1and 3 particularly, which unmasked the influence of individual difference. These are first considered before the experiments are discussed in a holistic context.

Aspects of coordination were determined from assessment of critical phenomena which precluded a loss of stability or, pattern change. It was argued in the introduction that the so-called regions of transition provide a logical entry point whereby the essential dimensions of the system are revealed. In order to examine these critical events in human performance under the constraints imposed, highly individualistic prescriptions of control parameter regimes were implemented, in the case of Experiment 1 and 4 for example, via tailored prescriptions of frequency of oscillation. By prescribing frequencies to subjects at an individual level, loss of stability emerged predictably in extant preparations of 1:1 coordination i.e., anti-phase to in-phase, and to a large extent, from multifrequency coordination to 1:1 patterns, supporting a dynamical basis for coordination in general. However, qualitative shifts in patterns from multifrequency to 1:1 patterns were not inevitable and as such, more fine-grained analyses of the order parameter relative phase (e.g., uniformity, phase attraction) were derived in order to assess the inherent stability of multifrequency assignments. This strategy was successful in providing a dynamical basis for stability differences in multifrequency coordination based on the assignment of hand to frequency. However, it was anticipated that other factors may also influence coordination, such as attention (e.g., Experiment 1), or the relation of limb frequency to the prescribed frequency of an auditory stimulus (e.g., Experiment 3). Quite simply, the effects of these manipulations were highly individualistic with respect to the subjects, and hence, the hypotheses regarding attention, and preferred assignment of limb to frequency in a person-environment multifrequency relation, were rejected. In the case of person-environment coordination in Experiment 3, this interpretation allowed for a more specific interpretation of multifrequency coordination dynamics for bimanual regimes specifically, and these are discussed further below. As a research strategy, the dynamics perspective adopts the tools of nonlinear dynamics as a basis for characterizing the essential features of coordination dynamics. Whether or not this strategy will flourish into a descriptor of the many facets of individual difference in human performance remains to be determined.

Stability and Loss-of-Stability

... do the intrinsic dynamics of bimanual coordination (as described by the HKB model) encapsulate the stability and loss-of-stability in multifrequency regimes?

The central prediction of the Haken et al (1985) model is that patterns of bimanual coordination, are prescribed *a posteriori*, as an inevitable consequence of the mutual interactions of the component oscillators which are coupled in a nonlinear fashion. When examined at the level of the relative phase between the limbs, patterns are governed by low-order equations of motion which evolve over the time course of observation, or more frequently, guided by the regular scaling of a known control parameter. Essentially, the control parameter regime guides the system through a parameter space toward instability, yet remains nonspecific with respect to the patterns themselves. For example, the regular scaling of oscillation frequency, a known control parameter in extant preparations of human coordination can lead to spontaneous, qualitative shifts in the relative phase. Frequency does not prescribe the pattern of coordination, but rather, the state of the system within an attractor landscape (Haken et al., 1985).

The notion of an attractor defines, or rationalizes, the stability of the pattern itself. A sudden shift from one stable pattern to another implies the annihilation of the attractor corresponding to the previous pattern or, a movement of the system to a parameter space which no longer furnishes stability for the respective frequency-locking. The phenomenon of the former are well documented in preparations of bimanual coordination (and interlimb coordination) for 1:1 frequency locking when prepared anti-phase. Bifurcations were also confirmed as regular features within the multifrequency preparations of the present Experiments 1 and 4. Namely, preparations of 1:2 (2:1) bimanual coordination often led to a spontaneous shift to 1:1 coordination. This bifurcation process demonstrated at least three unique characteristics. First, its emergence was not inevitable i.e., a scaling in frequency did not guarantee a shift from multifrequency to 1:1 frequency locking. Second, under the spontaneous occurrence of 1:1 patterns, the mode of coordination was always *in-phase*. Third, and finally, the frequency of oscillation of the emergent pattern 1:1 always exhibited the frequency of the driving (faster) frequency of the multifrequency preparation. These features are addressed within the remainder of the present discussion.

...are transition phenomena (of multifrequency coordination) an expression of the intrinsic dynamics, as identified by Haken et al. (1985)?

Transitions were not an inevitable consequence of multifrequency preparations. Herein lies a striking distinction from examinations of 1:1 coordination i.e., when the limbs are prepared "anti-phase". The present findings (Experiments 1 and 4), and the findings of many recent studies, suggest that preparations of non-homologous muscle groups active in synchrony inevitably become unstable under the scaling of frequency (but see Baldiserra, 1991; Kelso & Jeka, 1992; and Riek et al, in press; for alternative parameterizations of so-called "anti-phase"). It may be asked then, is frequency of oscillation the true control parameter? Although a complete loss of stability was not always an inevitable feature of the multifrequency preparations examined here, it would not be unwise to predict a loss-of-stability as an inevitable consequence over: a) longer time scales and, b) more stringent conformity to frequency regimes. However, the sporadic nature of bifurcation phenomena suggest that the multifrequency locking is not solely defined by an attractor per se, but rather by the strength of the frequency locking or ratio (the attractor) within the parameter space of the coupled frequencies *and* phase attraction.

