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# MANUAL ASYMMETRIES: DYNAMICAL ANALYSES

by

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# ABSTRACT

It was proposed that a dynamical description of human coordination may provide a means by which to elucidate the basis of manual asymmetries. Four experiments were conducted in which the dynamics of coordinated rhythmic movements of the ankle and the wrist, on each side of the body, were examined. In Experiment 1, a self paced protocol was employed. Four subjects were required to produce movements in two modes of coordination, anti-phase and in-phase, at what they determined to be their most comfortable sustainable frequency of oscillation. The dynamics of these movements were expressed in terms of a number of variables including variability of oscillation frequency, nominally a control parameter, and the variability of discrete relative phase, the putative collective variable or order parameter. The results of the first experiment indicated that movements of the left side exhibited greater variability of oscillation frequency and of relative phase than movements of the right side. In the second experiment, subjects attempted to execute their movements at frequencies (1 Hz or 2 Hz) specified by an external pacing regime. It was noted that when initially prepared in the anti-phase mode and paced at 2 Hz, three of the four subjects examined were unable to satisfy task requirements by reproducing the specified frequency and prescribed mode of coordination. Movements of the left and right side were not distinguished by the degree of adherence to external pacing, nor in terms of the variability with which oscillation frequencies were produced. A single subject conformed to task requirements in all conditions. Movements of the left and right side performed by this individual were distinguished from each other especially when prepared in the anti-phase mode and paced at 2 Hz. In these conditions, movements of the left side exhibited lower oscillation frequencies, and larger coefficients of variation of oscillation frequencies than movements of the right side. The third experiment comprised a scaled frequency protocol. Pacing frequency was increased from an initial value of 1.25 Hz to 2.75 Hz in steps of 0.25 Hz. When movements were initially prepared in the anti-phase mode of coordination, spontaneous transitions to the in-phase mode or to phase wandering were observed as the pacing frequency was increased. When initially prepared in the in-phase mode, transitions to phase wandering were observed. Signature features of nonequilibrium phase transitions including loss of stability were noted. The two observed stationary coordinative states, anti-phase and in-phase, were mapped unto attractors of the collective variable dynamics. Intrinsic dynamics were assessed using measures indexing the stability of these stationary (attractor) states. These measures included the variability of the collective variable relative phase about the mean value corresponding to each stationary state. Movements of the left and right side were not distinguished with respect to this measure of stability. The number of transitions from each preparation and the time at which those transitions occurred furnished measures of the relative stability of the attractor states. Movements of the left and right sides were also not differentiated on the basis of these measures. In a fourth experiment, coordinated movements of the left and right sides were compared with respect to the implementation of intentional perturbations of the intrinsic dynamics. Upon presentation of a visual signal, subjects were required to rapidly switch from the anti-phase to the in-phase pattern of coordination, or vice versa. The duration of transition was predicted to index the differential stability of the two patterns of coordination. However, transitions from the anti-phase to the in-phase mode were of equivalent duration to transitions from the in-phase phase to the anti-phase mode. In addition, analysis of transition durations failed to reveal differences between movements performed by the left and the right side. Transition durations were observed to scale inversely with increases in pacing frequency.

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Our nature lies in movement; complete calm is death

Pascal
Pensées

## Table of Contents

4 Experiment 2

5 Experiment 3

6 Experiment 4

## List of Figures

## List of Tables

# INTRODUCTION

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*... concepts which have proved useful for ordering things easily assume so great an authority over us, that we forget their terrestrial origin and accept them as unalterable facts. They then become labeled as "conceptual necessities," "*a priori *situations," etc. The road of scientific progress is frequently blocked for long periods by such errors. It is therefore not just an idle game to exercise our ability to analyse concepts, and to demonstrate the conditions on which their justification and usefulness depend, and the way in which these developed, little by little, from the data of experience. In this way they are deprived of their excessive authority.*

Albert Einstein

The expression of human handedness is a phenomenon which has recently generated widespread interest and extensive research. Progress has been made in elucidating both the circumstances in which asymmetries are exhibited and the physiological correlates of their expression. However, there has been little evidence of convergence upon unifying principles which would reconcile the many and varied expressions of handedness. The study of manual asymmetries to date has been characterised by a series of attempts to map the supposed information processing characteristics of the cerebral hemispheres onto variables which are ostensibly central to movement control.The present research has been motivated by the conviction that advances are possible through the application of novel, yet more general, analyses based on dynamics.

Any complex system of interest may, in theory, be described at a number of levels by employing a unitary set of descriptive tools, for example those of non-linear dynamics. The problem in studying coordinative systems is usually to obtain an appropriate level of description and identify the task relevant degrees of freedom therein. It is not often the case that these may be determined a priori. One means of delineation derives from situations in which there is a qualitative change of system behaviour, or "phase transition". Given that qualitative change, by definition, permits one pattern of behaviour to be distinguished from another, examination of the pre and post transition behaviour allows identification of the essential dimensions of the patterns. It is these essential dimensions which constitute the "collective variables" or "order parameters" which in turn encapsulate the pattern itself. The order parameter expresses the most relevant properties of a system engaged in task specific coordination. Analysis conducted in terms of the dynamics of order parameters represents a reduction of the degrees of freedom which describe the system from the potential to the essential. In rhythmic coordinative tasks, relative phase (the latency of one component with respect to the cycle of another component ) has been identified as an appropriate order parameter, as it permits characterisation of all observed coordinative patterns or stationary states.

In addition, the study of phase transitions allows one to examine the specific action of control parameters. These are the parameters responsible for inducing changes in the topology of the system's dynamics as a new pattern is achieved. Control parameters are considered to be unspecific to the resulting patterns, they carry no information whatsoever about the pattern that emerges. Signature features of self-organization include the spontaneous emergence of patterns under continuous changes in a control parameter. Patterns arise solely as a function of the dynamics of the system. In many coordinative tasks, as the frequency of oscillation serves to induce pattern transitions, it is identified as the control parameter.

To a degree of approximation, for movements of distal limb segments, each limb/flank-hemisphere complex may be characterized as an "independent" dynamical system. There exist multijoint and multilimb models which provide means of probing their dynamics and of distinguishing dimensions along which the organization of these systems are differentiated. It may be the case that these systems differ in the manner in which control parameter regimes are implemented. The joints of the left side are known to move less rapidly than those of the right side and are consistently more variable at maximal rates of responding. Indeed a large body of theoretical work is based explicitly upon the assumption that the left hemisphere contralateral to the preferred right hand assumes some privileged role in the execution of timing functions.

Another engaging possibility is that the limb-hemisphere systems are distinguished on the basis of their intrinsic dynamics. If this is the case, the preferred and non-preferred limbs may exhibit qualitative differences in the topology of the potential landscape for an appropriate collective variable such as relative phase. Such differences will be reflected by the absolute and relative stability of attractor states which are in turn indexed by a number of measures which can be derived experimentally.

The quintessential feature of human behaviour, is the ability to switch between movement patterns in a purposeful fashion Central to the application of dynamics to the realm of purposeful behaviour is the concept of information. Information such as that arising from conscious intent, is viewed as "meaningful and specific to the biological system only to the extent that it contributes to the order parameter dynamics attracting the intended behavioural pattern". As it is with respect to intentional behaviour that the clearest hand preferences are expressed and the greatest performance are observed, it is conceivable that the limb/flank hemisphere systems may be distinguished in their expression of intentional dynamics.

The dissertation is organized into seven chapters. The first chapter comprises an outline of current accounts of manual asymmetries. In Chapter 2, the dynamics approach to the study of movement regulation is introduced. Means by which the dynamics approach may be utilized in the study of manual asymmetries are discussed. It is suggested that asymmetries may be illuminated through consideration of the relative stability of stationary states, the variability with which control parameter regimes are instantiated, and the manner in which information contributes to the order parameter dynamics. Chapters 3 to 6 respectively outline four experiments predicated on a dynamical account of manual asymmetries. In Experiments 1 and 2 attention is focussed on the generation of rhythmic movement patterns. The stability and loss of stability of these patterns are examined in Experiment 3. Intentionally mediated transitions between movement patterns are addressed in Experiment 4. Finally, Chapter 7 is a general discussion.

**Who will change old lamps for new ones?**
**... new lamps for old ones?**

**Arabian Nights**
**From The History of Aladdin**

# 1 Manual Asymmetries: Old Problems

## 1.1 Introduction

In performing both simple and sophisticated motor tasks, most individuals are willing to express a clear preference for one hand over the other. However, the relationship between hand preference and proficiency is often equivocal (Peters, 1990a). There are tasks in which performance by the non-preferred[1] limb is superior to the preferred limb (e.g., Benton, Varney, & Hamsher, 1978; Carnahan & Elliott, 1987; Roy & MacKenzie, 1978; Witelson, 1974). In spite of extensive research, there exist few satisfactory accounts of these phenomena (Carson, 1989a). Nonetheless, the clarification of performance differences between the hands, and of the relationship of preference to performance, offers the prospect of insight into more general issues pertaining to the nature of movement regulation.

In this paper, it is argued that this potential has not been realised as existing accounts of manual asymmetries are artefacts of paradigms used to elicit generic principles of motor control. Constructs, which have proved useful in delineating levels of performance within the hands, have been scavenged in attempts to account for performance differences between the hands. This failure to generate independent explanatory constructs may be identified as a symptom of a more widespread malaise. The variables we can easily conceive of or manipulate are not necessarily those which are central to the regulation of movement (cf., Rosen, 1978). Similarly, these variables may not constitute the essence of what distinguishes the performance of the hand-

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[1] In this paper, any reference to hand advantage is with respect to right handers.

hemisphere systems. The study of manual asymmetries has been characterised by a series of attempts to map the putative "information processing" characteristics of the cerebral hemispheres onto variables which ostensibly capture the essential aspects of movement regulation. The general and specific problems of this approach are briefly outlined and discussed. An alternative strategy is proposed. This involves the use of dynamical systems theory (e.g., Thompson & Stewart, 1986) to describe the behaviour of the limb-hemisphere systems. The task relevant degrees of freedom or variable boundaries which are employed to elucidate manual asymmetries, are not selected a priori but emerge from the behaviour of the system itself. Although to date this approach has been especially well suited to the study of rhythmic movement, efforts are currently being made to extend its application to discrete movements (e.g., Schöner, 1990, in press). It is to be anticipated that the principles elucidated in a dynamical account of manual asymmetries which is formulated with specific reference to rhythmic movement will generalise to non-continuous behaviours.

## 1.2 Two Models

Although the regulation of movement in normals is clearly subserved by a continuous transaction between the two cerebral hemispheres (cf., Trevarthen, 1984), investigators have generally opted to discuss tasks in which right hand advantages for execution are noted in terms of the processing characteristics of the left hemisphere. This tendency has historical antecedent in claims by Liepmann (e.g., Liepmann, 1905; Liepmann & Maas, 1907) that there exists a unilateral left hemisphere specialization for motor function and in particular for timing (cf., Peters, 1989). Contemporary expressions of this position have ascribed to the left hemisphere an enhanced facility for the fine temporal resolution of both sensory input and motor output (e.g., Bradshaw & Nettleton, 1981; Ojemann, 1984; Tzeng & Wang, 1984).

It would be impractical in this context to provide an exhaustive review of the literature as it pertains to manual asymmetries. The interested reader is referred to Todor and Smiley (1985) for more extensive coverage. However classes of movement can be identified, for example visually guided reaching and manipulative behaviours, which exhibit strong performance asymmetries favouring the right hand (Elliott, 1991), and which have have been the focus of models purporting to provide general accounts of manual asymmetries. With respect to these movements, two pedigrees of explanation can be delineated. The "feedback processing" model encapsulates proposals that the left hemisphere/right hand system is more efficient in the execution of "error corrections" utilizing sensory feedback (e.g., Flowers, 1975; Todor & Cisneros, 1985; Todor & Doane, 1978). Whereas, the "output variability" model is predicated upon the assumption that superior right hand performance accrues from more precise control of net forces and force durations. It is supposed that the reputed left hemisphere propensity for temporal processing mediates more effectively the timing of onsets and offsets of muscular activity. These differences are thought be most clearly reflected by behavioural measures during reversals of the direction of motion (Peters, 1980; Todor & Smiley-Oyen, 1987) and postural transitions (Kimura, 1979). They have also been conceived of in terms of the parameterization of impulse characteristics (e.g., Roy & Elliott, 1986, 1989) or simply the variability of motor output (e.g., Annett, Annett, Hudson & Turner, 1979).

Unfortunately, what has been seen as a means to differentiate the hands has often been dependent upon that which has been regarded as a plausible basis for Fitts' Law. In a seminal paper, Flowers (1975) hypothesised that aiming movements were characterised by a "corrective mode of control", and that asymmetries were accounted for by differences in the efficiency with which this control regime was implemented. It was projected that individuals respond with "ballistic" movements for low index of difficulty (ID) value movements. Whereas, for more "difficult" combinations (high ID values) they necessarily implement a corrective procedure. Flowers observed that performance differences between the hands, as expressed by movement durations and by the proportion of targets misses, were more pronounced at ID values 4 and above. It was therefore concluded that the advantage for the preferred hand during "non-ballistic" movements was due to a higher rate of information transmission. As no asymmetries were elicited for aiming movements having ID values smaller than 4, it was concluded that the hands were equivalent for ballistic movements during which the transmission of sensory information was considered to be of little significance.

Todor and Doane (1978) reasoned that the "parallel or nonserial processing mode of the right hemisphere may be associated with nonadaptive (i.e., limited feedback usage) movements... usually referred to as preprogrammed" (p. 295). As such, it was posited that the right hand would be superior when the demands for precision and thus for feedback processing were enhanced. Conveniently, the Fitts' task permits independent manipulation of ID value and precision. The hypothesis was therefore tested, by examining the relative levels of performance for each hand, for movements (of equal ID value) defined by one of two levels of precision. It was noted that the performance of the right hand was not distinguished by precision requirements. The left hand was, however, superior in circumstances requiring less precision (relative to the high precision condition rather than to the right hand).

In a similar vein, Todor and Cisneros (1985) concluded that the differing efficiency with which accommodation was made to demands for precision "implicates hand differences in error corrective ability and/or the need for error correction in the terminal phase of the movement" (p. 366). This finding was based on the observation that the majority of accommodation to increased accuracy demands was accounted for by changes in the duration of the period from peak acceleration to target contact. The extent of this segment of the movement was greater for the non-preferred hand, a difference which covaried with demands for precision.

It can be seen that these accounts of manual asymmetries are contingent upon two implicit couplings. In the first case, it is supposed that precision as operationalised in the Fitts paradigm covaries with the demands for feedback processing. It is also assumed that the processing characteristics of the cerebral hemispheres and the mechanisms of sensory feedback processing are conjoined. Conclusions pertaining to the nature of manual asymmetries have been constrained by specific explications of what data obtained from the Fitts' type task reveal of the underlying control processes. Indeed, the supposition that the preferred hand advantage ensues from an enhanced efficiency in the use of feedback, rests upon the assumption that Fitts' Law may be accounted for in terms of feedback processes in general, and of visual feedback in particular (Carson, 1992).

There are alternative explanations of Fitts' Law (e.g., Meyer, Abrams, Kornblum, Wright, & Smith, 1988; Schmidt, Zelaznik, and Frank, 1978; Schmidt et al., 1979). Many share the assumption that movement endpoint variability is an indication of variability in the production an initial impulse. These models have also provided the "inspiration" for accounts of manual asymmetries. For example, the description outlined by Annett et al. (1979) is predicated on the assumption that asymmetries are due largely to differences in the "intrinsic variability or noise in the production of force time patterns" (p. 647), and is descended directly from the Schmidt, Zelaznik, and Frank model of 1978. In the Annett et al. (1979) study individuals were required to perform a variation of a pegboard task. Performance measures revealed that movement series were performed more rapidly by the preferred hand. Analysis of a film record of performance indicated that differences occurred primarily during the "positioning" element of the movement rather than during the "transport phase". The non-preferred hand more frequently missed the target hole, requiring on average 50% more corrective movements. The authors suggested that corrections were conducted on the basis of a "kinesthetic feedback loop", the duration of which did not differ between the hands. Movements to the target were assumed to be "open loop" and were made at an equivalent rate by each hand. Rather, it was in the accuracy of these movements that the hands differed. Annett et al. (1979) therefore concluded that the greater variability present in the output of the non-preferred hand was directly attributable to greater variability in the production of force time patterns.

The proposal that the hands differ in the efficiency with which feedback is processed (Flowers, 1975) has been explicitly interpreted as a supposition that the right hand/left hemisphere is transcendent in the processing of visual information (e.g., Roy & Elliott, 1986). This model, although not explicitly linked to the Fitts paradigm, identifies factors which are perceived as having some centrality in accounting for visually based movement regulation as those factors which underlie performance asymmetries. It is predicted that differences between the hands, as expressed by speed/accuracy functions, vary as a function of the form of visual information which is available. Although this "strong" form of the feedback processing hypothesis has been exhaustively tested, there is little evidence to suggest that the hands differ in terms of the efficiency with which visual feedback is utilized, (Carson et al., 1990; Carson, Goodman, Chua, & Elliott, in press; Carson, Goodman, & Elliott, 1992; Roy and Elliott, 1986, 1989; Roy, Elliott, and Rohr, 1990).

Further attempts to account for performance asymmetries in terms of output variability have been equally unsatisfying. On the basis of observations that hand differences in accuracy are accentuated for movements of shorter duration, Roy and Elliott (1989) reasoned that the right hand is less variable in generating force. Following Schmidt et al. (1979), it was hypothesised that increasing force requirements would result in proportionately greater increases in force variability, and thus movement endpoint variability, for the non-preferred hand. Force requirements in an aiming task (Roy & Elliott, 1989) were manipulated by changing movement amplitudes while constraining movement time. As their data demonstrated that differences in endpoint variability between the hands were not sensitive to changes in movement amplitude, they concluded that the greater variability exhibited by the left hand was "independent of the variability that is affected by the force demands of the aiming task" (p. 514). Carson, Elliott, Goodman, Thyer, Chua and Roy (submitted) directly manipulated force requirements by increasing the mass of the limb. Kinematic analyses allowed the computation of measures defining impulse parameters. Their results indicated that differences in output variability between the hands were orthogonal to changes in variability accruing to manipulation of limb mass. Changing the force requirements of the task did not alter the magnitude of the preferred hand advantage.

It thus appears that neither the feedback processing or output variability approaches can adequately account for the nature of right hand superiority in these movement tasks. The failure to provide support for these positions raises considerations of a more general nature. It may simply be the case that those elements which constitute the essence of regulation do not stand in simple correspondence with the motor variables which are amenable to measurement (Tuller & Kelso, 1990, see also Abbs & Connor, 1989).