In the circle map regime, the stability of a frequency lock is determined by the range of coupling functions which return stable locking at a given frequency ratio. The range of stability is termed an "Arnold tongue" (after Arnold, 1965), whereby stability in the mode lock is depicted by the width of the tongue and determined by the equation of motion for the coupled oscillator regime. The intrinsic dynamics of bimanual coordination as identified by Haken et al. (1985) may be extended to the discrete framework of the sine circle map (DeGuzman & Kelso), and as stated throughout, the map can be endowed with phase attractive dynamics such that the coupling, and phase attraction act as the relevant control parameters through an expanded coupling expression (e.g., Section 5.4, eq'n 2). Thus, the fate of the collective behaviour of bimanual coordination is not solely determined by the coupling, but rather by the coupling, the phase attraction (A), and/or, the function relating the two e.g., F(K,A).

...what features of coordination rationalize the loss of stability at higher order frequency relations?

This question was addressed predominantly in Experiment 1. First, it was noted that under the regular scaling of oscillation frequency, abrupt, qualitative shifts occurred in relative phase. These identified the evolution of the coordination through low-order resonances, namely through the frequency ratios 2:1 to 1:1. These comply with general Farey principles (Glazier & Libchaber, 1988) in that the frequency ratio of the components shift from higher order to lower order ratios, and hence, rationalize a fundamental feature of human coordination. Namely, it is *more difficult* to maintain a higher-order frequency relation between the limbs (DeGuzman & Kelso, 1991; Deutsch, 1983; Peper et al., 1991; Peters & Schwartz, 1989; Treffner & Turvey, 1993).

However, the present data suggest that the true control parameter of bimanual coordination may be phase attraction itself. The multifrequency preparations of Experiment 1 depicted a monotonic increase in phase attraction toward in-phase and corresponding decreases toward anti-phase. Granted this feature did arise under the scaling of frequency, but the scaling of frequency was not always sufficient to induce a (complete) loss of stability in the pattern. In the absence of transitions, the system had essentially become locked in frequency and in phase. With the occurrence of transitions through 1:1 preparations, phase, but not frequency, was altered. As one might suspect, the probability of induced transitions in phase only are greater. However, the occurrence of bifurcations in Experiment 1 and 4 were consistent in the sense that the post-transition pattern of 1:1 coordination always emerged in-phase, suggesting the underlying annihilation of the attractor corresponding to anti-phase. The annihilation metaphor has been examined in relaxation time measures indicative of critical slowing down by Scholz and Kelso (1989), and has been confirmed in the replications of 1:1 bimanual preparations of Experiment 4. The stability of the multifrequency patterns examined herein were shown to correspond to attraction in Φ to in-phase and anti-phase. The loss-of-stability was precluded by the loss of an existing region of attraction corresponding to anti-phase. It was suggested that the corresponding annihilation of the anti-phase attractor corresponded to a loss of synchronization such that the bimanual system became dependent on the synchronization at in-phase only. Thus, the (overwhelming) phase attraction to in-phase was implicated in the bifurcation phenomenon i.e., the formation of a dynamic which prescribes rigid locking in phase and frequency reminiscent of von Holst's absolute coordination . Unfortunately, measures of relaxation time did not provide the overwhelming support for critical slowing down in multifrequency preparations as were realized for 1:1 anti-phase preparations. The implications of this difference were discussed in Experiment 4 and suggest that the phase attractive dynamics may elude conventional assessments of critical slowing down.

The above discussion of phase attraction is not intended to suggest that the coupling between the limbs does not contribute to the coordination pattern, and to some extent, a change in pattern. Indeed, it is the respective coupling between the component oscillators, as well as the bi-directionality and proportionality of coupling strengths which define the basis of asymmetries described herein. These ideas are expanded in the discussion of asymmetries throughout, as well as in later discussions. However, the present discussion which is pertinent to loss-of-stability in general, concludes with a final consideration of experimental data which depict stability of Φ in the absence of pattern change. A fine-grained analysis at the level of the collective variable was derived which demonstrated instability in the *absence* of qualitative change. Namely, the uniformity of relative phase, a measure inversely proportional to variability, was obtained which demonstrated a degeneration in stability. A reduction in uniformity was predominant under the scaling of frequency (e.g., Experiment 1), and between multifrequency preparations (e.g., 1:2 versus 2:1) under the influence of pacing (prescribed externally or internally) at a constant frequency (e.g., Experiment 2). As has been stated (Section 1.4) variability is not only a ubiquitous feature of human movement, it is essential. For example Schöner et al (1986) demonstrated an essential role of critical fluctuations i.e., variability in Φ, in the spontaneous emergence of new patterns of coordination. However, the time scales and nature of variability in human movement, deterministic or stochastic, remain a feature yet to be resolved by the student of movement regulation.

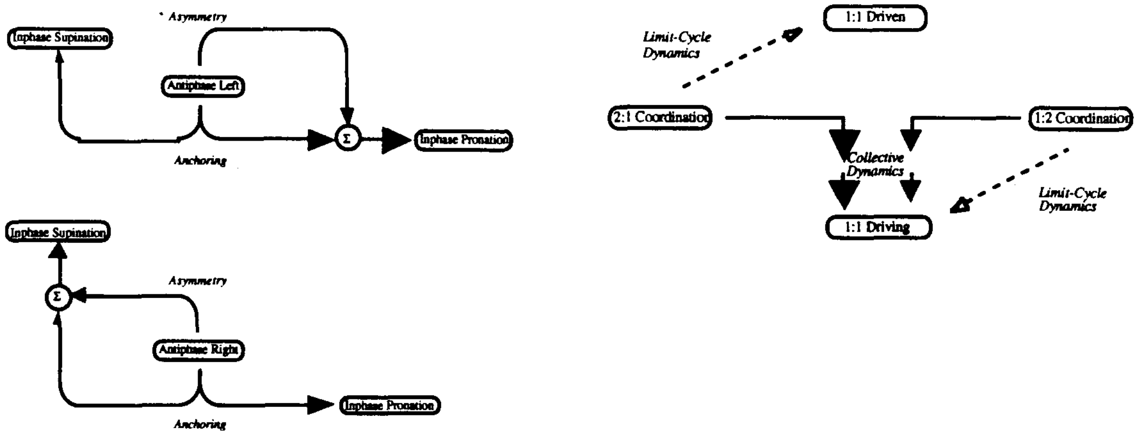
Asymmetries in Coordination

...are expressions of asymmetries consistent in multifrequency coordination i.e., ubiquitous to bimanual coordination in general?

Asymmetries are indeed ubiquitous in bimanual coordination whether prepared in 1:1 or multifrequency relations. Experiment 1, 2, and 4 served to note the difference in inherent stability between systems comprised of the left versus the right limb assigned to the dominant frequency in the relation. In Experiment 1, when the non dominant limb maintained the higher frequency in the relation, and under the scaling of frequency, the occurrence of bifurcations was greater, the time-to-onset of bifurcation was quicker, and variability of relative phase was greater. In general, the collective behaviour of the "left-hand-fast system" was quantifiably less stable than the "right-hand-fast" system. Importantly, these differences were evident in the absence of any clear dissociation between the frequency characteristics of the limbs at the level of the limit-cycles themselves. That is, at an individual limb level, neither limb was implicated as inherently more or less stable. This is not to suggest a complete absence of manual asymmetries in general. Indeed, such phenomena have received considerable exposure from current research efforts (e.g., Byblow et al., 1994; Byblow et al. ,in press; Carson et al., 1994), and throughout the literature (e.g., Carson, 1993; Marteniuk et al., 1984; Peters, 1990). However, it is important to note that at a performance level the prescribed frequency of oscillation was well within the maximal tolerance limits for the successful completion of the task. This condition was also supported throughout in preparations of the limbs in 1:1 patterns of coordination (e.g., in-phase, and anti-phase). Thus, the emergent performance asymmetries in multifrequency coordination are implicated within the interactions of the limbs at the level of coordination. In the language of von Holst, asymmetries emerge in the latent struggle between the limbs in cooperativity ("magnet effect") and competition ("maintenance tendency") through mutual interaction. The essence of asymmetries evident in multifrequency coordination (e.g., Experiments 1,2,4) have been identified within (as an expression of) the intrinsic dynamics which prescribe the patterns themselves- that is, the phase attractive dynamics.

...are asymmetries expressed as a feature of cooperativity or, will features of symmetry breaking emerge?

Clearly, it is our contention (e.g., Byblow et al, 1994; Carson, 1993; Carson et al., 1994) that in extant preparations of 1:1 bimanual coordination, asymmetries emerge *a posteriori* as a result of the differential coupling of one limb on the other. The basis of this difference may well be ascribed to maximal rates of responding (e.g., Peters, 1990), however, such conditions are not necessary for their emergence. It is perhaps puzzling, if not an unfortunate circumstance of nomenclature, that the predictions of broken symmetry are not identified with the expression of performance asymmetries described herein. For example, in preparations of 1:1 bimanual coordination Byblow et al. (1994) determined that although the phenomenon of isodirectional transitions emerge, the full predictions of broken symmetry were not fulfilled. Specifically, the occurrence of fixed point drift (stable value of Φ which "drifts" away from 0 and 180 degrees) was notably absent. The observation of isodirectional transitions revealed a tendency for the non dominant (left) limb to alter it's initial state in an anti-phase preparation in order for the collective to shift in-phase. In order to illustrate these data, Byblow et al (1994) proposed the force flow diagram of Figure 6.1a. The diagram depicts the transition pathways which emerge under preparations of 1:1 coordination (anti-phase) which are defined on the basis of asymmetries and anchoring (the coincidence of movement endpoints and external information such as a metronome beat). As stated in section 1.4, the phenomenon of isodirectionality in the absence of fixed point drift can be accommodated by the differential coupling of left limb on right and vice versa. The basis for this difference may arise from differences in the limit-cycle dynamics i.e., inherent variability at maximal rates of responding (e.g., Peters, 1990), or dynamics which are not stationary over time (Byblow et al., 1994). In either case, such differences are scaled to sub maximal levels such that they are observable at the level of the collective behaviour about the critical region of loss-of-stability and pattern change.



a. b.

Fig. 6.1 Isodirectional transition pathways of bimanual coordination. a) 1:1 coordination (from Byblow et al., 1994). The magnitude of the forces of asymmetries and anchoring are depicted by the size of arrows. b) Multifrequency coordination. Patterns of 1:1 coordination emerge always "in-phase", and at the dominant frequency of the multifrequency preparation. In this case, the *probability* of transition is depicted by the size of arrows.

Isodirectionality was also evident in critical behaviour in multifrequency coordination. That is, bifurcations occurred solely to 1:1 in-phase and maintained the frequency of the dominant (driving) limb, regardless of the assignment of hand to frequency. These features are depicted in Figure 6.1b and comport to the transition data of Experiments 1 and 4. As such, the apparent asymmetries at the level of limit-cycles remain latent with respect to transition pathways. That is, the non dominant limb in *hand preference* does not define the pathway through which transitions emerge, but rather, the pathway is defined by the non dominant limb in *frequency*. Thus, the broken symmetry which is imposed on the bimanual coordination regime via oscillation frequency, and which defines the multifrequency pattern itself, can be isolated in the extent of post-transition patterns. However, the feature of fixed point drift was absent in the present data, and thus the relation between the uncoupled eigenfrequencies did not express a difference between left and right limbs. Although a more fine-grained analysis might reveal a difference at the level of the limit-cycles themselves, any difference in the natural bimanual preparations of Experiment 1 and 4 (not physically altered in characteristic frequency by pendula or other means) were not significant contributors to pattern shifts, nor were they stationary over time (see Carson et al., 1994, for a discussion of "characteristic" frequencies). The features of broken symmetry are thus not supported in the present bimanual regimes although their relevance is apparent within interlimb regimes such as those of provided by Kelso & Jeka (1992). The diversity afforded to bimanual coordination thus emerges from sources of asymmetry which arise from sources other than those imposed by symmetry breaking dynamics.