### 1.3 Theoretical Considerations

An illustration of the problems inherent in translating facets of neuromuscular function into our vocabulary is provided by the catalogue of dichotomies which has been generated in characterizing the processing characteristics of the cerebral hemispheres. In addition to the traditional verbal/nonverbal distinction (e.g., Bradshaw & Nettleton, 1981), it has been proposed that the left cerebral cortex is specialized for, serial as distinguished from parallel processing (Cohen, 1973); analytic as opposed to holistic, global, synthetic or gestaltic apprehension (Nebes, 1978); verbal versus visuospatial activities (Kimura, 1961); focal rather than diffuse processing (Semmes, 1968), name matching in contrast to physical matching (Geffen, Bradshaw & Nettleton, 1972). This list is by no means exhaustive. The circumspect theorist maintains that strict dichotomies do not prevail (e.g., Bradshaw & Nettleton, 1981), that the capacities of each hemisphere lie at points on a continuum between two poles, and that differences are of degree rather than of kind (e.g., Corballis, 1981; Milner, 1971; Zangwill, 1960). However the demarcations are imposed by the texture of our concepts rather than by the nature of the physiology they presume to describe. We would be foolish to presume that the brain "divides up its functions into categories which correspond to our concepts or vocabulary" (Bullock, 1965, p. 473). In spite of suggestions that the assorted labels are merely reflections of a single underlying mechanism (Allen, 1983), it is clear that cerebral specialization of whatever form will not become "less complex or more 'captured' by labelling one of its attributes" (McKeever, 1981, p. 74). The resolute nature of these controversies indicate that the method itself has been inapposite.

The critique applies similarly to attempts to define the variables which are ostensibly "controlled" by the nervous system during limb movements (Stein, 1982). An obdurate problem for the field of motor behaviour has been that the descriptive variables which appear to capture some aspects of system function have been seen as internalized prescriptions for regulation and control (e.g., Gottlieb, Corcos & Agarwal, 1989). There is no evidence to suggest that the nervous system is rule guided (c.f., Dreyfus, 1987), although the outcomes of its functioning may be well described by various rules (Carson, 1992). This encumbrance applies to all existing accounts of manual asymmetries in that the variables which are nominally "controlled" by the nervous system are also those which must be controlled in variegated fashion in giving rise to asymmetries. When schemes relating control of such descriptive variables are conjoined with sublimations of cerebral functioning, we attain accounts of manual asymmetries which possess negligible generality.

The simplest description of any act is the act itself (cf., Maxwell, 1877/1952). However, we generally employ a scientific strategy which involves generating an abstraction of the act or system of interest (cf., Turvey, 1988). These abstractions are constrained not only by the nature of that which we aim to describe, but also by the conceptual tools which are brought to bear. In many cases, the principles so derived are not those the system has evolved to embody (Crick and Asanuma, 1986; Vogel, 1989). The tendency to assume that organizing principles are in some sense applied by the nervous system to produce regularity in behaviour appears rooted in a tradition of assigning mechanism or causality to regularity (cf., Swartz, 1985). Although causal attributions are presupposed by the structure of our language and are useful in conducting everyday relations, they may also be regarded as heuristics constrained by the macroscopic level of description (Carson, 1989b). There exist, however, means of characterizing behaviour which are more explicitly descriptive and are less sensitive to preconceptions regarding the presence of control. Dynamics, the study of change in systems over time, furnishes techniques with which to describe the self-organization and pattern generation intrinsic to many complex biological systems (see Haken, 1981). These methods may be applied to the study of movement regulation in general and of manual asymmetries in particular.

## 2. Manual Asymmetries: New Directions

### 2.1 Dimensions of Coordination

There are reasons to believe that the principles of dynamics provide a cogent basis on which to establish an account of manual asymmetries. As applied to the study of human coordination, there exist a number of expressions of this general approach. Although sharing the same set of analytical tools they differ with respect to methodological details and in particular the attention directed toward induced state transitions. In all cases emphasis is placed upon the derivation of laws of coordination which encapsulate behaviour at a variety of levels of observation.

Any system of interest may, in theory, be described at a number of levels by employing a unitary set of descriptive tools, for example those of non-linear dynamics. The problem for the student of motor regulation is usually to obtain an appropriate level of description and identify the task relevant degrees of freedom therein (Kay, 1988). It is not often the case that the latter may be determined a priori. One means of delineation derives from the examination of situations in which there is a qualitative change of system behaviour, or "phase transition". Given that qualitative change, by definition, permits one pattern of behaviour to be distinguished from another, examination of the pre and post transition behaviour allows identification of the essential dimensions of the patterns. It is these essential dimensions which constitute the "collective variables" or "order parameters" which in turn encapsulate the pattern itself (Jeka & Kelso, 1989). In addition, the study of phase transitions allows one to examine the specific action of control parameters. These are the parameters responsible for inducing changes in the topology of the system's behaviour as a new pattern is achieved. In short, the order parameter expresses the most relevant properties of a system engaged in task specific coordination (Turvey, 1990). Thus analysis conducted in terms of the dynamics of order parameters represents a reduction of the degrees of freedom which describe the system from the potential to the essential. However, the task and situation specificity of order parameters cannot be overemphasised. The essence of biological coordination is the assembly of special purpose solutions to the problems posed by environmental contingencies (Turvey, 1990).

## 2.2 The Dynamic Pattern Approach

The phase transition methodology is best represented by the "dynamical pattern approach" (e.g., Jeka & Kelso, 1989; Kelso & Schöner, 1987, 1988; Schöner & Kelso, 1988a). Based upon contemporary theories of pattern generation and self organization in dissipative dynamical systems, it traces lineage from Haken's (e.g., 1983) synergetics. This is an interdisciplinary field which studies "the self-organized behavior of complex systems (composed of many subsystems) and focuses its attention to those phenomena where dramatic changes of macroscopic patterns or functions occur owing to the cooperation of subsystems" (Haken, 1979, p. 357).

The seminal application of these constructs to the study of movement regulation was conducted by Kelso (1981, 1984). Human subjects performed rhythmic voluntary oscillations of the hands (Kelso, 1982, 1984) or of the fingers (Kelso, 1981). The frequency of oscillation is increased, usually through the use of a pacing metronome. In these circumstances only two phase locked modes can be stably and reliably reproduced. These are the in-phase mode, in which there is simultaneous contraction of homologous muscle groups, and the anti-phase mode, in which homologous muscle groups contract in an alternating fashion. When the system is initially prepared in the anti-phase mode, an involuntary shift to the in-phase mode is observed as the cycling frequency is increased. When, however, the system is initially prepared in the in-phase mode no switching is observed. Relative phase (the latency of one finger with respect to the cycle of the other finger) is identified as the appropriate order parameter, as it characterises all observed coordinative patterns or stationary states. As the frequency of oscillation serves to induce pattern transitions, it is identified as the control parameter (Jeka & Kelso, 1989).

## 2.3 Additional Methodologies

It is a central tenet of the dynamics approach that organizational principles apply across levels of description (Kelso & Schöner, 1987; Kelso, Schöner, Scholz, & Haken, 1987). As has been indicated, coordinated states are characterized by the dynamics of macroscopic collective variables such as relative phase. Extension entails application of this rubric to the component subsystems, with the aim of elucidating the manner in which the dynamics of the subsystems and the coupling between them gives rise to coordinated states. In bimanual movement, for example, the next level of description comprises the component oscillators, the individual hands. Behaviour at this level may be simply described in terms of the position $x$ and velocity $\dot{x}$ of the limbs (Kay, Kelso, Saltzman & Schöner, 1987). Displacement and velocity are now the collective variables, collective that is with respect to the next level of description. We could also conceive of description in terms of the coordinated activity of the agonist and antagonist muscles (Schöner & Kelso, 1988a).

It is not necessarily the case that all systems engaged in coordination will exhibit abrupt transitions given the boundary conditions encountered in a natural or an experimental context. Similarly, transitions are not inevitably to be anticipated at all levels of description. Thus, additional tools are required to complement the phase transition methodology. Analytic techniques based upon the paradigm introduced by Kugler and Turvey (1987) have been employed with some success in exploration of the dynamical basis of bimanual coordination (e.g., Bingham, Schmidt, Turvey, & Rosenblum, 1991; Kugler, Turvey, Schmidt, & Rosenblum, 1990; Rosenblum & Turvey, 1988; Schmidt, Beek, Treffner, & Turvey, 1991; Schmidt, Treffner, Shaw, & Turvey, 1992). In these cases the dynamics are monitored in a region of state space in which phase transitions are atypical.

The dynamics of the component subsystems, which are themselves typically oscillatory and non-linear, may be derived from phase portraits using a variety of graphical and analytic techniques. A mathematical argument has been presented that, for certain classes of human movements, only four elementary series of non-linearities are required to encapsulate the dynamics of the component oscillators(Beek & Beek, 1988, cf., Kay et al., 1987). These and additional methods permit one to establish whether kinematics derived experimentally are consistent with specific dynamical models (e.g., Kay, Saltzman, & Kelso, 1991).

## 2.4 Stability, Adaptability and Time Scales Relations

The notion of stability is central to consideration of the manner in which dynamical systems exhibit qualitative changes of behaviour. Often small changes in parameter values lead only to small changes in dynamics. However, as a control parameter crosses a critical point, qualitative changes in dynamics may occur. During nonequilibrium phase transitions, previously stable patterns become unstable, and the system switches to a pattern or patterns exhibiting stability beyond the critical point (Schöner & Kelso, 1988a).

Generally a system exhibiting nonequilibrium phase transitions will satisfy certain requirements. The collective variable or order parameter must be able to assume two or more distinct values corresponding to stationary states. This has been termed the property of modality. An attendant attribute is inaccessibility which indicates that values outside of the stationary states cannot be consistently sustained (Turvey, 1990). There exist a number of ways in which stability may be determined. If a perturbation (of sufficiently small magnitude) drives the system away from a stationary (attractor) state, the time required to return to that state will be independent of the magnitude of the perturbation and will be an index of the local relaxation time. This is an observable system property which directly reflects the stability of the attractor. However, all real systems described by low dimensional dynamics are also coupled to noise sources comprising many weakly interacting degrees of freedom corresponding to a multitude of individual subsystems (Kelso, Schöner, Scholz, & Haken, 1987). These noise sources act as "stochastic forces" on the collective dynamics (Haken, 1983), and may be considered "continuously applied perturbations" which force the system away from the attractor state (Schöner & Kelso, 1988a). It is the balance which exists between the stability of an attractor and the level of fluctuations which determines the stability and flexibility of behavioural patterns (Schöner & Kelso, 1988a).

An appreciation of this balance may be obtained through consideration of system time scales (e.g., Scholz, Kelso, & Schöner, 1987; Schöner, Haken, & Kelso, 1986; Schöner & Kelso, 1988a). In particular, the interpretation of observed states as stationary attractor states is consistent if the following relation is fulfilled

$$\tau_{rel} \quad << \quad \tau_{obs} \quad << \quad \tau_{equ} \tag{1}$$

Where $\tau_{rel}$ is an index of the time required for the system to relax onto an attractor in its immediate vicinity, $\tau_{obs}$ is the typical time period over which the system is observed, and $\tau_{equ}$ is the equilibration time which is determined largely by the time required to traverse from one stationary state to another (Schöner & Kelso, 1988a). It is anticipated that as transitions occur the times scale relation in (1) is violated. The phenomena of critical fluctuations (a marked increase in the variance of the order parameter) and critical slowing down ($\tau_{rel}$ tending toward infinity) are predicted as the transition region is approached.

As relation (1) is violated, an additional time scale becomes important. This is the time scale of (control) parameter change $\tau_{par}$. The nature of the phase transition is crucially determined by the relationship of the time scale of parameter change to other system time scales. Consider cases in which

$$\tau_{rel} \quad << \quad \tau_{par} \quad << \quad \tau_{equ} \tag{2}$$

In these circumstances the system remains at a specific value of the control parameter appreciably longer than the time required to relax upon a locally stable state (Jeka & Kelso, 1989). The system may, for conditions in which (2) holds, remain in a particular state even as fluctuations increase. Therefore the system changes state only as the initial state becomes unstable. As the system changes state, the feature of critical fluctuations is anticipated. Consider on the other hand the case in which

$$\tau_{rel} \quad << \quad \tau_{equ} \quad << \quad \tau_{par} \tag{3}$$

In (3) the time scale of parameter change is substantially greater than the time required for the system to equilibrate. In these circumstances no enhancement of fluctuations is anticipated as the system moves to the lowest potential minimum (most globally stable state) prior to the old state becoming unstable.

## 2.5 Asymmetries in Bimanual Coordination

The essential features of the switching phenomena evident in bimanual coordination were modelled by Haken, Kelso, and Bunz (1985) using the basic tools of the synergetic approach (e.g., Haken, 1983). Among the assumptions under which the system was modelled was that there was symmetry of the component oscillators. That is, the behaviour of the system would not change if the labelling of the left and right hands was reversed. However symmetry of the dynamics is unlikely to prove a ubiquitous feature of biological systems and recent advances have been made in delineating the effects of broken symmetry upon coordination dynamics (e.g., Jeka, 1992; Kelso, DeGuzman, & Holroyd, 1991, Sternad, Turvey, & Schmidt, 1992). Differences in the characteristic or eigen frequencies of the component oscillators have been encapsulated, in an extension of the Haken et al. (1985) model, through the inclusion of a symmetry breaking term (Kelso, DelColle, & Schöner, 1990). Specific predictions of the augmented model include fixed point drift, isodirectional state transitions and phase wandering. Fixed point drift refers to the tendency of the coupled system to exhibit phase relations corresponding to stationary states which deviate increasingly from values of 0 and $\pi$ as the difference in the eigen frequencies of the component oscillators is enhanced. This deviation is also predicted to increase in magnitude as control parameters are scaled (phase wandering). Transitions are characterized as isodirectional in that they are predicted to occur predominantly in the same direction as the fixed point drift (Kelso et al., 1990). Average Phase Difference (APD) Theory (Kopell, 1988; Rand, Cohen, & Holmes, 1988) also appears especially well suited to the treatment of these phenomena. This is a very general modelling scheme in which no assumptions are made regarding the dynamical substructure or "state space" of the individual oscillatory components. Notwithstanding these limitations, this phenomenological approach provides a convenient means through which the collective behaviour of a system of oscillators may be studied. The version of the Rand et al. (1988) model which is presented below illustrates one means by which asymmetries may be encapsulated, without it being the case that the model is exhaustive with respect to the dynamics which are observed in bimanual coordination.

In the nomenclature adopted by Rand et al. (1988) the characteristic frequencies of the left and right oscillators are given by $\omega_l$ and $\omega_r$ respectively. It is assumed that the magnitude of the coupling between them is a function of their phase difference. Such that

$$\frac{d\theta_l}{dt} = \omega_l + k_{lr} \sin(\theta_r - \theta_l) \tag{4}$$

$$\frac{d\theta_r}{dt} = \omega_r + k_{rl} \sin(\theta_l - \theta_r) \tag{5}$$

where $k_{rl}$ is the coupling coefficient representing the influence of the oscillator corresponding to the left hand on the oscillator corresponding to the right hand. The reverse applies in the case of the coupling coefficient $k_{lr}$.

The collective variable relative phase $\varphi(t)$ is defined as

$$\varphi(t) = \theta_l(t) - \theta_r(t) \tag{6}$$

subtracting (5) from (4) we obtain

$$\frac{d\varphi}{dt} = (\omega_l - \omega_r) - (k_{lr} + k_{rl}) \sin \varphi \tag{7}$$

In (7) stationary states (1:1 phase locking) exist as special solutions in which $\dot{\varphi} = 0$ and in which relative phase is constant over time. Thus, following Rand et al. (1988)

$$\varphi = \arcsin \frac{\omega_l - \omega_r}{k_{lr} + k_{rl}} \tag{8}$$

Phase and frequency locking are predicted to occur if the difference in the characteristic frequencies of the component oscillators ($\omega_l$ and $\omega_r$) is sufficiently small relative to the net coupling between them. Given two oscillators of fixed characteristic frequencies, a decrease in the net coupling strength will, at a critical value, engender a transition from phase-locked motion to phase-drift (Rand et al., 1988).

In modeling the interlimb coordination of rhythmic movements, it has generally been assumed that the coupling strengths ($k_{lr}$ and $k_{rl}$) are inversely proportional to the frequency of oscillation $\omega_v$. Sternad et al. (1992) have suggested that relevant quantities should not be expressed simply in terms of the frequency of oscillation but rather as a ratio of the actual and characteristic frequencies.

We may therefore introduce the following expressions

$$k_{rl} = G_l \frac{\omega_l}{\omega_v} \tag{9}$$

$$k_{lr} = G_r \frac{\omega_r}{\omega_v} \tag{10}$$

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 the frequency of oscillation.

Considerable emphasis has been placed upon the use of preferred frequency as an index of the characteristic frequency (e.g., Schmidt et al., 1991; Turvey, Schmidt, & Rosenblum, 1989) or eigen frequency (e.g., Jeka, 1992) of component oscillators. The limited amount of data which are available pertaining directly to this issue provide little evidence to suggest that the hands differ in terms of preferred frequency (Kay et al., 1987). In addition, fixed point drift or phase wandering are not usually observed in bimanual coordination. On initial inspection, these observations appear to support the assumption of symmetry (Haken et al., 1985). However detailed analyses of transition pathways reveals that it is predominantly the kinematic pattern of the left hand which is modified (Carson, Byblow, & Goodman, in press). This finding of a preferred transition path between stationary states fulfills at least one of the predictions of symmetry breaking dynamics. It also suggests that there may exist asymmetries which are not fully expressed in terms of unimanual preferred frequencies.

In (8) the key quantity determining stability is the ratio of the difference in the component eigen frequencies to the coupling strength. As the frequency of oscillation $\omega_v$ is increased and the transition region is approached $|k_{lr} + k_{rl}|$ decreases to a critical value relative to $|\omega_l - \omega_r|$. In order for the transition to proceed predominantly in a single direction, that of left to right at transition, it is necessary that $k_{lr} > k_{rl}$ and as such that $\left|\frac{k_{lr}-k_{rl}}{k_{lr}+k_{rl}}\right|$ is larger at the transition frequency than at pretransition values of $\omega_v$. This would occur in circumstances in which $G_l$ is larger than $G_r$ resulting in a rate of depression of $k_{lr}$ with increases in $\omega_v$ that is larger than that of $k_{rl}$. Although there is no evidence directly in support of this proposition, it is known that maximal rates of response are consistently higher for the right hand than for those of the left hand (see section 2.8) while preferred frequencies appear to be equivalent. It has been noted that preferred frequencies are sensitive to task exposure (Carson et al., in press) suggesting that $G_l$ and $G_r$ are not stationary over time. It remains to be determined whether $G_l$ and $G_r$ are distinguished from each other on a consistent basis. Appraisal of the maximum sustainable frequencies of oscillation for single limbs on these types of task may help establish whether this is the case. In this regard it is also interesting to note the suggestion that in juggling the right hand appears to "dominate" the left hand (Beek, 1989).