The expression of asymmetries through the assignment of hand to frequency in multifrequency preparations, as evidenced in the present experiments, were evident at the level of relative phase. This was not surprising since these preparations usually relegated the slower limb to frequencies well within its maximal frequency limits (e.g., Carson, 1993; Peters, 1987). As such, performance asymmetries which emerged between assignments of hand and frequency were expressed primarily through the parameters which defined the collective behaviour, despite the apparent absence of inherent limitations at the level of the limit-cycles themselves. For example, the data of Experiment 1 did not implicate either limb as inherently more or less stable under the multifrequency constraints imposed, although the expression of performance asymmetries between the respective preparations 1:2 versus 2:1, was clear. It has been argued above and in the discussions of Experiments 1 and 4, that the function which relates the coupling strength between the oscillators to the relative importance of the intrinsic dynamics (phase attraction) may determine the basis for the observed phenomenon. Under this strategy, separate coupling terms are not prescribed as in section 1.4, or in Carson et al. (1994). Instead the strength of coupling remains generic between limbs i.e., as a consistent feature of the driver/driven frequency relations. However, the coupling strength is guided, enhanced, etc., by the parametric influence of phase attraction, which delineates the respective assignments, and consequently, forces the bimanual system into parameter spaces where transitions are more (2:1) or less (1:2) likely to occur.

...does the two-process model (Wing & Kristofersson, 1973) extend to account for asymmetries in the domain of rhythmic, multifrequency coordination?

It was anticipated that a meaningful expression of manual and performance asymmetries could be determined through analyses which may isolate sources of timekeeping and neuromuscular delay in repetitive rhythmic movement. Experiment 2 was specifically directed toward the identification of the underlying neural correlates between unimanual and bimanual rhythms, and specifically the timekeeping constraints imposed in multifrequency coordination. Would sources of variability attributable to timekeeping or pattern generation, or inherent delay processes, form the basis of the anticipated and observed performance asymmetries as depicted throughout? Experiment 2 provides an extensive body of data which suggest that this was not the case. Although performance asymmetries were evident in the relative phase dynamics of multifrequency preparations between the fingers, neither oscillator was identified as more or less variable in terms of their underlying neural architecture. These data are in agreement with the earlier work of Wing et al. (1989) who did not show an expression of hand (left versus right) in preparations of alternate finger tapping. The present data suggest that the model of Wing & Kristofersson (1973) was not sensitive to the underlying system dynamics which form the basis for the dissociation between the respective multifrequency preparations examined herein. The main limitation was suggested to be the isolation of analyses to the level of the components in isolation. It has been argued throughout that differences at this level may only arise near maximal tolerance limits of the respective limb. These conditions were not explored fully in Experiment 2, since they did not preclude the emergence of performance asymmetries and, they were not well suited to multifrequency preparations in general.

Turvey and colleagues (1986, 1989) have implicated variability, and fluctuations in relative phase in preparations of 1:1 wrist-pendulum oscillations to the neural componentry as identified by the two process model of Wing & Kristofersson (1973) (see section 3.1.2 and 3.1.3). The present data however, did not clearly implicate the influence of Φ on timekeeping or delay variances in preparations of natural i.e., not physically driven, oscillations. It is not clear whether a difference in paradigms of rhythmic movement served as a basis for differences between the findings of Experiment 2 and Turvey et al. (1986). The reader is reminded that the paradigm of rhythmic movement chosen for Experiment 2 was such that it closely approximated the paradigm (and frequencies) of the original studies of Wing and colleagues.

A final consideration of the strategy of timekeeping and pattern generation determination is provided. Recently, Kelso et al. (1992) have expanded the dynamical framework of human coordination to the level of cortical activity i.e., the identification of the pattern formation process in EEG and MEG signals. There is mounting evidence to suggest that a shared dynamical basis exists between the patterns of overt rhythmic movement and the patterns of neural/cortical activity which underlie rhythmicity. As such, further evaluation of models such as those of Wing & Kristofersson (1973), which serve to link these levels of analyses, yet remain at the level of movement behaviour, may still hold considerable promise for students of coordination.

...is stability in the limb-stimulus relation dependent upon whether the dominant versus non dominant limb is comprised within the collective?

Although an attractive hypothesis from the viewpoint of symmetry (and asymmetry) in human coordination, there was no support for this hypothesis. However the features of person-environment coordination from Experiment 3 shed insight into the phenomenon of multifrequency coordination in general, and interlimb coordination specifically. First, stability in Φ was determined on an individual basis by the assignment of limb frequency to driving or driven status (in frequency). It was apparent from Experiment 3, that this preference did not differ between coordination patterns between limb and metronome when the left versus the right limb was chosen. Since only the limb component was free to vary in phase and frequency (as opposed to the stimulus), the system is said to be forced, or coupled, in a unilateral manner. Although this condition implicates the limb in the role of the driven oscillator, it was apparent that certain subjects expressed a preference to maintain the dominant frequency with either limb. It was suggested that this preference, as identified in the stability portrait of Φ, may provide a basis for correlates in the realm of psychosocial interactions. Similar hypotheses have been advanced, and studied formally, by Schmidt et al (1993) in between-person coordination. With respect to interlimb coordination, the multifrequency preparations of person-environment coordination implicate the reciprocal coupling between limbs as a basis of performance asymmetries, as opposed to a preferential assignment of limb (based on hand preference) to frequency (based on driving/driven relations) in the multifrequency relation. In principle, these data lend support to the position that performance asymmetries emerge through the *mutual* interaction of the limbs in coordination. This feature of bimanual coordination has been proposed in the circle map framework of DeGuzzman & Kelso (1991) which relates coupling to phase attraction i.e., F(K,A), based on assignment of hand to frequency.

...are asymmetries expressed as a feature of flexibility reflected in Φ space, or more specifically, those regions which are not consistently accessible to interlimb coordination?

There was limited evidence from Experiment 3 which suggested that the maintenance of coordination in near-mode-locked regions of Φ space identified a basis for asymmetries. These data may thus rationalize the contention that the dominant limb is better suited to creative expression (Guiard, 1989). In a recent study, Treffner & Turvey (1993) provide an extensive account of resonance constraints on rhythmic movement. Their paradigm was similar to that of Experiment 3 and examined the evolution of person-environment coordination through a number frequency lockings. Their data supported a dynamical basis for shifts from one frequency locking to another, and in princpile, support the utility of person-environment regimes in the study of coordination dynamics. The present paradigm of person-environment coordination implicated a means for assessing the ability of human movement to "live" near, but not in, mode-locks It was suggested that this provides a novel expression of flexibility in human coordination. Another recent study by Byblow et al. (in press) adopted the paradigm of Experiment 3 to demonstrate a novel expression of manual asymmetries in the stability of Φ in 1:1 frequency regimes. Although potentially useful in the expression of asymmetries between rhythmic units of coordination, the person-environment paradigm has more importantly provided a means of expression of the underlying tendencies identified by von Holst (1937/1973). Shifts between absolute and relative coordination are more readily accessible and better demonstrate the latent struggle between the cooperative and competitive tendencies generic to human coordination. If as suggested, a dynamical basis determines the stable and flexible phase relations which define absolute and relative coordination respectively, it is anticipated that a similar dynamical basis may underlie the assembly of task-relevant degrees of freedom across a broad spectrum of coordinated human movement.

References

Abernethy, B. & Sparrow, W.A. (1992). The rise and fall of dominant paradigms in motor behaviour research. In J. Summers (Ed.), *Approaches to the Study of Motor Control and Learning*. Elsevier.

Adams, J.A. (1971). A closed-loop theory of motor learning. *Journal of Motor Behavior, 3*, 111-150.

Allen, G.D. (1972). The location of rhythmic beats in English I: An experimental study. *Language and Speech, 15*, 72-100..

Asch, S.E. (1952). *Social psychology.* Englewood NJ: Prentice-Hall.

Baldissera, F., Cavallari, P., Civaschi, P. (1982). Preferential coupling between voluntary movements of ipsilateral limbs. *Neuroscience Letters, 34*, 95-100.

Beek, P.J. (1989). *Juggling dynamics.* PhD. Thesis. Amsterdam: Free University Press.

Beek, P. J., & Beek, W.J. (1988). Tools for constructing dynamical models of rhythmic movement. Human Movement Science, 7, 301-342.

Beek, P.J. & Bingham, G.P. (1991). Task-specific dynamics and the study of perception and action: A reaction to von Hofsten (1989). *Ecological Psychology, 3*, 35-54.

Beek, P.J., Peper, C.E, van Wieringen, P.C.W. (1992). Frequency locking, frequency modulation, and bifurcations in dynamic movement systems. In G.E. Stelmach & J. Requin (Eds.), *Tutorials in Motor Behaviour II*, Amsterdam: Elsevier.

Bellman, R. (1961). *Adaptive control processes: A guided tour.* Princeton University Press.

Bernstein, N.A. (1967). *The coordination and regulation of movements.* London: Permagon.

Burgess-Limerick, R., Abernethy, B., & Neal, R.J. (1991). A statistical problem in testing invariance of movement using the phase plane model. *Journal of Motor Behavior, 23 (4),* 301-303.

Byblow, W.D., Carson, R.G., & Goodman, D. (1994). Expressions of asymmetries and anchoring in bimanual coordination. *Human Movement Science, 13,* 3-28.

Byblow, W.D., Carson, R.G., Goodman, D., & Storlund, C. (1992). Measurement problems encountered in a dynamical analysis of multijoint and multilimb movements. *Presented at the North American Society for the Psychology of Sport and Physical Activity*, Pittsburgh, PA, June 1992.

Byblow, W.D., Chua, R. & Goodman, D. (in press). Asymmetries in coupling dynamics of perception and action. *Journal of Motor Behavior.*

Carson, R.G. (1993). Manual asymmetries: Old problems and new directions. *Human Movement Science, (12),* 479-506.

Carson, R.G., Byblow, W.D., & Goodman, D. (in press). The dynamical substructure of bimanual coordination. In S.P. Swinnen, H. Heuer, J. Massion, & P. Casaer (Eds.)*Interlimb Coordination: Neural, dynamical, and cognitive constraints.* Orlando, Fl: Academic Press.