In bimanual tasks requiring absolute coordination, the right hand is characterized by a smaller degree of variability in frequency (Carson at al., in press; Kay et al., 1987). There is also considerable evidence (see section 2.8) to support the observation that in simple oscillatory movements such as finger tapping the left hand exhibits maximal rates of movements which are consistently more variable than those of the right hand. However this variability represents subsystem specific noise. While it is likely that this variability will impinge upon the coupled system dynamic, current models do not speak clearly to the manner in which this might occur. It is conceivable however that in bimanual coordination, asymmetries in the degree of frequency variability will impact upon preferred transition pathways.

## 2.6 Asymmetries in Unimanual Coordination

There exist other systems which make asymmetries expressed in "unimanual" multijoint rhythmic coordination amenable to these forms of analysis. In single limb movements involving flexion and extension of the elbow and wrist, relative phase of the component joint angles has been identified as an appropriate order parameter (Kelso, Buchanan & Wallace, 1991). The control parameters are oscillation frequency, and the spatial orientation of the forearm. Studies of multilimb coordination of the arms and legs (Jeka, 1992, Kelso & Jeka, 1992; Serrien, Swinnen, & Lee, 1992) and of the hands and feet (Baldissera, Cavallari & Civaschi,1982; Baldissera, Cavallari, Maarini, & Tassone, 1991) provide evidence that collective variables for these systems are defined in terms of the relative phasing of the elbow and knee, and of the wrist and ankle joints respectively.

To some degree of approximation, for unimanual movements, each limb/flank-hemisphere complex may be characterized as an "independent" dynamical system. The multijoint and multilimb models described above provide means of probing their dynamics and of distinguishing dimensions along which the organization of these systems are differentiated.

## 2.7 Intrinsic Dynamics

The most engaging possibility is that the limb-hemisphere systems are distinguished on the basis of their intrinsic dynamics. If this is the case, the preferred and non-preferred limb/flank joint couples will exhibit qualitative differences in the topology of the potential landscape for an appropriate collective variable such as relative phase. Such differences will be reflected by the relative stability of attractor states which are in turn indexed by a number of measures which can be derived experimentally. These include (a) The (local) relaxation time which is the time required for the system to return to the stationary state following an externally applied perturbation; (b) The variability of the collective variable over time under stationary conditions; (c) The time scale over which correlations of the pattern variables decay (correlation time), which is derived either from correlation functions or from the corresponding power spectra (Schöner, in press). An additional indirect measure gauging the difference in stability between two adjacent states can be estimated as the length of the transient switching process (Schöner & Kelso, 1988b).

It may be useful to consider the advantages which would be conferred upon the limb-hemisphere system for which stationary states exhibit less dynamic stability. This can also be conceived of as a shallower or less confining basin of attraction. We would anticipate that this system would possess greater flexibility in switching from one pattern of coordination to another (Kelso, Scholz, & Schöner, 1988). This difference should also be expressed as a greater sensitivity to informationally based perturbations of the intrinsic dynamics resulting in an enhanced ability to deal effectively with environmental contingencies (see section 2.9).

Is there evidence to suggest that the limb-hemisphere systems may be differentiated on this basis? Recent studies conducted by Newell and van Emmerik (Newell & van Emmerik, 1989; van Emmerik & Newell, 1990; van Emmerik, 1991), although not specifically motivated by a commitment to the dynamics approach, suggest that preferred and non-preferred limb couples may indeed be discriminated by their intrinsic dynamics. In a task in which subjects were required to repetitively produce both cursive alphabetic characters and signatures in a rhythmic fashion, correlations of the linear displacements of the wrist, elbow and shoulder were significantly higher for movements of the left arm as compared to the right arm (Newell & van Emmerik, 1989). In a further study comprising a circle drawing task.(van Emmerik & Newell, 1990) it was again noted that correlations were higher in the left arm than in the right arm. Although these data were expressed in terms of the correlations of linear displacements rather than the phase relations of joint angles, they suggest that a greater degree of mode-locking is exhibited between the joints of the left arm compared to the right arm. More recently, van Emmerik (1991) extended these findings, noting that when the pattern of coordination was mechanically perturbed, compensation in the non-dominant limb was equivalent across all degrees of freedom, whereas in the dominant limb this was not the case. The higher inter-joint coupling for the non-dominant limb was in turn subserved by greater joint damping and stiffnesses. These data offer some insight concerning the manner in which asymmetries at the level of the collective variable could be explored at the level of the component oscillators.

## 2.8 Control Parameters

In the dynamics approach the instantiation of control parameters is treated as formally distinct from order parameter dynamics. Although control parameters (e.g., oscillation frequency) are deemed nonspecific with respect to order parameter dynamics, it has been noted that the order parameter is subject to fluctuations arising from noise in the control parameter (Haken & Wunderlin, 1990). Stochastic fluctuations of the order parameter, arising from the interaction of the many subcomponents from which the system is assembled, assume both conceptual and technical importance (Kelso & Ding, in press; Schöner, Haken, & Kelso, 1986). These fluctuations are constructive in the sense that they permit the system to explore new regions of state space, and thus effect transitions to new modes of behaviour. In addition they are thought to play a crucial role in determining various system time scales and the relations between them (e.g., Kelso & Schöner, 1987). As has been noted above, the nature of these time scale relations account for both qualitative and quantitative characteristics of macroscopic coordination, and in particular, for switching among multiple behavioural patterns (cf. Schöner & Kelso, 1988b). In contrast, the implications of control parameter fluctuations, lacking adequate theoretical treatment, remain abstruse. Stochastic fluctuations live on a time scale much faster than variation of the order parameter. This is not the case for variability arising from vagaries in the implementation of control parameter regimes. While most theoretical treatments (e.g., Haken et al., 1985) have stressed the non-specificity of control parameters, in an experimental context a strong association between variability of the putative control parameter and variability of the order parameter has been demonstrated (Carson et al., 1992).

In the unimanual and bimanual coordination tasks discussed thus far, frequency of oscillation has been identified as an appropriate control parameter. It is well known that the fingers of the right hand tap more rapidly than those of the left hand (e.g., Peters, 1977, 1987, 1990a) and with less variability at maximal rates of responding (e.g., Hammond, Bolton, Plant, & Manning, 1988; Peters, 1980; Peters & Durding 1978, 1979a; Todor & Kyprie, 1980; Todor & Smiley-Oyen, 1987). These findings have been reproduced for movements of more proximal upper limb segments (e.g., Harrison, 1991; Rouselle & Wolff, 1991; Todor, Kyprie, & Price, 1982) and of the foot (Augustyn & Peters, 1986; Peters & Durding, 1979b). In addition, the left hand has been observed to be more variable in following a pacing signal and in reproducing a simple rhythm (Wolff, 1977; Wolff, Hurwitz, & Moss, 1977)

Task specific factors and environmental constraints often demand stability in maintaining a particular posture or mode of coordination, rather than flexibility in achieving new modes of behaviour. In these circumstances variability of the order variable is undesirable if it serves to drive the system away from the required coordinative state. Generally then a balance must exist between the stability that is demanded by task constraints and the variability which arises either from fast stochastic noise sources or from variability of the control parameter. It can be seen that variability of the control parameter which contributes to variability of the order parameter compromises the dynamic stability of the coordination pattern. Consistent with the expectations expressed in section 2.7, it is proposed that movements of the left side, which it appears are characterised by greater variability of the control parameter (oscillation frequency), may maintain a dynamic stability equivalent to that of the right side only through compensatory reconfigurations of the intrinsic dynamics. However, it is to be anticipated that reconfigurations of this nature will incur costs in terms of flexibility and sensitivity to evolving task requirements. In support of this view is the observation made by van Emmerik & Newell (1990) that in executing the cyclic drawing task, the left limb "does not change its style of organization with the scaling of circle diameter" (p. 188).

These data suggest that the greater degree of joint coupling exhibited by the nondominant limb, is contiguous with a less efficient response to environmental contingencies (specification of circle size).

## 2.9 Information Mediated Behavioural Change

We have thus far neglected the quintessential feature of human behaviour, the ability to switch between movement patterns in a purposeful fashion (c.f. Kelso, Scholz & Schöner, 1988). Central to the extension of the dynamic pattern theory to the realm of purposeful behaviour is the concept of information. Information is viewed as "meaningful and specific to the biological system only to the extent that it contributes to the order parameter dynamics attracting the system to the required (e.g., perceived, learned, memorized, intended) behavioural pattern " (Jeka & Kelso, 1989, p.29). As such, information, and in particular, intentional information is defined in the same space as the collective variables which characterize the behaviour under study (Jeka & Kelso, 1989; Schöner & Kelso, 1988b).

Intentional information may be viewed as a perturbation of the pre-existing dynamics to a new (intended) behavioural pattern. The structure of intentional perturbations have been modelled by Kelso, Scholz and Schöner (1988) (see also Schöner & Kelso, 1988b) and have been subjected to experimental investigation (Scholz & Kelso, 1990). The characterization of intention as a perturbation contributing to the intrinsic dynamics appears to provide an acceptable account of intentional switching between modes of coordination. In addition, as Kelso, Scholz and Schöner (1988) highlight, it illuminates a means through which otherwise intrinsically unstable modes of behaviour may be maintained through the imposition of the appropriate intentional dynamics.

As it is with respect to intentional behaviour that the clearest hand preferences are expressed, and the greatest performance asymmetries are observed, it is conceivable that the limb/flank-hemisphere systems may be distinguished in their expression of intentional dynamics. It would therefore be valuable to determine whether these systems differ in terms of the strength of the intentional influence upon the intrinsic dynamics. Suggestions that the hands differ in their relation to conscious intent are not without precedent. Peters (e.g., 1987, 1989, 1990b) has proposed that the activity of the preferred hand thrives upon and demands focussed attention, whereas, the non-preferred hand receives a more diffuse form of attention. It has also been proposed that in bimanual movements, right handers have a propensity to direct attention preferentially to the right body half (Peters, 1987), and that it is this feature which accounts for the superiority of the right hand in producing complex rhythmic sequences such as polyrhythms.

## 2.10 Concluding Comments

It has been suggested that manual asymmetries may be illuminated through consideration of the relative stability of stationary states, the variability with which control parameter regimes are instantiated, and the manner in which information contributes to the order parameter dynamics. Means have therefore been provided of characterising performance differences between the hands independently of special purpose explanatory constructs and of presuppositions regarding the presence of control. One might question whether these factors capture all non-trivial aspects of the relevant systems' behaviour and if their identification is theory neutral. It remains to be determined whether these variables are exhaustive with respect to manual asymmetries. However, the trenchant difference between this and traditional approaches is that the variables employed, although preselected, are not arbitrary with respect to the system's dynamics.

The use of dynamical principles does not entail selection of a privileged level of description. Rather these techniques constitute an "entry point" for the study of manual asymmetries at other scales of observation (cf., Kelso, 1990). To the extent that, at present, this means of analysis is more readily applied to asymmetries in neuromuscular coordination at the level of the joint kinematics in rhythmic movements, the limitation is one of implementation rather than of principle.

**Si nous ne trouvons pas des choses agréables, nous trouverons du moins des choses nouvelles.**

**If we do not find anything pleasant, at least we shall find something new.**

**Candide, Voltaire**

# 3 Experiment 1

## 3.1 Introduction

There is considerable evidence to document asymmetries in timing functions. The fingers of the right hand tap more rapidly than those of the left hand (e.g., Peters, 1977, 1987, 1990a) and are consistently less variable at maximal rates of responding (e.g., Hammond et al., 1988; Peters, 1980; Peters & Durding 1978, 1979a; Todor & Kyprie, 1980; Todor & Smiley-Oyen, 1987). These findings have been reproduced for movements of more proximal upper limb segments (e.g., Harrison, 1991; Rouselle & Wolff, 1991; Todor, Kyprie, & Price, 1982) and of the foot (Augustyn & Peters, 1986; Peters & Durding, 1979b). In bimanual tasks requiring absolute coordination, the right hand is characterized by a smaller degree of variability in frequency (Carson at al., in press; Kay et al., 1987). Indeed a large body of theoretical work has been based explicitly upon the assumption that the left hemisphere assumes some privileged role in the execution of timing functions (e.g., Bradshaw & Nettleton, 1981; Ojemann, 1984; Tzeng & Wang, 1984). There is as yet little evidence to suggest the presence of asymmetries at subcortical levels (Trevarthen, 1984). It may thus seem paradoxical that a number of investigators have proposed that motor timing functions are largely mediated by subcortical mechanisms (e.g., Grillner, 1981; Ivry & Keele, 1989).

This contrariety may be resolved if it is noted that the bulk of experimental work countenancing the role of subcortical structures in timing functions has been concerned with human and animal locomotion. It may be the case that the control processes mediating cycling of the limbs in locomotion are assembled to optimize energy consumption through exploitation of the pendular properties of the limbs (Keele & Ivry, 1987; cf., Bach, Chapman, & Calvert, 1983). Indeed it has been contended that the maximum rate of reciprocation in running can be accounted for largely in terms of inertial properties of the limbs (Heglund, Taylor, & McMahon, 1974). However, rhythmical movements of other effectors may be less sensitive to energetic considerations and may be modulated by combinations of "control modules" which are different from those involved in locomotion (Keele & Ivry, 1987). It is not even clear that the most comfortable or preferred "styles" of locomotion in humans are such as to minimize energy expenditure (Lonergan, 1988). When the other effectors are considered, it is evident that the longer and most massive effectors are not necessarily the slowest. It appears that the finger, thumb and foot are the slowest, while the forearm and wrist exhibit the fastest maximal rates of reciprocal movement. These frequencies are themselves in the order of twice those observed at maximal rates of locomotion (Keele & Ivry, 1987). The observation that the maximal rate of reciprocal movement is not necessarily dependent upon the inertial properties of the limb has implications for the estimation of eigenfrequencies (Jeka, 1992), and for the generality of tasks in which characteristic frequencies of oscillation, inferred from preferred frequencies, are manipulated through the addition of mass to limb pendulums (Kugler & Turvey, 1987). In addition, in some experimental systems, preferred frequencies are demonstrably sensitive to task exposure (Byblow, Carson, & Goodman, submitted). The mutability of these attributes and the lack of dependence upon purely mechanical or inertial properties suggests that preferred and maximal sustainable frequencies of rhythmic movement may provide a window upon cortical organization vis a vis timing functions.

Rhythmic (multijoint) movements may be examined in a number of nonlocomotory effector systems. Coordination dynamics have been examined in multijoint (elbow and wrist) arm movements (Buchanan & Kelso, in press). Features such as stability, loss of stability and switching between coordinative modes were studied as a function of forearm rotation. Enhancement of fluctuations and critical slowing down were noted en route to transitions, as the putative control parameter forearm position was manipulated. Baldissera, Cavallari and Civaschi (1982) studied the coupling of flexion and extension of the hand, in the parasaggital plane, with movements of the foot. Subjects were seated in an armchair which allowed the right forearm to be supported, in a horizontal position, in either a prone or supine position. This arrangement permitted free full range flexion and extension of the wrist and of the ankle. In the first of two experiments, the arm was placed in the prone position. Subjects were asked to make simultaneous movements (alternate flexions and extensions) of the right hand and foot. It was observed that all individuals inevitably adopted a pattern in which hand extension was associated with foot dorsal flexion, and hand flexion with foot plantar flexion. As the hand and foot were moving in the same direction in this arrangement, the pattern may be represented as an in-phase relationship. Although the analysis was of a qualitative nature, the authors noted that this was the only phase relationship which remained stable as oscillation frequency was increased. Individuals were, with some effort, able to adopt the anti-phase pattern (hand extension associated with foot plantar flexion, and hand flexion with foot dorsal flexion) for low oscillation frequencies. However, as oscillation frequency was scaled upward, subjects demonstrated what the authors describe as "hesitations and/or errors". In addition, abrupt phase transitions were noted as subjects spontaneously reverted to the in-phase pattern. Baldissera, Cavallari, and Civaschi (1982) noted that the in-phase and anti-phase patterns were primarily differentiated in terms of the ease with which they could be reproduced. They further observed (p. 97) that other "intermediate phase relationships are impossible".

In a second experiment, subjects' hands were supported in a supine position, such that for instances in which the hand and foot were moving in the same direction, hand flexion was associated with foot dorsal flexion and hand extension was associated with foot plantar flexion. Again, it was noted that the in-phase relationship (in which the hand and foot moved in the same direction) was "easier" than the anti-phase relationship. It was however evident that the phase transitions from the anti-phase to in-phase pattern were less abrupt than when the arm was in the prone position, and that the anti-phase pattern could be more reliably reproduced (Baldissera, Cavallari, & Civaschi, 1982). The greater stability observed for the in-phase pattern did not appear to depend upon a preferential coupling between specific muscles. The groups which were co-activated in the in-phase pattern when the hand was supinated were those which were coactivated in the anti-phase pattern when the hand was pronated (Baldissera, Cavallari & Civaschi, 1982). Dynamic stability was thus more sensitive to spatial than to anatomical constraints. These findings have been reproduced and extended through the recording of EMG from the muscles supporting the antigravity portion of the movement in this task (Baldissera, Cavallari, Maarini, & Tassone, 1991).

In unimanual movement each limb/flank-hemisphere complex may be characterized as an "independent" system. Rhythmic multilimb coordination tasks (e.g., Baldissera et al., 1982; Baldissera et al., 1991) make these systems amenable to dynamical analyses. The present experiment was conducted to determine whether putative asymmetries in cortical organization with respect to timing functions.are expressed in the dynamics of self paced rhythmic coordinative tasks. The specific aims of this study were to ascertain whether the greater variability of movement frequency exhibited by a variety of effectors on the left side of the body at maximal rates of response, are reproduced at preferred frequencies. Flexion and extension movements of the wrist and the ankle were examined both when these joints were moving singly and when coupled, following the paradigm introduced by Baldissera et al. (1982). In addition, the dynamics of coupled movements were assessed to determine whether putative asymmetries are expressed in terms of the collective variables which appear to encapsulate stable coordinative states. These features were examined at both the kinematic and the neuromuscular levels of observation.

## 3.2 General Methodology (Experiments 1 to 4).

### Subjects

Three normal adult females (24-27 years) and one normal adult male (24 years) from the university population were employed in these experiments. All were right-handers (Oldfield 1971) and were paid $110.00 for their participation.