Carson, R.G., Goodman, D., Elliott, D., & Kelso, J.A.S. (submitted a). Asymmetires in the dynamics of interlimb coordination. *Manuscript submitted for publication.*

Carson, R.G., Goodman, D., Elliott, D., & Kelso, J.A.S. (submitted b). Phase transitions in interlimb coordination. *Manuscript submitted for publication.*

Carson, R.G., Goodman, D., Elliott, D., & Kelso, J.A.S. (submitted c). Intentional switching between patterns of interlimb coordination. *Manuscript submitted for publication.*

Cohen, L. (1971). Synchronous bimanual movements performed by homologous and non-homologous muscles. *Perceptual and Motor Skills, 32*, 639-644.

Condon, W.S. (1982). Cultural microrhythms. In M. Davies (Ed.), *Interactional rhythms: Periodicity in communication and behavior.* (pp. 53-78). New York: Human Sciences.

DeGuzman, G.C. & Kelso, J. A. S. (1991). Multifrequency behavioral patterns and the phase attractive circle map. *Biological Cybernetics, 64(6)*, 485-495.

Deutsch, D. (1983). The generation of two isochronous sequences in parallel. *Psychophysics, 34*, 331-337.

Glazier, J.A. & Libchaber, A. (1988) Quasi-periodicity and dynamical systems, *IEEE Transactions on Circuits and Systems, 35 (7)*, 790-810.

Grillner, S. (1975). Locomotion in vertebrates: Central mechanisms and reflex interaction, *Physiological Review, 55,* 247-304.

Guiard, Y. (1989). Failure to sing the left-hand part of the score during piano performance: loss of the pitch and stroop vocalizations. *Music Perception, 6*, 299-314.

Haken, H. (1977). *Synergetics: An introduction.* Berlin: Springer.

Haken, H. (1983). *Advanced Synergetics.* Berlin: Springer.

Haken, H. (1988). *Information and Self-Organization.* Berlin: Springer.

Haken, H., Kelso, J.A.S., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biological Cybernetics, 51,* 347-356.

Hinton, G. (1984). Parallel computations for controlling an arm. *Journal of Motor Behavior, 16*, 171-194.

Iberall, A. (1993). A physical foundation for the Gibsonian theory of perception and action. *Paper presented at the VIIth International Conference on Event Perception and Action. Vancouver, B.C.*

Ivry, R. & Corcos, D.M. (1993). Slicing the variability pie: Component analysis of coordination and motor dysfunction. In K. Newell & D. Corcos (Eds.), *Variability and Motor Control* (pp. 415.447). Champaign, Il: Human Kinetics.

Ivry, R., & Keele, S. (1989). Timing functions of the cerebellum. *Journal of Cognitive Neuroscience, 1*, 136-152.

Jordan, M.I. (1989). Indeterminate motor skill learning problems. In M. Jeannerod (Ed.), *Attention and Performance, XIII.* Hillsdale, NJ: Erlbaum.

Kay, B.A. (1988). The dimensionality of movement trajectories and the degrees of freedom problem: A tutorial. *Human Movement Science, 7*, 343-364.

Kay, B.A., Kelso, J.A.S., Saltzman, E.L., & Schöner, G. (1987). The space-time behavior of single and bimanual movements: Data and model. *Journal of Experimental Psychology: Human Perception and Performance, 13*, 178-192.

Kay, B. A., Saltzman, E. L., & Kelso, J. A. S. (1991). Steady-state and perturbed rhythmical movements: Dynamical modeling using a variety of analytical tools. *Journal of Experimental Psychology: Human Perception and Performance, 17*, 183-197.

Kelso, J.A.S. (1981). On the oscillatory basis of movement. *Bulletin of the Psychonomic Society, 18*, 63.

Kelso, J.A.S. (1984). Phase transitions and critical behavior in human bimanual coordination. *American Journal of Physiology: Regulatory, Integrative, and Comparative Physiology, 15,* R1000-1004.

Kelso, J.A.S., Buchanan, J.J., DeGuzman, G.C., & Ding, M. (1993). Spontaneous recruitment and annihilation of degrees of freedom in biological coordination. *Physics Letters, A179,* 364-371

Kelso, J.A.S., Bressler, S.L., Buchanan, S., DeGuzman, G.C., Ding, M., Fuchs, A., & Holroyd, T. (1992). A phase transition in human brain and behaviour, *Physics Letters A, 169,* 134-144.

Kelso, J. A. S., DeGuzman, G. C., & Holroyd, T. (1991). The self-organized phase attractive dynamics of coordination. In A. Babloyantz (Ed.), *Self-organization, emerging properties and learning*. New York: Plenum Press.

Kelso, J.A.S., Delcolle, J.D., & Schöner, G.S. (1990). Action-perception as a pattern formation process. In M. Jeannerod (Ed.), *Attention and performance XIII* (pp. 139-169). Hillsdale, NJ: Erlbaum.

Kelso, J.A.S. & Ding, M. (1993). Fluctuations, intermittency and controllable chaos in biological coordination. In K.M. Newell & D.M. Corcus (Eds.) *Variability and motor control.* Champaign, IL: Human Kinetics.

Kelso, J.A.S., Holt, K.G., Rubin, P, & Kugler, P.N. (1981). Patterns of human interlimb coordination emerge from the properties of non-linear, limit-cycle oscillatory processes: Theory and data, *Journal of Motor Behavior, 4,* 226-261.

Kelso, J.A.S., & Jeka, J.J. (1992). Symmetry-breaking dynamics of human limb coordination. *Journal of Experimental Psychology: Human Perception and Performance, 18(3),* 645-668.

Kelso, J.A.S. & Kay, B. (1987). Information and control: A macroscopic analysis of perception-action coupling. In H. Heuer & A.F. Sanders (Eds.), *Perspectives on Perception and Action.* Hillsdale NJ: Erlbaum.

Kelso, J.A.S., Putnam, C.A., & Goodman, D. (1983). On the space-time structure of human interlimb co-ordination. *The Quarterly Journal of Experimental Psychology, 35A*, 347-375.

Kelso, J. A. S. , & Scholz, J. P. (1985). Cooperative phenomena in biological motion. In H. Haken (Ed.), *Complex Systems: Operational approaches in neurobiology, physical systems and computers,*. (pp.124-149). Berlin: Springer.

Kelso, J.A.S., Scholz, J.P. & Schöner, G. (1986). Non-equilibrium phase transitions in coordinated biological motion: Critical fluctuations. *Physics Letters, A118*, 279-284.

Kelso, J.A.S., Southard, D.L., & Goodman, D. (1979). On the coordination of two-handed movements. *Journal of Experimental Psychology: Human Perception and Performance, 5*, 229-238.

Killeen, P. & Weiss, N. (1978). Optimal timing and the Weber function. *Psychological Review, 94*, 455-468.

Kugler, P.N., Kelso, J.A.S., & Turvey, M.T. (1980). Coordinative structures as dissipative structures I: Theoretical lines of convergence. In G.E. Stelmach & J. Requin (Eds.), *Tutorials of Motor Behavior.* Amsterdam: North Holland.

Kugler, P.N., & Turvey, M.T. (1987). *Information, natural law, and the self assembly of rhythmic movement.* Hillsdale, NJ: Erlbaum.

LaFrance, M. (1985). Postural mirroring and intergroup relations. *Personality and Social Psychology Bulletin, 11*, 207-217.

Lashley, K. (1951). The problem of serial order in behaviour. In L.A. Jeffress (Ed.), *Cerebral mechanisms in behaviour.* New York: Wiley.

Lennard, R.P. (1985). Afferent perturbations during monopodal swimming movements in the turtle: phase dependent cutaneous modulation and proprioceptive resetting of the locomotor rhythm. *Journal of Neuroscience, 5,* 1434-1445.

MacKay, D.G. (1987). *The organization of perception and action.* Berlin: Springer-Verlag.

Mardia, K.V. (1972). *Statistics of directional data.* London: Academic Press.

Marteniuk, R.G., & MacKenzie, C.L, & Baba, P. (1984). Bimanual movement control: Information processing and interaction effects, *The Quarterly Journal of Experimental Psychology, 36A*, 335-365.

Meijer, O.G., & Roth, K. (1988). *Complex movement behaviour: The motor-action controversy.* Amsterdam: North-Holland.

Morowitz, H.J. (1968). *Energy flow in biology: biological organization as a problem in thermal physics.* New York: Academic Press.

Newell, K.M. & Corcos, D.M. (1993). *Variability and motor control.* Champaign IL: Human Kinetics.

Peper, C.E., Beek, P.J. & Van Wierengen, P.C.W. (1991). Bifurcations in polyrhythmic tapping: In search of Farey principles. In J. Requin and G.E. Stelmach (Eds.), *Tutorials in Motor Neuroscience,* (pp. 413-431). Netherlands: Klewer Academic.

Peters, M. (1985). Constraints in the performance of bimanual tasks and their expression in unskilled and skilled subjects, *Quarterly Journal of Experimental Psychology, 37A*, 171-196.

Peters, M. (1977). Simultaneous performance of two motor activities: the factor of timing. *Neuropsychologia, 15*, 461-465.

Peters, M. (1987). A nontrivial motor performance difference between right handers and left handers: Attention as intervening variable in the expression of handedness. *Canadian Journal of Psychology, 41*, 91-99.

Peters, M. (1990). Interaction of vocal and manual movements. In G.E. Hammond ed., *Cerebral control of Speech an Limb Movements,* (pp 535-574). North Holland.

Peters, M. & Schwartz, S. (1989). Coordination of the two hands and effects of attentional manipulation in the production of a bimanual 2:3 polyrhythm. *Australian Journal of Psychology, 41,* 215-244.

Rand, R.H., Cohen, A.H., Holmes, P.J. (1988). Systems of coupled oscillators as models of central pattern generators. In A.H., Cohen, S. Rossignol, & S. Grillner (Eds.) *Neural control of rhythmic movements in vertebrates* (pp. 333-367). New York: Wiley.

Riek, S., Carson, R.G., & Byblow, W.D. (in press). Spatial and muscular dependencies in bimanual coordination. *Journal of Human Movement Studies.*

Runeson, S. (1977). On the possibility of "smart" perceptual mechanisms, *Scandinavian Journal of Psychology, 18*, 172-179.

Saltzman, E. & Kelso, J.A.S. (1987). Skilled actions: A task dynamic approach. *Psychological Review, 94*, 84-106.

Schmidt, R.A. (1975). A schema theory of discrete motor skill learning. *Psychological Review, 83,* 225-260.

Schmidt, R.C., Carello, C., & Turvey, M.T. (1990). Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 227-247.

Schmidt, R.C., Christianson, N., & Carello, C. (1993 a). Effects of social and physical variables on between-person coordination. In S.S. Valenti & J.B. Pittenger (Eds.), *Studies in Perception and Action II: VIIth International Conference on Event Perception and Action.* Vancouver, BC.