### Apparatus

Subjects were positioned in a padded wooden seat. Custom built manipulanda were used to monitor the flexion and extension of the wrist, and the plantar flexion and dorsi flexion of the foot. Linear potentiometers (Bourns Instruments, Model # 3540, 0.25%) located coaxially with the center of rotation of each manipulandum allowed for the continuous transduction of angular displacement. Wrist manipulanda were mounted on a frame in front of the subject, and could be moved in the transverse plane such that they were located a comfortable distance from the subject's midline. The height of the frame was adjustable so that subjects could passively rest their forearms, on semi-rigid foam blocks, in a fully pronated or supinated position. Subjects' hands were attached to the manipulandum by means of two rubber loops passing over the second and third, and fourth and fifth fingers at about the metacarpal phalangeal joint. These loops ensured that it was unnecessary for subjects to "grip" the manipulandum. The manipulanda were adjusted for each subject to ensure that the axis of rotation was coaxial with the wrist joint. Subjects' forearms were secured with a wide velcro belt, ensuring that movements were restricted to flexion/extension of the wrist. Foot manipulanda comprised freely rotating, neoprene padded foot plates. Subjects' feet were placed on these plates and secured by a heel support and five velcro straps applied over the upper surface of the foot. The length of the shafts from which the foot plates were suspended could be adjusted such that the axes of rotation of the manipulanda were coaxial with subjects' ankle joints. The manipulanda were positioned on a sliding trackway mounted in front of the subject. When seated, subjects' thighs were in a horizontal position with knees flexed at approximately 45°. Fine, "comfort", adjustments could be performed by moving the manipulanda along the trackway either towards or away from the subject (Figure 3.1).

Fig. 3.1 Apparatus (Experiments 1 - 4)

Auditory signals providing pacing for movements (metronome) or indicating either the initiation or termination of data collection were presented via a loudspeaker mounted on the floor directly in front of subjects. These signals (50 ms square waves) were output through a Scientific Solutions Inc. LABMASTER board mounted in a microcomputer. Control routines for the production of auditory signals and for the control of data collection devices were developed using TURBO C (Borland) and LABPAC (Scientific Solutions Inc.) procedures. EMG signals (Experiment 1) and the voltage signals from each potentiometer and metronome pulses were sampled at 500 Hz by an 8-channel WATSCOPE (Northern Digital) A/D converter and stored to disk upon completion of each trial.

### Data Reduction (kinematic data)

Fast fourier transforms of kinematic (angular displacement) data were performed for sample trials. It was determined that in all cases the power of the signal was predominantly distributed over harmonics below 5 Hz. Kinematic data were then low pass filtered using a 2nd order Butterworth dual pass filter with a cut off frequency of 10 Hz. The maximum and minimum angular displacements for each movement cycle were delineated using a custom "peak peaking" algorithm. Discrete (cycle to cycle) estimates of oscillation frequency were thus obtained.

### Sample Time Series

Examples of time series are presented in Figures 3.8 and 3.9 (Exp. 1), Figures 4.1 to 4.4 (Exp. 2), Figures 5.1 to 5.3 (Exp. 3), and Figures 6.1 to 6.4 (Exp. 4). In Figures 3.8 and 3.9 angular displacements of the wrist and ankle joint, and activity of the Flexor Carpi Radialis and Tibialis Anterior are represented. In all subsequent figures of time series, angular displacements of the wrist and ankle joint, and the relative phase relations between these joints are illustrated.

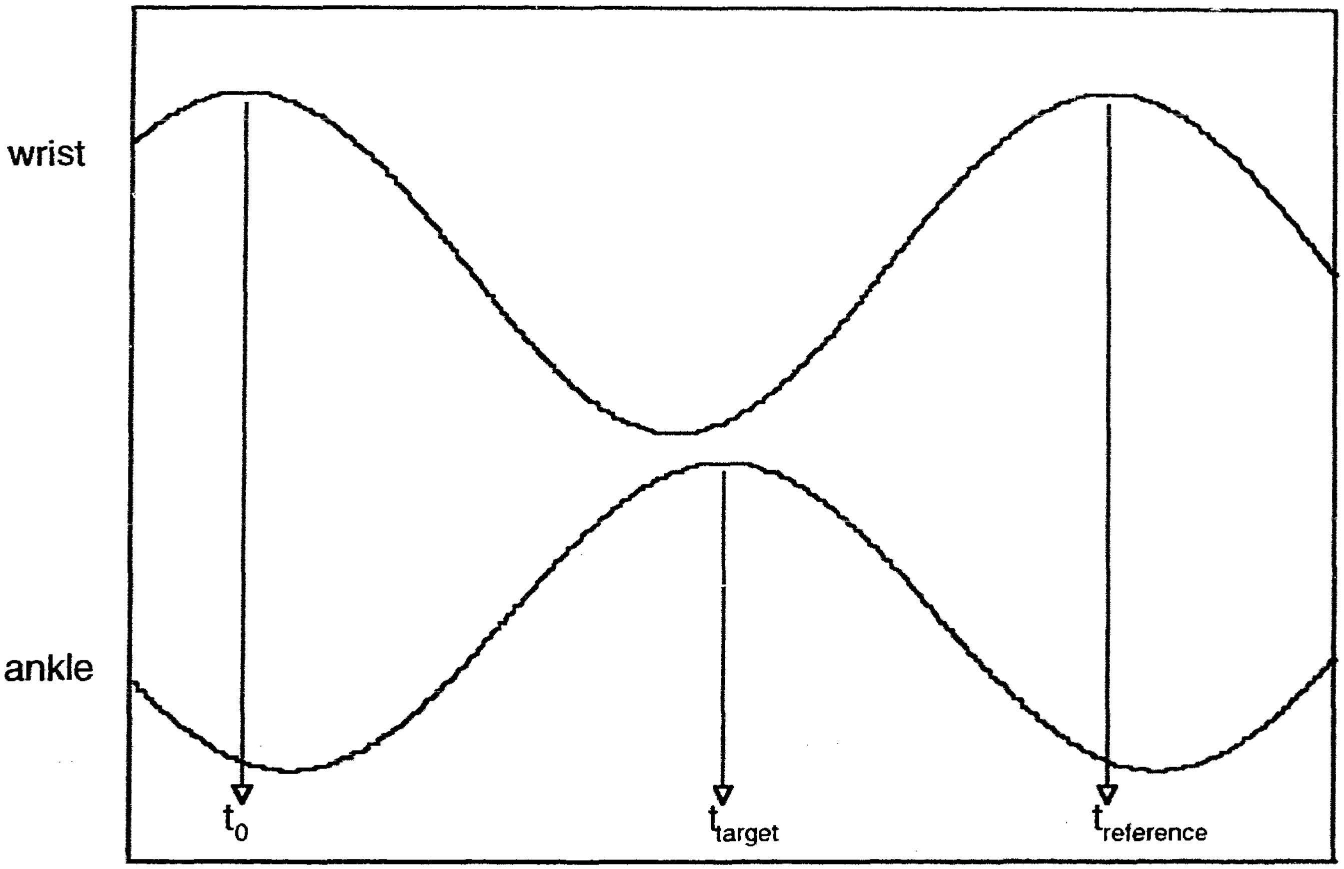

Fig. 3.2 Representation of a single measurement of relative phase from simulated data.

Discrete estimates of relative phase were derived in the following fashion. The wrist was chosen as the reference, and the ankle chosen as the target signal. An uncorrected relative phase value was first calculated according to the formula (1) below (Jeka, 1992).

$$RP = \frac{t_{target} - t_0}{t_{reference} - t_0} \tag{1}$$

This formula returns a relative phase value in the range 0 to 1. It can be noted that if, for example, $t_0$ is the 2nd peak identified for the reference channel and $t_{target}$ is the 2nd peak identified for the target channel, a positive value for RP will be returned. However, in actuality the target signal lags the reference signal by the calculated value of RP. In addition, as values are always returned in the range 0 to 1 (wrapped), no indication is provided of the history of the relative phase relationship. A corrected (unwrapped) relative phase value was therefore calculated as follows

$$RP_{unwrapped} = ( - (360 \times RP) ) - (360 \times (i_0 - j_{target}) ) \qquad (2)$$

where $i_0$ is the ith peak of the reference channel (wrist) and $j_{target}$ is the jth peak of the target channel.

The mean direction of relative phase obtained within a given interval was calculated following Mardia (1972) (see also Batschelet, 1981 and Burgess-Limerick, Abernethy, & Neal, 1991). Circular variables such as relative phase are characterized by the von Mises distribution function. This distribution plays a key role in statistical inference on the circle, and in this sense its role is similar to that of the normal distribution on the line (Mardia, 1972). There exist inferential tests for samples drawn from von Mises distributions which may be considered analogues of the standard normal theory tests. In the analyses reported in this dissertation, comparisons of directional data from multiple groups were conducted using the equivalent of a one-way ANOVA described by Watson and Williams (1956) (see also Burgess-Limerick et al., 1991). Measures of circular variance (uniformity) were calculated following Mardia (1972). The circular variance takes values in the range 0 to 1, unlike measures of variability on the line which take values in the range 0 to ∞. However a suitable transformation of the circular variance to the range (0, ∞) is of the form

$$s_0 = \{ - 2 \log_e (1 - S_0) \}^{0.5} \qquad (2)$$

where $S_0$ is the measure of uniformity in the range (0, 1), and $s_0$ is the transformed uniformity measure (Mardia, 1972). The measure thus derived corresponds to the ordinary sample standard deviation on the line, and permits the use of inferential tests based on standard normal theory.

## 3.3 Methodology (Experiment 1).

### Apparatus

Electromyographic recordings (Experiment 1) of the wrist flexor (Flexor carpi radialis) and extensor (Extensor carpi radialis) and foot plantar flexor (Medial head gastrocnemius) and dorsi flexor (Tibialis anterior) were obtained using a multichannel electromyographic system (Strawbridge Technologies, Waterloo, Ontario). Using standard skin preparation procedures, silver/silver chloride electrodes were mounted on the surface of the subject's forearm and lower leg over the muscles of interest (Delagi, Perotto, Iazzetti, and Morrison, 1975). EMG signals were monitored on oscilloscopes and input gains (1000, 2000, 5000, 10000) adjusted when necessary. Following preamplification, all EMG signals were passed through a 4th order butterworth (hardware) filter (20 - 500 Hz) prior to digital sampling.

### Procedure

Subjects performed self-paced oscillatory motions of the wrist and foot in two conditions, coupled and uncoupled. These movements, conducted seperately for the left and right side, consisted of the rhythmic flexion and extension of the wrist joint and the plantar-flexion and dorsi-flexion of the ipsilateral foot. Movements of the wrist were performed with the forearm either in a supine or a prone position. In all conditions, emphasis was placed upon the adoption of a comfortable frequency and amplitude such that the movements "could be performed all day" if necessary.

### Single Joint Trials

All subjects first performed single joint trials in the following order, wrist alone (forearm supinated), foot alone, wrist alone (forearm pronated). Six trials were conducted in each condition, representing a total of 18 uncoupled trials. In all conditions, subjects were permitted one practice trial.

### Coupled Trials

Subjects performed rhythmic oscillatory motions in two modes of coordination, in-phase and anti-phase. In the in-phase (forearm supinated) mode, flexion (extension) of the wrist was required to be coincident with dorsi-flexion (plantar-flexion) of the foot . In the anti-phase (forearm supinated) mode, flexion (extension) of the wrist was required to be coincident with plantar-flexion (dorsi-flexion) of the foot. This coupling was reversed when the forearm was in a pronated position whereby in the in-phase mode, flexion (extension) of the wrist was required to be coincident with plantar-flexion (dorsi-flexion) of the foot and in the anti-phase mode, flexion (extension) of the wrist was required to be coincident with dorsi-flexion (plantar-flexion) of the foot.

In each forearm position, trials alternated between in-phase and anti-phase trials, commencing with an in-phase trial. Trial blocks for which the forearm was placed in a supinated position preceded those in which the forearm was in a prone position. For each side (left or right) six trials were performed for each combination of coordination mode and forearm position, for a total of 24 coupled trials. In all conditions, subjects were permitted one practice trial. Two subjects first performed 24 trials for the left side followed by 24 trials for the right side. For the other two subjects, the order was reversed.

On all trials, subjects were instructed to move at their preferred frequency. Upon achieving this frequency, subjects made a verbal signal to the experimenter. Data collection was then initiated. Following 500 msec an auditory tone was output, coincident with a reference pulse output to one channel of the A/D unit. Following 30 seconds, a second auditory tone and reference pulse were output, signalling to the subject the termination of the data collection period.

### Data Reduction (kinematic data)

Kinematic data were treated as indicated in section 3.2 to allow for the identification of maximum and minimum angular displacements. These features served as the bases for the calculation of oscillation frequency and discrete relative phase. In order to assess variability of oscillation frequency, coefficient of varation (CV) was used, since mean frequency varied between experimental conditions.

### Data Reduction (EMG data)

EMG data were treated by removing bias and were then rectified. Having ascertained, on the basis of analysis of kinematic data, that frequencies of oscillation were in no instances above 1.5 Hz, EMG profiles were enveloped through the application of a low pass filter (dual pass 2nd order Butterworth, cutoff 2 Hz). These data were differentiated using a two-point central difference algorithm. A custom "peak peaking" algorithm was applied to the resulting "velocity" profiles in order to delineate points corresponding the maximum rate of increase of activity for each EMG burst. Discrete (cycle to cycle) estimates of oscillation frequency and discrete estimates of relative phase were based upon these peaks. Figure 3.3 illustrates the signal processing steps involved in implementing these procedures for a subsection of a representative trial. Vertical dashed lines correspond to the points in time corresponding to peaks of the 1st time derivative of the enveloped signal.

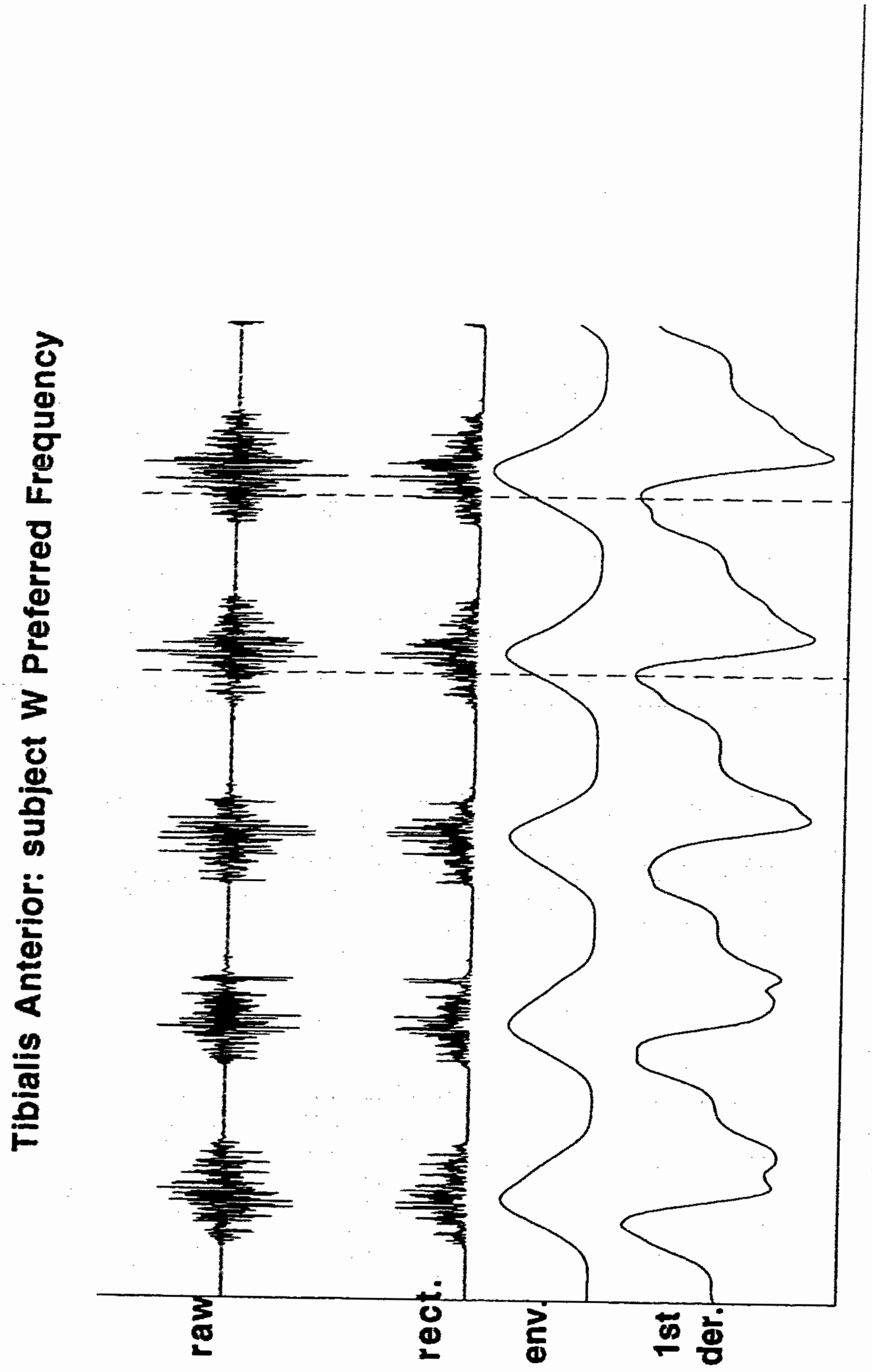

Fig. 3.3 Sample time series (Tibialis Anterior: subject W) illustrating the signal processing stages implemented to determine the maximum rate of increase of activity for EMG bursts.

## 3.4 Results (single joint trials)

### 3.4.1 Discrete Frequency

Independent analyses of variance for mean preferred frequency and coefficient of variation (CV) were performed for each subject using a 2 side (left, right) by 3 joint condition (wrist-forearm pronated, wrist forearm-supinated, ankle) design. Each trial was treated as a single case.

Subject: W

Mean frequency:

The mean frequency was unaffected by side ($F<1$). As examination of Figure 3.4 suggests there was a statistically significant main effect for joint condition ($F(2, 30) = 29.25$, $p < 0.0001$). Post hoc analysis of means using the Tukey (HSD) procedure indicated that the mean preferred frequency for movements of the ankle (1.02 Hz) was higher ($p < 0.01$) than that for the wrist when the forearm was pronated (0.90 Hz) and when supinated (0.90 Hz).

Coefficients of Variation:

Coefficients of variation were larger for the left side (4.42) than for the right side (3.46) ($F(1, 30) = 13.31$, $p < 0.001$). There was also a main effect for condition ($F(2, 30) = 4.33$, $p < 0.05$). Less variability was exhibited by the ankle than by the wrist (supine) ($p < 0.05$, Tukey HSD) with the wrist (prone) being intermediate.