Schmidt, R.C., Shaw, B.K. & Turvey , M.T. (1993 b). Coupling dynamics in interlimb coordination, *Journal of Experimental Psychology: Human Perception and Performance, 19*, 397-415.

Schmidt, R.C., Treffner, P.J., Shaw, B.K., & Turvey, M.T. (1992). Dynamical aspects of learning an interlimb rhythmic movement pattern. *Journal of Motor Behavior, 24*, 67-83.

Scholz, J. P. & Kelso, J. A. S. (1989). A quantitative approach to understanding the formation and change of coordinated movement patterns. *Journal of Motor Behavior, 21(2)*, 122-144.

Scholz, J. P., Kelso, J. A. S., & Schöner, G. S. (1987). Non-equilibrium phase transitions in coordinated biological motion: Critical slowing down and switching time. *Physics Letters, A123*, 390-394.

Schöner, G.S., Haken, H., & Kelso, J.A.S. (1986). A stochastic theory of phase transitions in human hand movement, *Biological Cybernetics, 53*, 442-452.

Schöner, G.S. & Kelso, J.A.S. (1988a). Dynamic pattern generation in behavioral and neural systems, *Science, 239*, 1513-1520.

Schöner, G., & Kelso, J.A.S. (1988b). Dynamic patterns of biological coordination: Theoretical strategy and new results. In J.A.S. Kelso, A.J. Mandell, & M.F. Shlesinger (Eds.) *Dynamic patterns in complex systems.* Singapore: World Scientific.

Stein, R.B. (1982). What muscle variable(s) does the nervous system control in limb movements? *Behavioral and Brain Sciences, 5,* 535-577.

Sternad, D., Beek, P.J. & Turvey, M.T. (1993). Mechanical perturbations of rhythmic forearm movements. *Presented at the VIIth International Conference on Event Perception and Action, Vancouver, B.C, August, 1993.*

Sternad, D., Turvey, M.T., & Schmidt, R.C. (1992). Average phase difference theory and 1:1 phase entrainment in interlimb coordination. *Biological Cybernetics, 67,* 223-231.

Stevens, L.T. (1886). On the time sense. *Mind, 11,* 393-404.

Summers, J.J., Rosenbaum, D., Burns, B.D., & Ford, S.K. (1993). Production of polyrhythms. *Journal of Experimental Psychology: Human Perception and Performance, 19 (2),* 416-428

Swinnen, S.P. & Walter, C.B. (1991). Toward a movement dynamics perspective on dual-task performance, *Human Factors, 33(4),* 367-387.

Treffner, P.J. & Turvey, M.T. (1993). Resonance constraints on rhythmic movement. *Journal of Experimental Psychology: Human Perception and Performance, 19,* 1221-1237.

Turvey, M.T. (1990). Coordination. *American Psychologist, 45(8),* 938-953.

Turvey, M.T., Rosenblum, L.D., Schmidt, R.C., & Kugler, P.N. (1986). Fluctuations and phase symmetry in coordinated rhythmic movements, *Journal of Experimental Psychology: Human Perception and Performance, 12,* 564-583.

Turvey, M.T., Schmidt, R.C., & Beek, P.J. (1993). Fluctuations in interlimb coordination. In K. Newell & D. Corcos (Eds.), *Variability and Motor Control* (pp. 381-411). Champaign, Il: Human Kinetics.

Turvey, M.T., Schmidt, R.C., Rosenblum, L.D. (1989). 'Clock' and 'motor' components in absolute coordination of rhythmic movements, *Neuroscience, 33(1),* 1-10.

von Holst, E. (1937/1973). Relative coordination as a phenomenon and as a method of analysis of central nervous function. In R. Martin (Ed.), *The collected papers of Erich von Holst*, (pp. 33-135) Florida: University of Miami.Press.

Vorberg, D. & Wing, A.M. (in press). Modeling variability and dependence in timing. In H.Heuer & S.W. Keele (Eds.), *Handbook of preception and action. Vol. 3: Motor skills*. London: Academic Press.

Welch, J.C. (1898). On the measurement of mental activity through muscular activity and the determination of a constant of attention. *American Journal of Physiology, 1*, 283-306.

Wimmers, R.H., Beek, P., & van Wieringen, P.C.W. (1992). Phase transitions in rhythmic tracking movements: A case of unilateral coupling. *Human Movement Science, 11,* 217-226.

Winfree, A.T. (1972). *The geometry of biological time*. Berlin: Springer-Verlag.

Wing, A.M. (1980). The long and short of timing response sequences. In G.E. Stelmach & J. Requin (Eds.), *Tutorials of Motor Behavior.* (pp. 469-486). Amsterdam: North Holland.

Wing, A.M., Church, R.M., & Gentner, D.R. (1989). Variability in the timing of responses during repetitive tappting with alternate hands, *Psychological Research, 51,* 28-37.

Wing, A. M. & Kristofferson, A.B. (1973). Response delays and the timing of discrete motor responses. *Perception and Psychophysics, 14*, 3-12.

Woodworth, R.S. (1899). The accuracy of voluntary movement. *Psychology Review, 3*, 1-114.

Yaminishi, J., Kawato, M., & Suzuki, R. (1979). Studies on human finger tapping neural networks by phase transition curves. *Biological Cybernetics, 33*, 199-208.

Yates, E. & Iberall, A.S. (1973). Temporal and hierarchical organization in biosystems. In J. Urquart and E. Yates (Eds.) *Temporal aspects of therapeutics.* Plenum: New York.