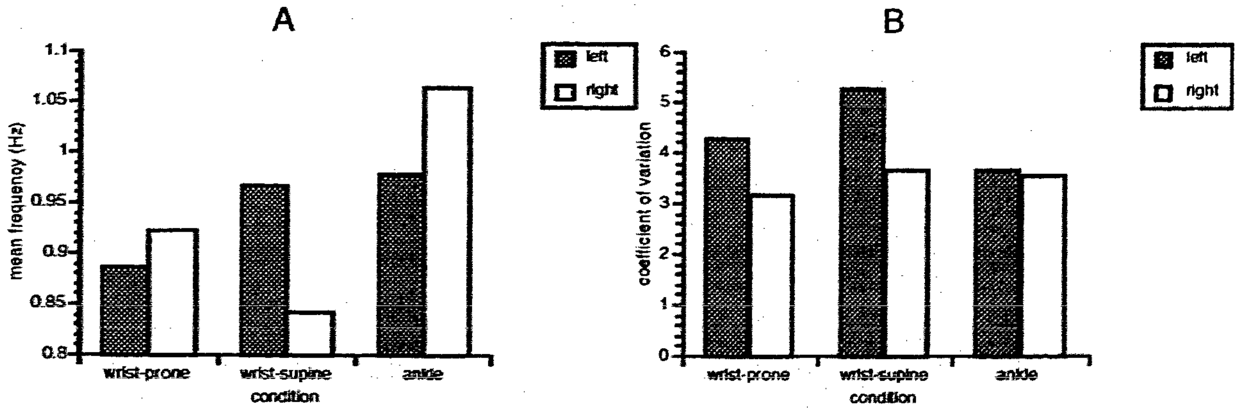

Fig. 3.4. Mean (A) and Coefficient of variation (B) discrete frequency for subject W in single joint conditions, shown as a function of side, and joint condition.

Subject: X

Mean frequency:

A main effect for side was noted (F(1, 30) = 293.69, $p < 0.0001$). Mean frequencies were higher for movements made by the left side (0.92 Hz) than by the right side (0.74 Hz). There was also a main effect for condition (F(2, 30) = 12.23, $p < 0.0001$). Movements of the wrist when the forearm was supinated (0.79 Hz) were characterized by lower mean frequencies than movements both of the ankle (0.86 Hz) and of the wrist when the forearm was pronated (0.83 Hz) ($p < 0.05$, Tukey HSD).

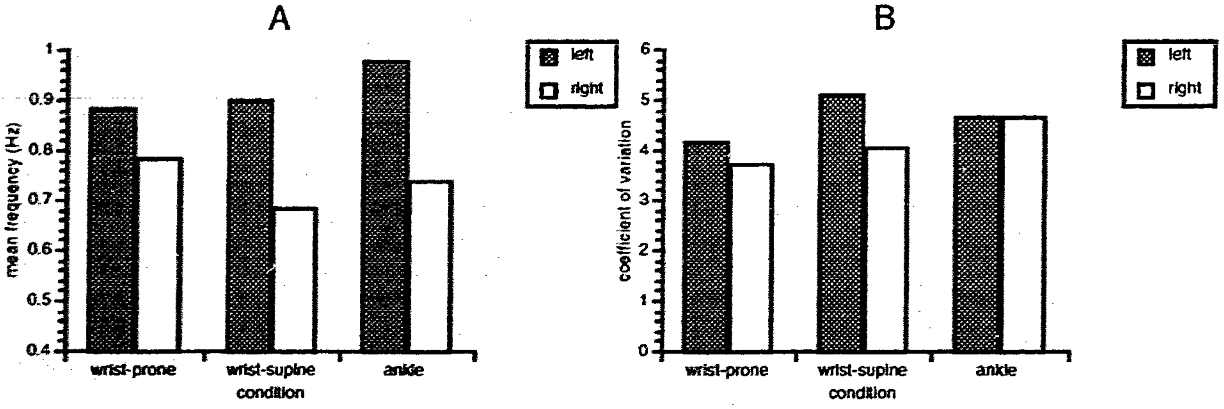

Fig. 3.5. Mean (A) and Coefficient of variation (B) discrete frequency for subject X in single joint conditions, shown as a function of side, and joint condition.

Coefficients of Variation:

Coefficients of variation (Figure 3.5 (B)) were essentially equivalent for all conditions ($p > 0.10$).

Subject: Y

Mean frequency:

There were no statistically significant main effects for either side or condition ($p > 0.05$) (Figure 3.6).

Coefficients of Variation:

Movements made by the left and right side were essentially equivalent in terms of variability ($F < 1$) (see Figure 3.6 (B)). A main effect for condition was noted ($F(2, 30) = 8.08$, $p < 0.01$). Movements made by the ankle were characterized by less variability than movements made by the wrist in both forearm positions ($p < 0.05$, Tukey HSD).

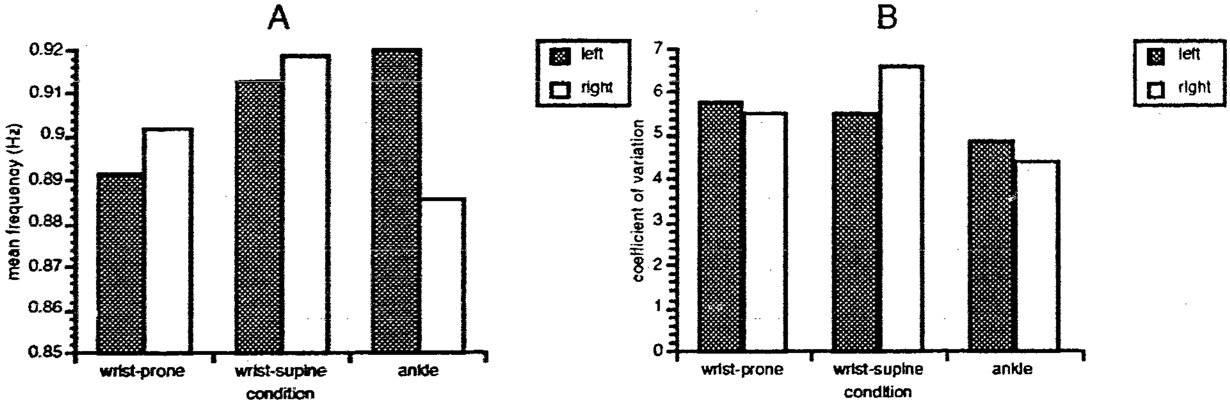

Fig. 3.6. Mean (A) and Coefficient of variation (B) discrete frequency for subject Y in single joint conditions, shown as a function of side, and joint condition.

Subject: Z

Mean frequency:

A main effect for side was observed ($F(1, 30) = 67.44$, $p < 0.0001$). Mean frequencies were higher for movements made by the right side (2.32 Hz) than by the left side (1.93 Hz). There was also a main effect for condition ($F(2, 30) = 75.38$, $p < 0.0001$). Movements of the ankle (2.44 Hz) were performed at higher frequencies than movements of the wrist when the forearm was pronated (2.19 Hz) which were in turn executed at higher frequencies than movements of the wrist when the forearm was supinated (1.74 Hz). All pairwise differences between means were statistically significant ($p < 0.01$, Tukey HSD).

Coefficients of Variation:

Coefficients of variation were larger for the left side (6.93) than for the right side (4.93) ($F(1, 30) = 14.86$, $p < 0.001$). There was also a main effect for condition ($F(2, 30) = 29.58$, $p < 0.0001$). Greater variability was exhibited by the ankle joint (8.75) than by the wrist when the forearm was supinated (4.65) and when the forearm was pronated (4.39) ($p < 0.01$, Tukey HSD). The latter two conditions did not differ from each other.

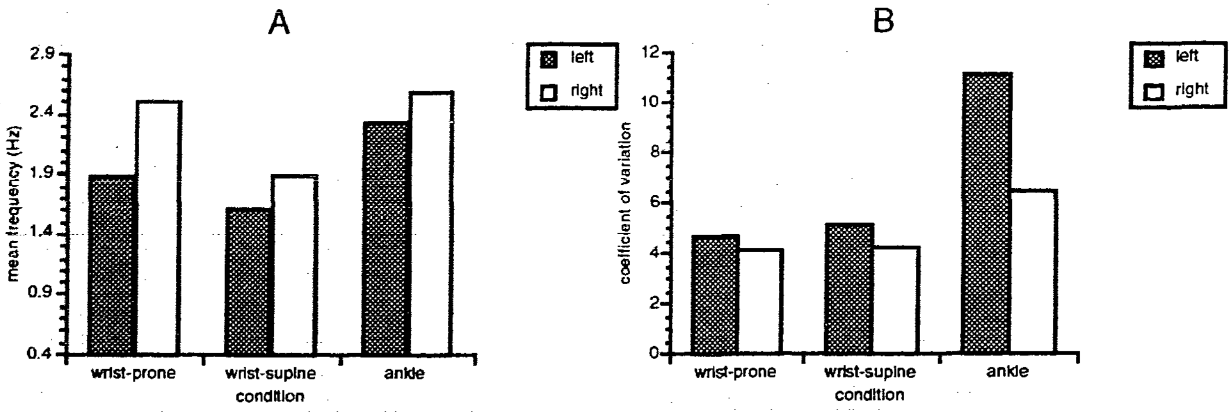

Fig. 3.7. Mean (A) and Coefficient of variation (B) discrete frequency for subject Z in single joint conditions, shown as a function of side, and joint condition.

TABLE 3.1 Summary table for Mean and Coefficients of Variation discrete frequency for all subjects (single joint conditions).

| | | | Effect | | |
|---|---|---|---|---|---|
| | | side | | | joint condition |
| mean freq. | | | | | |
| W | left | = | right | | ankle > (wrist (prone) = wrist (supine)) |
| X | left | > | right | | (ankle = wrist (prone)) > wrist (supine) |
| Y | left | = | right | | ankle = wrist (prone) = wrist (supine) |
| Z | left | < | right | | ankle > wrist (prone) > wrist (supine) |
| CV freq. | | | | | |
| W | left | > | right | | (ankle < wrist (prone)) = wrist (supine) |
| X | left | = | right | | ankle = wrist (prone) = wrist (supine) |
| Y | left | = | right | | ankle < (wrist (prone) = wrist (supine)) |
| Z | left | > | right | | ankle > (wrist (prone) = wrist (supine)) |

< and > indicate the direction of statistically significant ($p < 0.05$) main effects or pairwise differences (see text for details)

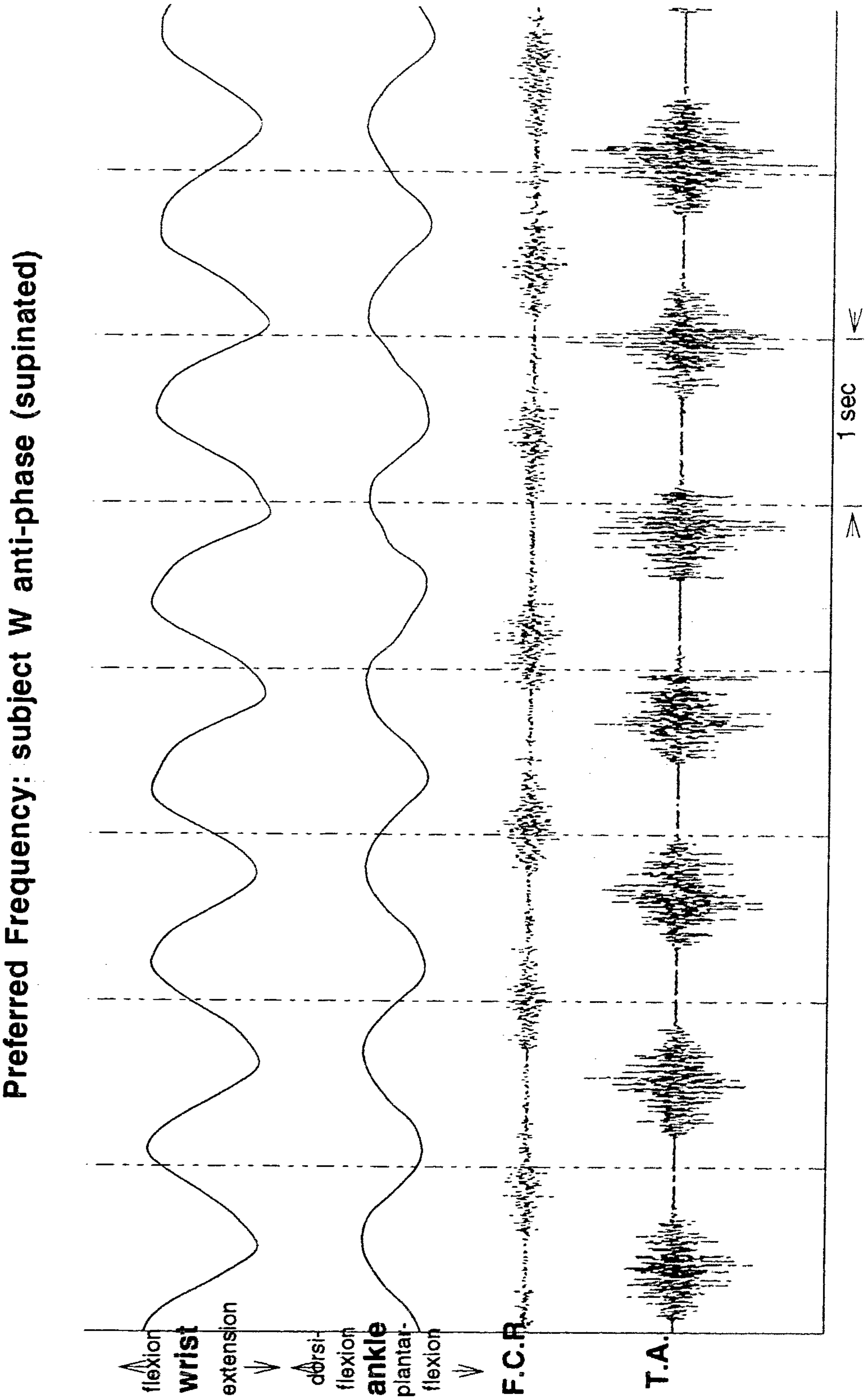

Fig. 3.8 Sample time series of a movement prepared in the anti-phase mode with the forearm in a supinated position (subject W).

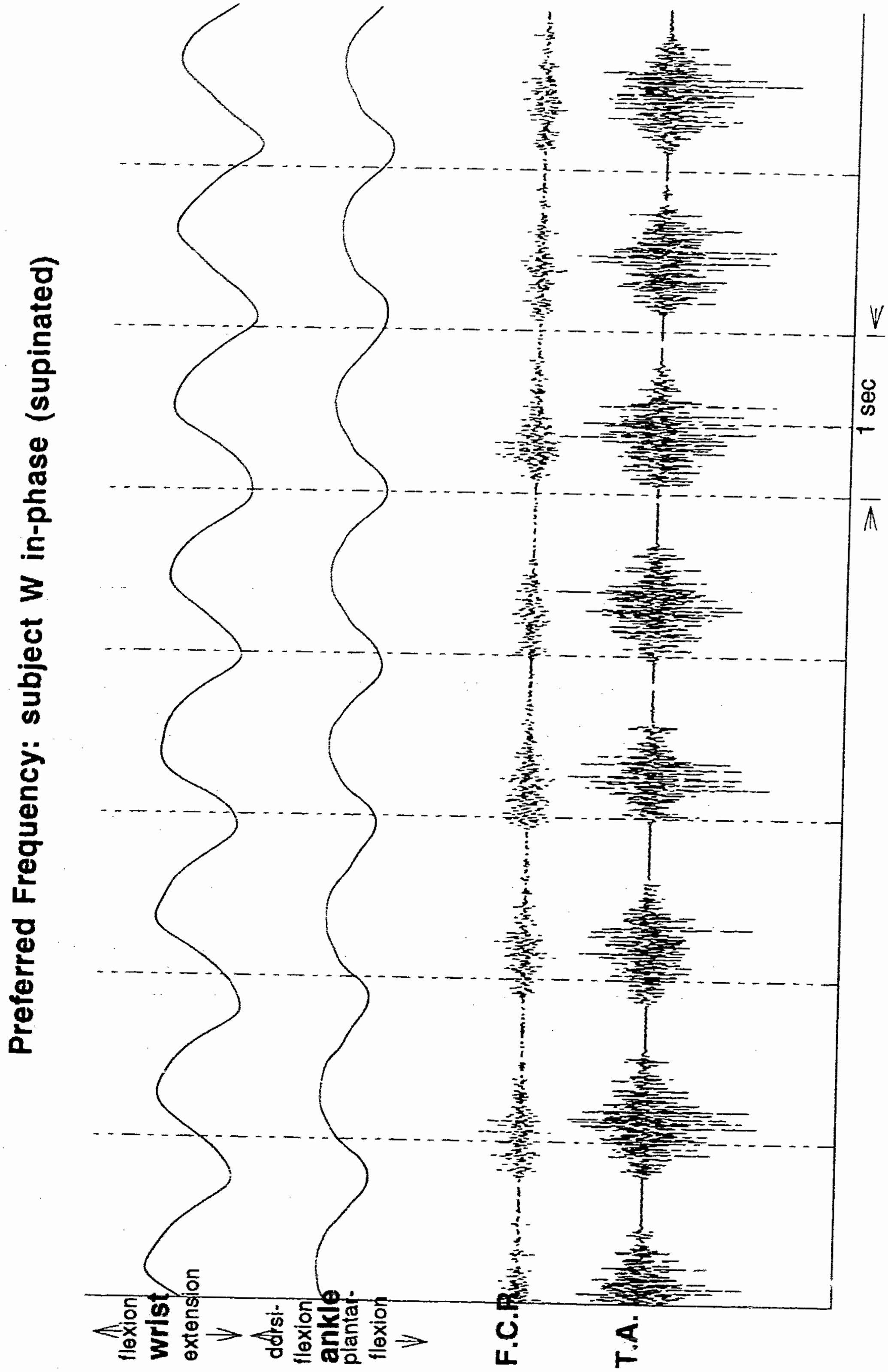

Fig. 3.9 Sample time series of a movement prepared in the in-phase mode with the forearm in a supinated position (subject W).

## 3.5 Results (coupled trials)

### 3.5.1 Discrete Frequency:

Independent analyses of variance for mean preferred frequency and coefficient of variation (CV) were performed for each subject using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 2 forearm position (pronated, supinated) by 2 joint (wrist, ankle) design. Each trial was treated as a single case. Side, mode and forearm position were grouping factors, joint was a within case factor.

Subject: W

Mean frequency:

Mean discrete frequencies for coupled movements were higher for the right side (0.90 Hz) than for the left side (0.84 Hz) ($F(1, 40) = 132.67, p < 0.0001$). In addition, movements prepared in the in-phase mode (0.89 Hz) were characterized by higher preferred frequencies than movements prepared in the anti-phase mode (0.85 Hz) ($F(1, 40) = 47.04, p < 0.0001$). Coupled movements performed with the forearm in a pronated position exhibited higher mean frequencies (0.88 Hz) than movements made with the forearm supinated (0.86 Hz) ($F(1, 40) = 5.09, p < 0.05$). The three way interaction of side, mode, and forearm position also attained statistical significance ($F(1, 40) = 4.38, p < 0.05$). The statistically significant pairwise diffferences comprised by this interaction are outlined in Table 3.2.

Coefficients of Variation:

Although there was a tendency for coefficients of variations to be larger for movements of the left side, this trend failed to attain conventional levels of statistical significance ($p = 0.07$). Similarly, while mean coefficients of variation were larger in the anti-phase mode (4.18) than in the in-phase mode (3.82), this tendency was not statistically significant ($p = 0.07$). Movements of the wrist joint (4.23) in the coupled condition exhibited greater variability of frequency than movements of the ankle (3.77) ($F(1, 40) = 6.94, p < 0.02$). This effect was accounted for largely by differences exhibited in the anti-phase mode of coordination ($F(1, 40) = 8.18, p < 0.01$). The variability of the wrist exceeded that of the ankle by a margin of 0.96 in the anti-phase mode (F(1,

40) = 15.10, $p < 0.001$), whereas in the in-phase mode they were essentially equivalent ($F < 1$). An interaction of joint with forearm position ($F(1, 40) = 11.86$, $p < 0.01$) was also present. The variability of the wrist exceeded that of the ankle by a margin of 1.06 when the forearm was supinated ($F(1, 40) = 18.48$, $p < 0.001$), whereas when the forearm was pronated they were essentially equivalent ($F < 1$). In addition there was a three way interaction of side, forearm position and joint ($F(1, 40) = 5.86$, $p < 0.05$). Visual inspection of means suggested that the forearm position by joint interaction was most pronounced for movements of the left side.

TABLE 3.2 Mean discrete frequency for subject W (coupled conditions): pairwise differences between combinations of side, mode and joint condition (Tukey HSD).

| | | | A | B | C | D | E | F | G | H |
|---|---|---|---|---|---|---|---|---|---|---|
| A. | left | anti-phase (supine)(0.81 Hz) | x | - | s | s | s | s | s | s |
| B. | left | anti-phase (prone)(0.82 Hz) | - | x | - | s | s | s | s | s |
| C. | left | in-phase (supine)(0.85 Hz) | - | - | x | - | - | s | s | s |
| D. | left | in-phase (prone)(0.87 Hz) | s | s | - | x | - | - | - | s |
| E. | right | anti-phase (supine)(0.88 Hz) | s | s | - | - | x | - | - | s |
| F. | right | anti-phase (prone)(0.90 Hz) | s | s | s | - | - | x | - | - |
| G. | right | in-phase (prone)(0.91 Hz) | s | s | s | - | - | - | x | - |
| H. | right | in-phase (supine)(0.92 Hz) | s | s | s | s | s | - | - | x |

Upper Triangle: $p < 0.05$; Lower Triangle: $p < 0.01$.

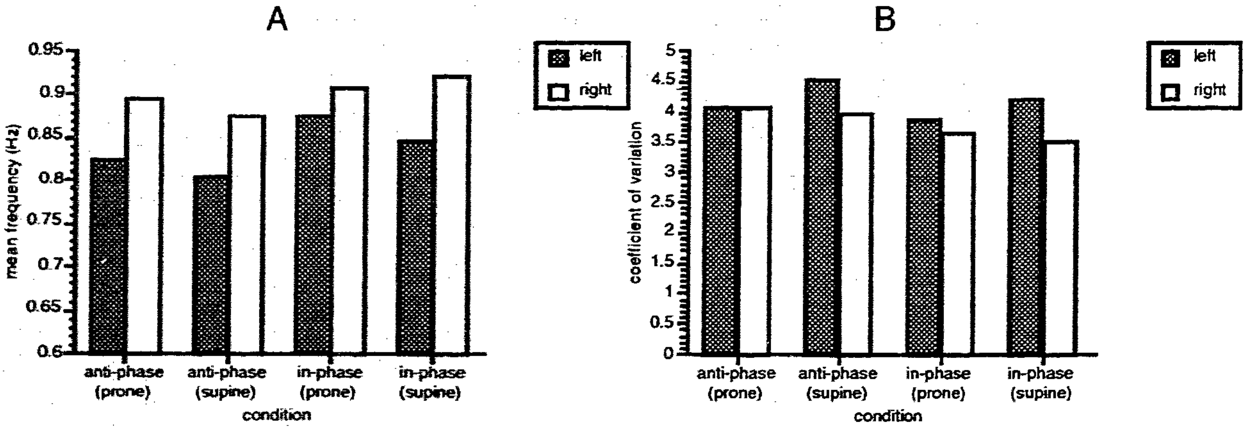

Fig. 3.10. Mean (A) and Coefficient of variation (B) discrete frequency for subject W in coupled conditions, shown as a function of side, mode and forearm position.

Subject: X

Mean frequency:

As is evident in Figure 3.11, mean discrete frequencies in the coupled conditions were larger for the left side (1.11 Hz) than for the right side (0.91 Hz) ($F(1, 40) = 183.66, p < 0.0001$). There was a tendency for movements in the in-phase mode (1.02 Hz) to be characterized by higher frequencies than movements in the anti-phase mode (1.00 Hz). This effect approached conventional levels of statistical significance ($F(1, 40) = 3.97, p = 0.053$). Coupled movements made with the forearm in a pronated position (1.05 Hz) exhibited higher frequencies than movements made with the forearm in a supinated position (0.97 Hz) ($F(1, 40) = 30.71, p < 0.0001$). There was an interaction of side and forearm position ($F(1, 40) = 7.18, p < 0.02$). Post-hoc analysis of means using the Tukey HSD procedure indicated that all pairwise comparisions other than between left side (supinated) and left side (pronated) were statistically significant ($p < 0.01$). Movements of the wrist (1.012 Hz) ) exhibited marginally higher frequencies than movements of the ankle (1.009 Hz). This gave rise to an effect of statistical significance ($F(1, 40) = 6.00, p < 0.02$). As the mean difference of 0.0029 Hz was barely within the temporal resolution of the system, this effect can be regarded as artefactual and thus will be excluded from further consideration.

Coefficients of Variation:

Coefficients of variation were larger for the left side (8.12) than the right side (6.05) ($F(1, 40) = 18.01, p < 0.001$). Greater variability was also exhibited in the anti-phase mode (8.32) relative to the in-phase mode (5.85) ($F(1, 40) = 25.76, p < 0.0001$). There was also an interaction of side and forearm position ($F(1, 40) = 6.09, p < 0.02$). As Figure 3.11 illustrates, movements of the left side when the forearm was supinated (8.68) were associated with greater variability than movements of the right side both when the forearm was supinated (5.41) and pronated (6.69) ($p < 0.05$, Tukey HSD). Movements of the left side when the forearm was pronated (7.56) were more variable than movements of the right side when the forearm was supinated ($p < 0.05$, Tukey, HSD). The summary of pairwise comparisions (Table 3.3) illustrates that these effects were most pronounced in the anti-phase mode of coordination.

TABLE 3.3 Coefficients of variation discrete frequency for subject X (coupled conditions): pairwise differences between all combinations of side, mode and joint condition (Tukey HSD).

| | | | A | B | C | D | E | F | G | H |
|---|---|---|---|---|---|---|---|---|---|---|
| A. | right | in-phase (supine)(5.22) | x | - | - | - | - | - | s | s |
| B. | right | in-phase (prone)(5.24) | - | x | - | - | - | - | s | s |
| C. | right | anti-phase (supine)(5.61) | - | - | x | - | - | - | - | s |
| D. | left | in-phase (supine)(6.42) | - | - | - | x | - | - | - | s |
| E. | left | in-phase (prone)(6.52) | - | - | - | - | x | - | - | s |
| F. | right | anti-phase (prone)(8.14) | - | - | - | - | - | x | - | - |
| G. | left | anti-phase (prone)(8.60) | - | - | - | - | - | - | x | - |
| H. | left | anti-phase (supine)(10.95) | s | s | s | s | s | - | - | x |

Upper Triangle: $p < 0.05$; Lower Triangle: $p < 0.01$.

A main effect for joint ($F(1, 40) = 5.95$, $p < 0.02$) reflected the greater variability exhibited by the wrist (7.34) relative to the ankle (6.83). An interaction of joint with forearm position ($F(1, 40) = 10.21$, $p < 0.01$) was also present. The variability of the wrist exceeded that of the ankle by a margin of 1.19 when the forearm was supinated ($F(1, 40) = 15.88$, $p < 0.001$), whereas when the forearm was pronated they were essentially equivalent ($F < 1$).

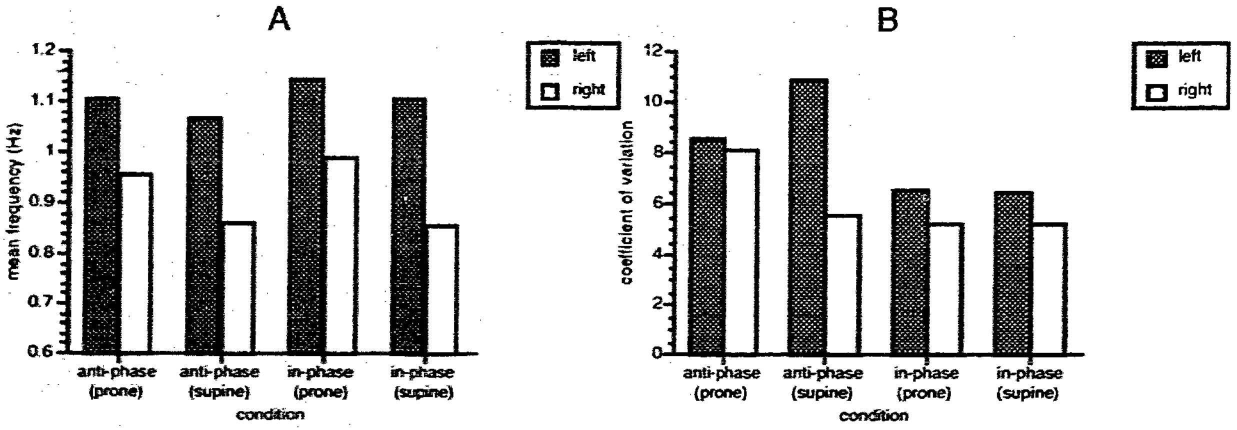

Fig. 3.11. Mean (A) and Coefficient of variation (B) discrete frequency for subject X in coupled conditions, shown as a function of side, mode and forearm position.

Subject: Y

Mean frequency:

Figure 3.12 illustrates that mean discrete frequencies in the coupled conditions were larger for the left side (0.94 Hz) than for the right side (0.89 Hz) ($F(1, 40) = 57.69$, $p < 0.0001$). Movements in the in-phase mode (0.93 Hz) exhibited higher frequencies than those in the anti-phase mode (0.90 Hz) ($F(1, 40) = 23.79$, $p < 0.0001$). Higher frequencies were also associated with those movements made with the forearm in a supinated position (0.92 Hz) compared to those made with the forearm pronated (0.90 Hz) ($F(1, 40) = 11.21$, $p < 0.01$). This effect was mediated by side. Movements of the left side (supine) exhibited higher frequencies than all other combinations ($p < 0.01$, Tukey HSD). The frequency of movement in the left side (prone) condition was also higher than that for the right side in both forearm position conditions ($p < 0.05$, Tukey HSD).

Coefficients of Variation:

The variability of discrete frequency, as reflected by coefficients of variation, was greater for movements of the left side (6.47) than those of the right side (5.20) ($F(1, 40) = 12.19$). Although the mean variability was apparently greater for movements in the anti-phase mode (6.14) compared to the in-phase mode (5.52), this tendency was not statistically significant ($p > 0.05$). An interaction of side and mode was noted ($F(1, 40) = 8.38$, $p < 0.01$). Decomposition of this interaction using the Tukey HSD procedure indicated that movements of the left side in the anti-phase mode exhibited greater variability ($p < 0.01$) than all other combinations of side and mode, which were essentially equivalent. This interaction is evident in Figure 3.12.

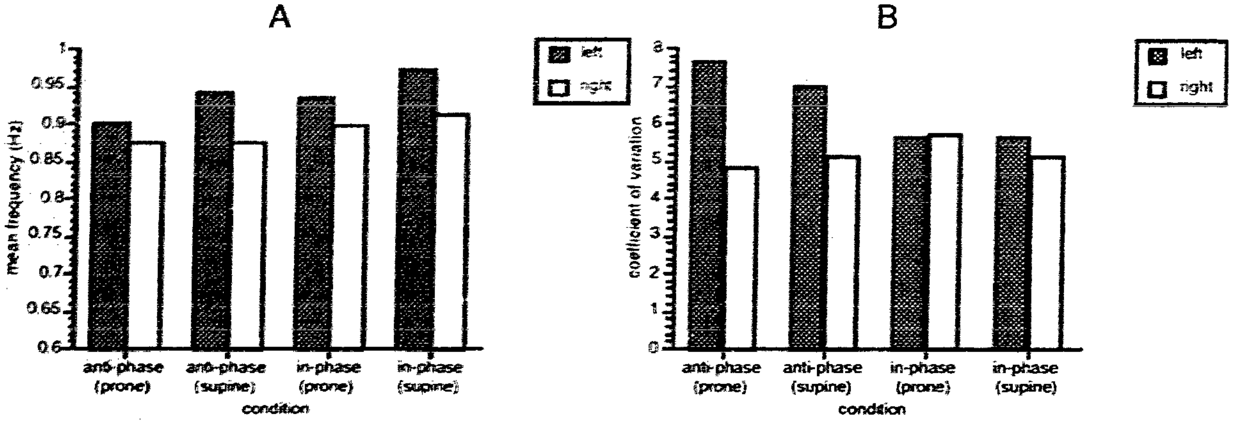

Fig. 3.12 Mean (A) and Coefficient of variation (B) discrete frequency for subject Y in coupled conditions, shown as a function of side, mode and forearm position.

Subject: Z

Mean frequency:

Mean discrete frequencies for coupled movements were higher for the right side (1.46 Hz) than for the left side (1.30 Hz) (F(1, 40) = 37.84, $p < 0.0001$). In addition, movements prepared in the in-phase mode (1.58 Hz) were characterized by higher preferred frequencies than movements prepared in the anti-phase mode (1.19 Hz) (F(1, 40) = 247.10, $p < 0.0001$). These factors also interacted to a statistically significant degree (F(1, 40) = 12.28, $p < 0.01$). Post hoc analysis of means using the Tukey HSD procedure indicated that the mean frequencies exhibited in the right in-phase condition were higher ($p < 0.01$) than in all other conditions. Also movements made in the left in-phase condition were characterized by frequencies that were higher than those observed in both anti-phase conditions ($p < 0.01$). Coupled movements performed with the forearm in a pronated position exhibited higher mean frequencies (1.43 Hz) than movements made with the forearm supinated (1.33 Hz) (F(1, 40) = 14.74, $p < 0.001$). There was an interaction of side and forearm position (F(1, 40) = 45.75, $p < 0.0001$). As Figure 3.13 illustrates, the frequencies exhibited in the left supine condition were on the average lower than in all other combinations of side and forearm position ($p < 0.01$, Tukey, HSD). The presence of two higher order interactions involving the factor of joint was noted. The three way interaction of mode of corrdination, forearm position and joint ($F(1, 40) = 6.17$, $p < 0.05$) indicated that the tendency for higher mean frequencies to be exhibited for the prone forearm position was more pronounced in the ankle joint in the anti-phase mode of coordination. This tendency was in turn somewhat more pronounced when movements were also performed by the left side ($F(1, 40) = 4.21$, $p < 0.05$).

Coefficients of Variation:

Coefficients of variation were larger for the left side (11.94) than the right side (8.90) ($F(1, 40) = 9.45$, $p < 0.01$). Greater variability was also exhibited in the anti-phase mode (14.13) relative to the in-phase mode (6.71) ($F(1, 40) = 56.24$, $p < 0.0001$).

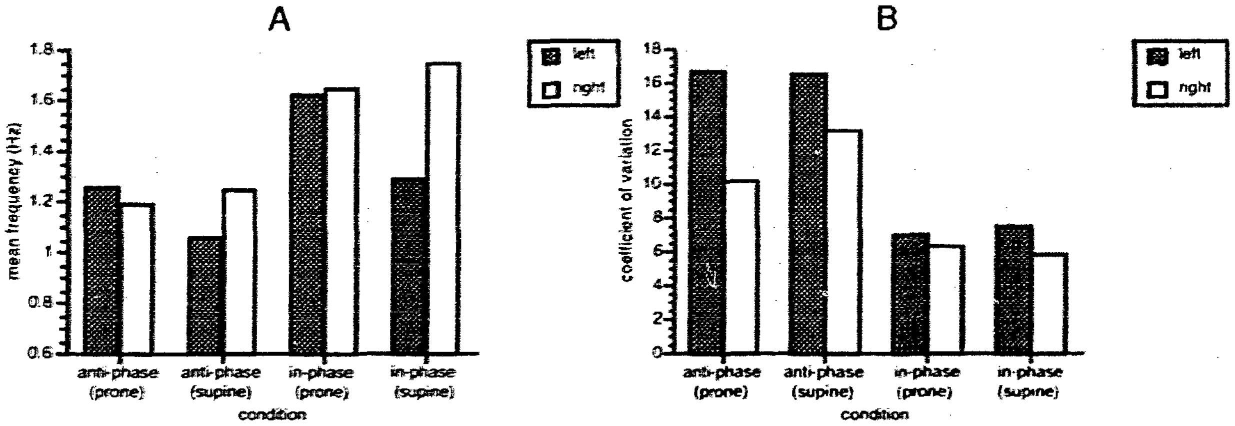

Fig. 3.13. Mean (A) and Coefficient of variation (B) discrete frequency for subject Z in coupled conditions, shown as a function of side, mode and forearm position.

TABLE 3.4 Summary table for Mean and Coefficients of Variation discrete frequency for all subjects (coupled conditions).

| | Effect | | | | | | |
|---|---|---|---|---|---|---|---|
| | side | | | mode | | | s x m |
| mean freq. | | | | | | | |
| W | left | < | right | anti-phase | < | in-phase | - |
| X | left | > | right | anti-phase | ≤ | in-phase | - |
| Y | left | > | right | anti-phase | < | in-phase | - |
| Z | left | < | right | anti-phase | < | in-phase | * |
| CV freq. | | | | | | | |
| W | left | ≥ | right | anti-phase | ≥ | in-phase | - |
| X | left | > | right | anti-phase | > | in-phase | - |
| Y | left | > | right | anti-phase | = | in-phase | * |
| Z | left | > | right | anti-phase | > | in-phase | - |

< and > indicate the direction of statistically significant ($p < 0.05$) main effects (see text for details)
≥ indicates the direction of main effect ($p = 0.07$) (see text for details)
* indicates the presence of statistically significant interaction (see text for details)

TABLE 3.5 Summary table for Mean and Coefficients of Variation discrete frequency for all subjects (coupled conditions).

| | Effect | | | | | |
|---|---|---|---|---|---|---|
| | forearm position | | | joint | | |
| mean freq. | | | | | | |
| W | prone | > | supine | wrist | = | ankle |
| X | prone | > | supine | wrist | ≠ | ankle |
| Y | prone | < | supine | wrist | = | ankle |
| Z | prone | > | supine | wrist | = | ankle |
| CV freq. | | | | | | |
| W | prone | = | supine | wrist | > | ankle |
| X | prone | = | supine | wrist | > | ankle |
| Y | prone | = | supine | wrist | = | ankle |
| Z | prone | = | supine | wrist | = | ankle |

< and > indicate the direction of statistically significant ($p < 0.05$) main effects (see text for details)

### 3.5.2 Discrete Relative Phase

The relative phase values obtained for each trial were tested for uniformity using the Rayleigh test (Mardia, 1972). It was confirmed for all subjects that for all trials the hypothesis of uniformity was rejected ($p < 0.01$) indicating that in every case there existed a dominant direction of relative phase. Test statistics for mean relative phase were calculated separately for anti-phase and in-phase trials. In the first instance, in order to compare left side to right side conditions, data were collapsed over forearm position. In the second instance, in order to compare forearm pronated to forearm supinated conditions, data were collapsed over side. In order to control for the potential inflation of Type I errors resulting from multiple comparisons, alpha was assigned as 0.01. In addition mean relative phase values were also assessed with respect to the target relative phase value for each mode of coordination. In performing these analyses, data were in the first instance pooled by collapsing over forearm position, and in the second instance by collapsing over side. Confidence intervals (99%) were calculated following Mardia (1972) (see also Batschelet. 1981). Analyses of variance for transformed uniformity scores were performed for each subject using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 2 forearm position (pronated, supinated) design. Each trial was treated as a single case.

#### Subject: W

#### Mean Relative Phase

In the anti-phase mode of coordination the mean value of relative phase exhibited by movements of the left side (164.8°) and the right side (171.9°) were different to a statistically significant degree from 180° ($p < 0.01$). When prepared in the in-phase mode of coordination the mean relative phase adopted for movements of the left side (352.1°) was reliably less than 0° ($p < 0.01$). The corresponding mean value for right side movements (358.6°) was not different from 0° ($p > 0.01$). Movements made with the forearm in a pronated position (170.9°) exhibited mean relative phase values different from 180° when prepared in the anti-phase mode ($p < 0.01$). This was also the case when the forearm was placed in a supinated position (165.8°) ($p < 0.01$). When prepared in the in-phase mode movements conducted with the forearm pronated (1.5°) were characterised by mean relative phase values which were essentially equivalent to 0° ($p > 0.01$) In contrast when the forearm was placed in a supinated position (349.1) mean relative phase values were reliably less than 0° ($p < 0.01$).

Mean relative phase values were essentially equivalent for movements of the left side and the right side both when movements were prepared in the anti-phase ($F(1, 22) = 6.41$, $p > 0.01$) and in the in-phase modes of coordination ($F(1, 22) = 3.48$, $p > 0.01$). In addition when movements were prepared in the anti-phase mode, the mean relative phase relation adopted when the forearm was pronated was equivalent to that adopted when the forearm was supinated ($F(1, 22) = 2.86$, $p > 0.01$). However, when prepared in the in-phase mode the mean phase relation exhibited when the forearm was in a pronated position differed to a statistically significant degree from the mean phase relation exhibited when the forearm was in a supinated position ($F(1, 22) = 21.79$, $p < 0.01$).

### Uniformity of Relative Phase

The measure of uniformity of relative phase failed to consistently distinguish between movements made by the left and right side ($p = 0.10$), and between movements prepared in the anti-phase and in-phase modes of coordination ($p > 0.20$).

## Subject: X

### Mean Relative Phase

The mean value of relative phase exhibited by movements of the left side (161.6°) and the right side (159.3°) were different to a statistically significant degree from 180° ($p < 0.01$) when prepared in the anti-phase mode of coordination. When prepared in-phase, mean relative phase values evident for movements of the left side (354.4°) were reliably less than 0° ($p < 0.01$). The corresponding mean value for right side movements (354.4°) was also different from 0° ($p < 0.01$).

Movements made with the forearm in a pronated position (160.8°) and in a supinated position (160.1°) exhibited mean relative phase values reliably different from 180° when prepared in the anti-phase mode ($p < 0.01$). When prepared in the in-phase mode, movements conducted with the forearm pronated (353.2°) were characterised by mean relative phase values which were consistently different from the target value of 0° ($p < 0.01$) This was not the case when the forearm was supinated (355.5°) ($p > 0.01$).

Mean relative phase values were essentially equivalent for movements of the left side and the right side both when movements were prepared in the anti-phase ($F < 1$) and in the in-phase modes of coordination ($F < 1$). In addition the mean relative phase relation adopted when the forearm was pronated was equivalent to that adopted when the forearm was supinated both when movements were prepared in the anti-phase ($F < 1$) and in-phase ($F < 1$) modes of coordination.

Uniformity of Relative Phase

Uniformity of relative phase was greater when movements were performed on the right side (2.64) compared to the left side (2.39) ($F(1, 40) = 29.00$, $p < 0.0001$). In addition, movements made in the in-phase (2.61) mode of coordination exhibited greater uniformity of relative phase than those prepared in the anti-phase mode (2.43) ($F(1, 40) = 14.27$, $p < 0.001$). Although movements made in each forearm position were not distinguished on the basis of uniformity ($p > 0.20$), a statistically significant interaction of side and forearm position was noted ($F(1, 40) = 8.01$, $p < 0.01$). It was evident that movements made by the left side when the forearm was supinated (2.29) exhibited less uniformity than movements in all other combinations ($p < 0.05$, Tukey HSD). Movements made by the left side when the was forearm pronated (2.49) were less consistent than movements made by the right side when the forearm was supinated (2.68) ($p < 0.05$, Tukey HSD), which were in turn not distinguished from those of the right side when the forearm was pronated (2.61).

Subject: Y

Mean Relative Phase

The mean values of relative phase exhibited by movements of the left side (166.7°) and the right side (172.6°) were both consistently different from the target value of 180° when prepared anti-phase ($p < 0.01$). When prepared in-phase, mean relative phase values evident for movements of the left side (357.4°) were not distinguished from 0° ($p > 0.01$). The corresponding mean value for right side movements (356.0°) was however different from 0° ($p < 0.01$). When prepared anti-phase mode, movements made with the forearm in a pronated position (171.4°) and in a supinated position (168.0°) exhibited mean relative phase values reliably different from 180° ($p < 0.01$). When prepared in-phase mode, movements conducted with the forearm pronated (359.7°) exhibited mean relative phase values which were essentially equivalent to the target value ($p > 0.01$). However when the forearm was supinated (353.7°) movements were characterised by mean relative phase values which were consistently different from 0° ($p < 0.01$).

Mean relative phase values were essentially equivalent for movements of the left side and the right side both when movements were prepared in the anti-phase ($F(1, 22) = 7.14$, $p > 0.01$) and in the in-phase modes of coordination ($F < 1$). In addition the mean relative phase relation adopted when the forearm was pronated was equivalent to that adopted when the forearm was supinated both when movements were prepared in the anti-phase ($F(1, 22) = 1.90$, $p > 0.01$) and in-phase ($F(1, 22) = 7.90$, $p > 0.01$) modes of coordination.

Uniformity of Relative Phase

Movements of the right side (2.75) were characterized by a higher degree of uniformity than those of the left side (2.51) ($F(1, 40) = 27.95$, $p < 0.0001$). As is revealed by inspection of Figure 3.14, the magnitude of this difference was contingent upon the mode of coordination in which the movements were prepared ($F(1, 40) = 4.70$, $p < 0.05$). Pairwise comparison of means using the Tukey HSD procedure indicated that movements of the left side prepared in the anti-phase (2.45) mode evidenced less uniformity than movements of the right side in both the in-phase

(2.71) and anti-phase (2.78) modes ($p < 0.05$). Movements of the left side prepared in the in-phase mode (2.57) were less consistent than those of the right side in the anti-phase mode ($p < 0.05$).

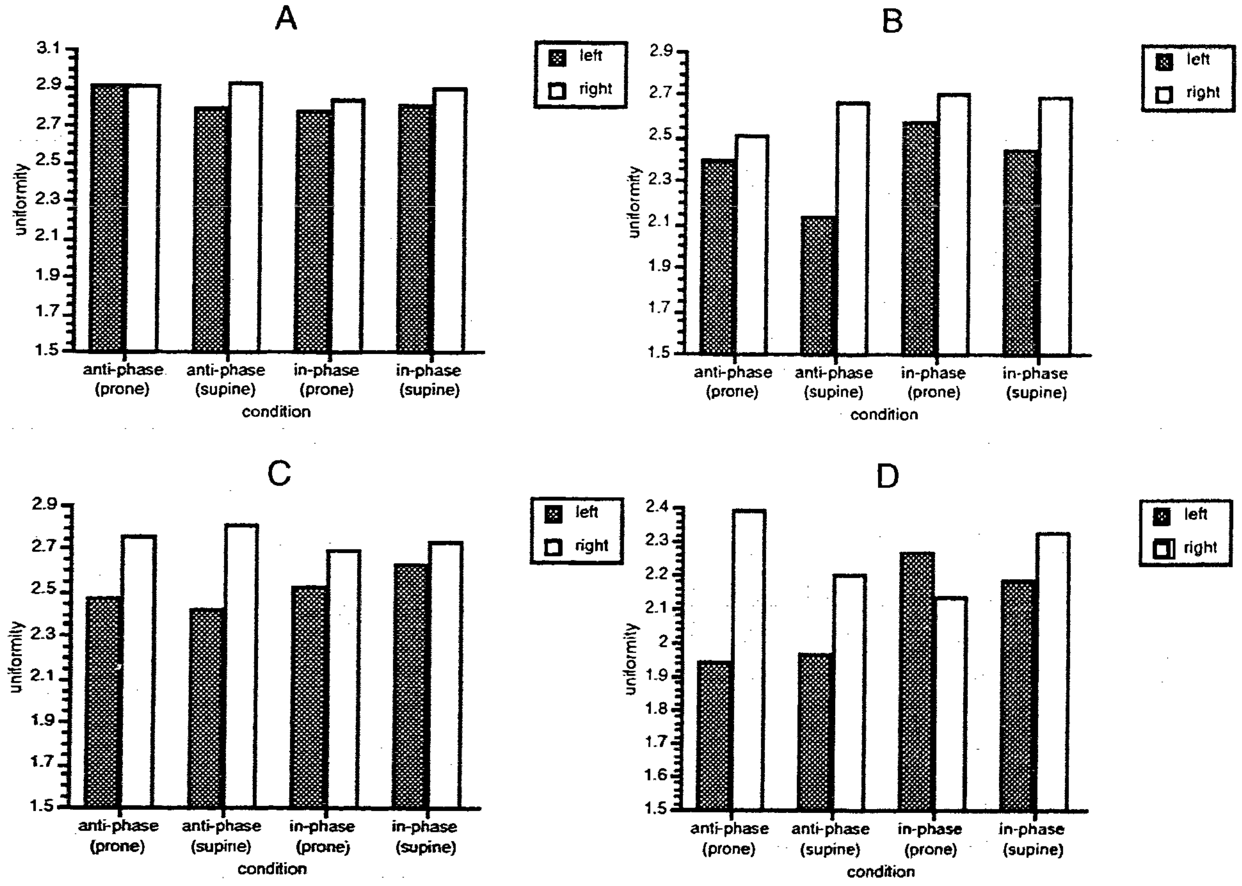

Fig. 3.14. Mean uniformity for subject W (A), X (B), Y (C), Z (D) in coupled conditions, as a function of side, mode and forearm position.

Subject: Z

Mean Relative Phase

When prepared in the anti-phase mode of coordination, the mean values of relative phase exhibited by movements of the left side (173.1°) and the right side (184.7°) were equivalent to 180° ($p > 0.01$). When prepared in-phase, mean relative phase values evident for movements of the left side (10.2°) and the right side (13.0°) were appreciably greater than 0° ($p < 0.01$). When prepared anti-phase mode, movements made with the forearm in a pronated position (184.7°) were reliably greater than 180° ($p < 0.01$), whereas those made with the forearm in a supinated position (173.1°) were not different from the target value ($p > 0.01$). When prepared in the in-phase mode, movements conducted with the forearm pronated (9.2°) and with the forearm supinated (14.0°) exhibited mean relative phase values which were reliably greater than the target value ($p < 0.01$). Mean relative phase values were essentially equivalent for movements of the left side and the right side both when movements were prepared in the anti-phase ($F(1, 22) = 5.97$, $p > 0.01$) and in the in-phase modes of coordination ($F < 1$). In addition the mean relative phase relation adopted when the forearm was pronated was equivalent to that adopted when the forearm was supinated both when movements were prepared in the anti-phase ($F(1, 22) = 6.00$, $p > 0.01$) and in-phase ($F(1, 22) = 1.22$, $p > 0.01$) modes of coordination.

### Uniformity of Relative Phase

Movements of the right side (2.26) exhibited greater uniformity of relative phase than movements of the left side (2.09) ($F(1, 40) = 5.81$, $p < 0.05$). As is illustrated by Figure 3.14, the magnitude of this difference was contingent upon the mode of coordination in which the movements were prepared ($F(1, 40) = 5.61$, $p < 0.05$). Pairwise comparison of means using the Tukey HSD procedure indicated that movements of the left side prepared in the anti-phase (1.96) mode evidenced less uniformity than movements movements of the left side prepared in the in-phase (2.23) mode and of the right side in both the in-phase (2.23) and anti-phase (2.30) modes ($p < 0.05$).

TABLE 3.6 Summary table for Mean Relative Phase for all subjects.

| | Effect | |
|---|---|---|
| | side | forearm position |
| mean relative phase | | |
| anti-phase | | |
| W | (left < 180°) = (right < 180°) | (prone < 180°) = (supine < 180°) |
| X | (left < 180°) = (right < 180°) | (prone < 180°) = (supine < 180°) |
| Y | (left < 180°) = (right < 180°) | (prone < 180°) = (supine < 180°) |
| Z | (left = 180°) = (right = 180°) | (prone > 180°) = (supine = 180°) |
| in-phase | | |
| W | (left < 0°) = (right = 0°) | (prone = 0°) > (supine < 0°) |
| X | (left < 0°) = (right < 0°) | (prone < 0°) = (supine < 0°) |
| Y | (left = 0°) = (right < 0°) | (prone = 0°) = (supine < 0°) |
| Z | (left > 0°) = (right > 0°) | (prone > 0°) = (supine > 0°) |

< and > indicate the direction of statistically significant main effects or comparisons (p < 0.05) (see text for details)

TABLE 3.7 Summary table for Uniformity Relative Phase for all subjects.

| | Effect | | | | | | |
|---|---|---|---|---|---|---|---|
| | | side | | | mode | | s x m |
| Consistency | | | | | | | |
| W | left | = | right | anti-phase | = | in-phase | - |
| X | left | < | right | anti-phase | < | in-phase | - |
| Y | left | < | right | anti-phase | = | in-phase | * |
| Z | left | < | right | anti-phase | = | in-phase | * |

< indicates the direction of a statistically significant (p < 0.05) main effect (see text for details)
* indicates the presence of statistically significant interaction (see text for details)

## 3.6 EMG (coupled trials)

### 3.6.1 Discrete Frequency:

Independent analyses of variance for coefficients of variation (CV) were performed for each subject using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 2 forearm position (pronated, supinated) by 2 joint (wrist, ankle) design. Each trial was treated as a single case. Side, mode of coordination, and forearm position were grouping factors, joint was a within case factor. Planned orthogonal comparisons of means were performed to highlight a limited number of preselected contrasts.

Subject: W

Coefficients of variation were larger for the left side (8.95) than the right side (6.35) ($F(1, 40) = 5.48$, $p < 0.05$). Greater variability was also exhibited in the anti-phase mode (8.96) relative to the in-phase mode (6.35) ($F(1, 40) = 5.50$, $p < 0.05$). The differences between movements of the left and right side were exhibited when movements were prepared in the anti-phase mode ($F(1, 40) = 4.65$, $p < 0.05$), and not when movements were prepared in the in-phase mode ($F(1, 40) = 1.33$, $p > 0.20$).

Subject: X

Coefficients of variation were larger for the left side (12.22) than the right side (6.43) ($F(1, 40) = 48.18$, $p < 0.0001$). Greater variability was also exhibited in the anti-phase mode (10.59) when compared with the in-phase mode (8.06) ($F(1, 40) = 9.26$, $p < 0.01$). Differences between movements of the left and right side were present both when movements were executed in the anti-phase ($F(1, 40) = 32.41$, $p < 0.0001$) and in the in-phase ($F(1, 40) = 17.00$, $p < 0.001$) modes of coordination.

Subject: Y

Movements made by the left (6.15) and right (5.98) sides were not distinguished in terms of coefficients of variation ($F < 1$). Similarly movements prepared in the anti-phase (6.04) and in-phase (6.09) modes of cooridnation were equivalent with respect to this measure ($F < 1$). There was also no interaction of these factors, as indicated by the absence of differences between movements of the left and right sides in both modes of coordination ($F < 1$).

Subject: Z

Movements prepared in the anti-phase mode (21.11) were associated with larger coefficients of variation than those in the in-phase mode (6.28) ($F(1, 20) = 33.66$, $p < 0.0001$).

### 3.6.2 Discrete Relative Phase

Analyses of variance for transformed uniformity scores were performed for each subject using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 2 forearm position (pronated, supinated) design. Each trial was treated as a single case. Planned orthogonal comparisons of means were performed to highlight a limited number of preselected contrasts. Values reported in the text correspond to transformed uniformity scores.

Subject: W

Uniformity of relative phase was lower for movements of the left (2.30) and right side (2.53) ($F(1, 40) = 21.41$, $p < 0.0001$). Movements made in the in-phase (2.40) and anti-phase (2.53) modes were equivalent in terms of this measure ($F < 1$). Movements performed by the left and right side were distinguished both when conducted in the anti-phase ($F(1, 40) = 13.12$, $p < 0.001$) and in-phase modes of coordination ($F(1, 40) = 8.53$, $p < 0.01$).

Subject: X

Movements of the left side (2.13) were associated with lower uniformity values than those of the right side (2.53) ($F(1, 40) = 26.14$, $p < 0.0001$). Uniformity of relative phase was also lower for movements conducted in the anti-phase mode (2.25) than those conducted in the in-phase mode (2.42) ($F(1, 40) = 4.45$, $p < 0.05$). The difference in uniformity values between movements of the left and right side was evident when movements were conducted in the anti-phase ($F(1, 40) = 24.88$, $p < 0.0001$) and the in-phase ($F(1, 40) = 5.03$, $p < 0.05$) modes of coordination.

Subject: Y

Measures of uniformity were equivalent for movements conducted by the left (2.66) and right (2.64) sides ($F < 1$), and for movements in the anti-phase (2.68) and in-phase (2.63) modes of coordination ($F< 1$). Movements of the left and right sides were not dissociable by this measure when prepared anti-phase ($F < 1$) or in-phase ($F < 1$).

Subject: Z

Movements prepared in the anti-phase mode (1.60) were associated with lower uniformity values than those prepared in the in-phase mode (2.40) ($F(1, 20) = 44.66$, $p < 0.0001$).

## 3.7 Summary and Discussion

### 3.7.1 Single joint trials.

There was little evidence to suggest the expression of asymmetries in the mean preferred frequencies of oscillation for movements of the wrist or the ankle. Subjects were as likely to exhibit higher preferred frequencies for movements of the left side as for the right side. Consideration of the variability of the elicited frequencies proved to be marginally more revealing. Where asymmetries were present, in two of the four subjects, larger coefficients of variation were associated with movements of joints on the left side. It was of some interest to determine whether the preferred frequencies of oscillation for movements of the ankle joint in isolation differed from the frequencies of movements of the wrist either when the forearm was in a pronated or supinated position. It has been suggested that preferred frequencies for single joint motion provide an index of the characteristic frequency (e.g., Schmidt et al., 1991; Turvey et al., 1989) or eigen frequency (e.g., Jeka, 1992) of the oscillator constituted by the CNS-muscle-joint complex (cf., Carson et al., in press). In three subjects, preferred frequencies for movements of the ankle were higher than for movements of the wrist, when the forearm was placed in a supinated position. The frequencies exhibited for movements of the wrist when the forearm was pronated were intermediate. Coefficients of variation for movements of the wrist were uninfluenced by the position of the forearm. However, in three subjects the degree of variability was different for movements of the ankle and of the wrist. The direction of these effects was inconsistent and it is doubtful whether any particular significance can be attached to these data.

### 3.7.2 Coupled Trials

The asymmetries expressed in terms of mean frequency, which were present for two subjects in the single joint trials, were reproduced for coupled movements. The two subjects who failed to exhibit differences in the single joint conditions, did so in the coupled conditions. Overall, two subjects presented preferred frequencies which were higher for movements of the right side, while two subjects presented frequencies which were higher for the left side. All subjects exhibited higher coefficients of variation for discrete frequency for movements of the left side. Two of three subjects for whom this comparison could be made, also exhibited higher coefficients of variation for the left side when movement onsets were defined in terms of EMG activity. These data suggest that asymmetries, latent in single joint movements, were elicited only when the additional requirement of interlimb coordination was imposed.

The mode of coordination in which the system was prepared had a consistent influence upon both the mean frequency of oscillation and its associated variability. Preferred frequencies were lower in the anti-phase mode than in the in-phase mode. Where differences were present, the variability of frequency was greater for movements prepared anti-phase. This was also found to be the case, in three of four subjects, when movement onsets were defined in terms of EMG activity. In general, the highest frequencies were exhibited in conditions in which the forearm was placed in a pronated position, although for a single subject the reverse was true. In contrast, the position of the forearm failed to influence the variability of frequency. In two of the four subjects, coefficients of variation for movements of the ankle were larger than for those of the wrist.

While subjects apparently experienced little difficulty in maintaining the prescribed modes of coordination, systematic deviations from the required value of relative phase were observed. When instructed to maintain an anti-phase mode of coordination, mean relative phase values were consistently below 180°, in three of four subjects. These data suggest that the ankle lagged the wrist to a greater degree than was prescribed. This characteristic was evident in movements of both sides, and when the forearm was placed in the pronated and supinated positions. When instructed to maintain an in-phase mode of coordination, three subjects exhibited relative phase values which deviated systematically from the target value. These trends were again generally present for movements of both sides and for both forearm positions.

Side of movement had reliable influence upon the uniformity of discrete relative phase. In three of four subjects, the degree of uniformity was smaller for movements of the left side. In two of these subjects this effect was further influenced by the mode of coordination in which the system was prepared. The smaller degree of uniformity associated with movements of the left side was most clearly expressed when these movements were conducted in the anti-phase mode. In two of three subjects, measures of uniformity based upon EMG activity were also smaller for movements of the left side. It was generally the case that the uniformity of relative phase was equivalent for movements prepared in the in-phase and anti-phase modes. One subject evidenced a smaller degree of uniformity for the anti-phase mode, both when movements were defined in terms of kinematic and EMG indices. The position of the forearm had essentially no bearing on these measures.

When measures of variability, whether defined at the level of the joint kinematics or the EMG, distinguished movements made by the left and right sides, the left side was in every instance more variable. These data are consistent with those obtained using other rhythmic tasks such as tapping. It was notable that differences were present in the absence of the requirement for maximal rates of response (cf. Hammond et al., 1988). In the coupled trials in which the constraint of absolute coordination was imposed, the prescribed relative phase relationship was equally well satisfied for movements of both sides. Thus, differences in uniformity between the left and right sides could not be ascribed to "trade-offs" between maintainence of the appropriate phase relation and the variability of relative phase. Similarly, while oscillation frequencies were more variable for movements of the left side, the number of subjects exhibiting higher preferred frequencies for movements of the left side was equal to the number showing higher frequencies for the right hand.

# 4 Experiment 2

## 4.1 Introduction

In extant modelling of the dynamics of human coordinative systems (e.g., Haken et al., 1985) the instantiation of control parameters has been treated as formally distinct from order parameter dynamics. Control parameters such as oscillation frequency are deemed nonspecific with respect to order parameter dynamics. Although fluctuations arising from noise in the control parameter are predicted to imbue fluctuations in the order parameter (Haken & Wunderlin, 1990), dynamics are not generally ascribed to the control parameter. That is, changes in the parametric influence are not anticipated to occur on the same time scale as fluctuations of the order parameter.

Stochastic fluctuations of the order parameter, arising from the interaction of many subsystems assume technical and conceptual importance (Kelso & Ding, in press; Schöner, Haken, & Kelso, 1986). In contrast, the implications of fluctuations in the instantiation of control parameter regimes lack adequate theoretical treatment. Clearly in an experimental context, when movements are self paced or externally paced, the frequency of oscillation is not stationary over time but rather exhibits some degree of variability. Thus there exists variability in the instantiation of what is ostensibly the control parameter. It has been demonstrated that, in bimanual coordination, there is an association between variability of oscillation frequency and variability of the order parameter relative phase (Byblow et al., submitted). It remains to be determined whether these fluctuations of the order parameter impinge upon the dynamics and upon time scales relations in the same fashion as predicted for fluctuations arising from interactions of the component subsystems. It is also not clear whether, in an experimental context, the control parameter is best represented by the externally administered pacing frequency or by the instantiated oscillation frequency.

In Experiment 1 it was demonstrated that, in coupled movements, there exist differences between movements of the left and right sides in terms of the variability of spontaneously elicited oscillation frequencies and the variability of relative phase. The question arises as to whether the larger degree of variability evident for movements of the left side engenders greater variability in the implementation of externally provided frequency regimes. There exists evidence to suggest that the left hand is generally more variable in following a pacing signal and in reproducing a simple rhythm (Wolff, 1977; Wolff, Hurwitz, & Moss, 1977).

When coordinative systems are "driven" in some fashion, the pattern of successive response intervals or cycle durations exhibits a fine structure which is contingent upon both the nature of the movement response and of the driving signal. For example, the degree of compliance with predictions of negative lag 1 autocorrelations of response intervals (Wing & Kristofferson, 1973), and the means by which changes in response interval durations are effected, are dependent upon whether movements are conducted in the induction or continuation phase of the protocol (Wrisberg & Liemohn, 1990). Movements made by individuals swinging wrist pendulums, following the protocol introduced by Kugler and Turvey (1987), yield response intervals which are in accordance with the predictions of the Wing and Kristofferson model (e.g., Turvey, Schmidt & Rosenblum, 1989). This may be due in large part to the physical properties of the compound system, and in particular the amplitude-frequency relations which characterize pendular motion. Movements made under the bimanual (Kelso, 1981, 1984) and unimanual (Kelso, Buchanan, & Wallace, 1991) protocols fail to comply with the predictions of the Wing and Kristofferson model (Byblow, unpublished data; Carson, unpublished data). The present experiment was therefore conducted to determine whether the asymmetries revealed by the use of a self-paced protocol (Experiment 1) would be reproduced when subjects were required to follow an external pacing signal. External pacing was provided at two frequencies, at 1 Hz which approximated the preferred frequencies of oscillation observed in coupled conditions in Experiment 1, and also at 2 Hz.

## 4.2 Methodology

Procedure

Subjects performed paced oscillatory motions of the wrist and foot commencing in two modes of coordination, in-phase and anti-phase. Pacing was provided by means of an auditory metronome at two frequencies, 1Hz and 2 Hz. These movements were performed with the forearm either in a supine or a prone position. In all conditions, emphasis was placed upon maintainence of a 1:1 frequency relation with the auditory metronome.

In the in-phase (forearm supinated) mode, flexion (extension) of the wrist was required to be coincident with dorsi-flexion (plantar-flexion) of the foot . In the anti-phase (forearm supinated) mode, flexion (extension) of the wrist was required to be coincident with plantar-flexion (dorsi-flexion) of the foot. In the in-phase (forearm prone) mode, flexion (extension) of the wrist was required to be coincident with plantar-flexion (dorsi-flexion) of the foot . In the anti-phase (forearm prone) mode, flexion (extension) of the wrist was required to be coincident with dorsi-flexion (plantar-flexion) of the foot.

In each forearm position, trials alternated between in-phase and anti-phase trials, commencing with an in-phase trial. Blocks of trials for which the forearm was placed in a supinated position preceded those in which the forearm was in a prone position. For each forearm position, a block of trials at 1 Hz preceded a block of trials at 2 Hz. Thus, for each side (left or right), four blocks of trials were performed, one for each combination of forearm position and oscillation frequency. Eight trials were performed in each block (four in each coordination mode) for a grand total of 64 trials. In all conditions, subjects were permitted one practice trial. Two subjects first performed all trials for the left side followed by all trials for the right side. For the other two subjects, the order was reversed.

Subjects were instructed to maintain a 1:1 frequency relation with the auditory metronome. They were also made aware that, should the pattern of coordination begin to change, they were to attempt to maintain the initial mode of coordination. Subjects were given no direction concerning the temporal locus of the metronome pulse with respect to the movement cycle. Rather, individuals were free to establish their own metronome-movement cycle coordinative pattern, subject to the constraint of isofrequency coordination.

Trials commenced with 2 seconds of "lead-in" metronome pulses (two pulses at 1 Hz, four pulses at 2 Hz) at which point the initiation of data collection was automatically triggered. A reference pulse was output to one channel of the A/D unit following 1 second of data collection. This pulse was included for the purposes of data analysis to indicate the start of a 30 second data window. A second reference pulse marked the end of this window. Data collection was terminated 1 second following the second reference pulse. One second of "lead-out" pulses followed to ensure that any anticipation of the end of the trial occurred following the termination of data collection.

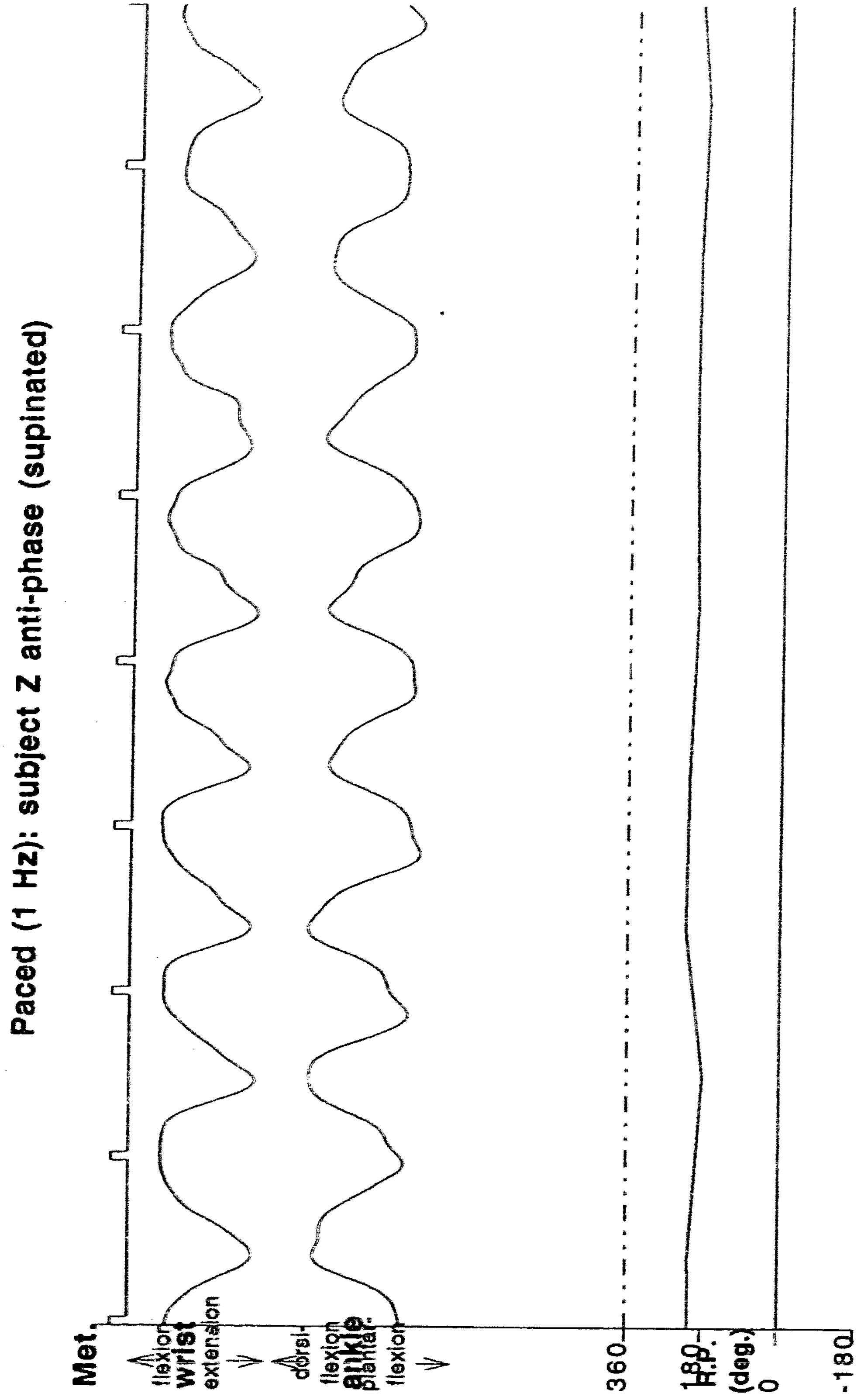

Fig. 4.1 Sample time series of a movement prepared in the anti-phase mode and paced at a frequency of 1 Hz with the forearm in a supinated position (subject Z).

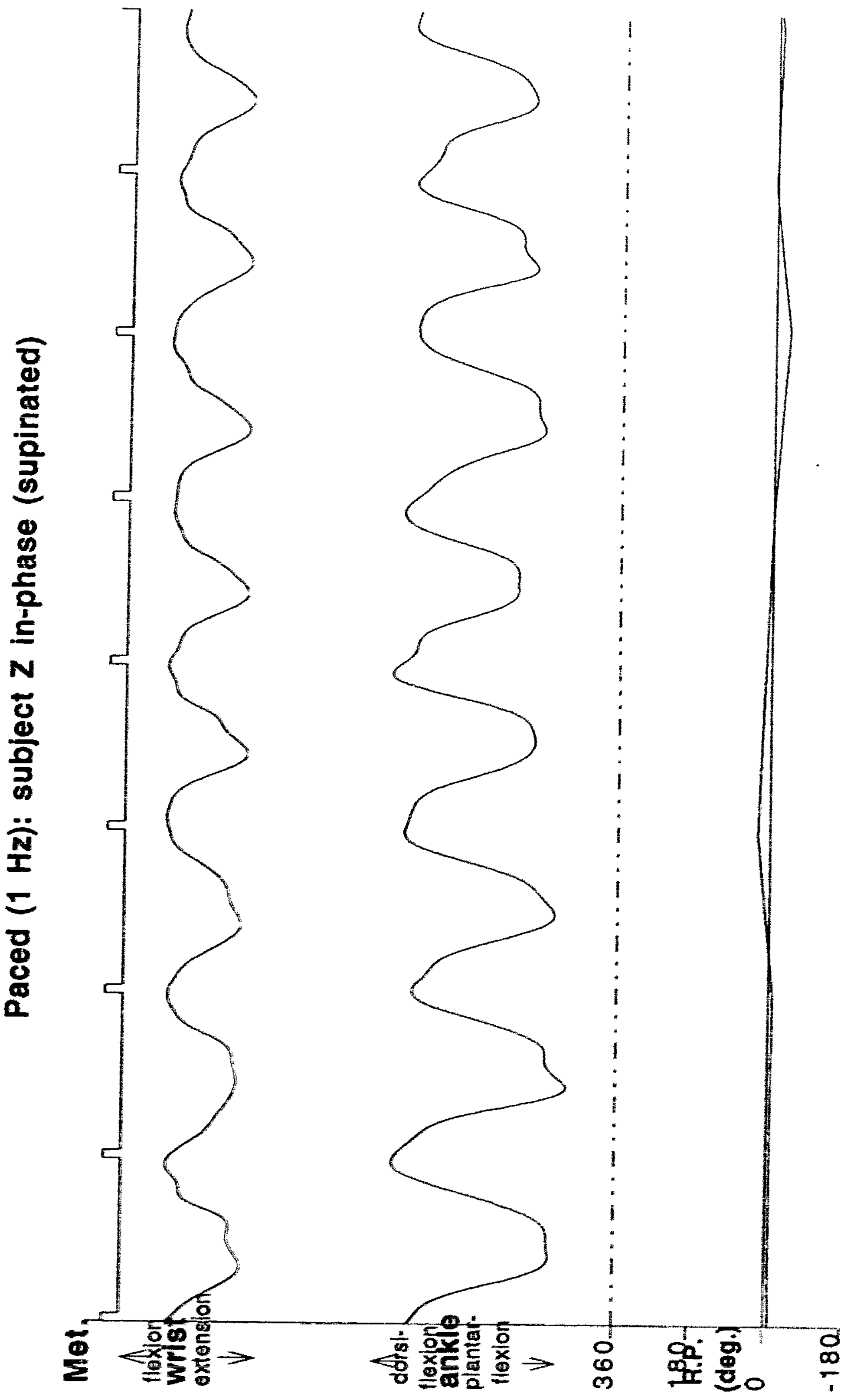

Fig. 4.2 Sample time series of a movement prepared in the in-phase mode and paced at a frequency of 1 Hz with the forearm in a supinated position (subject Z).

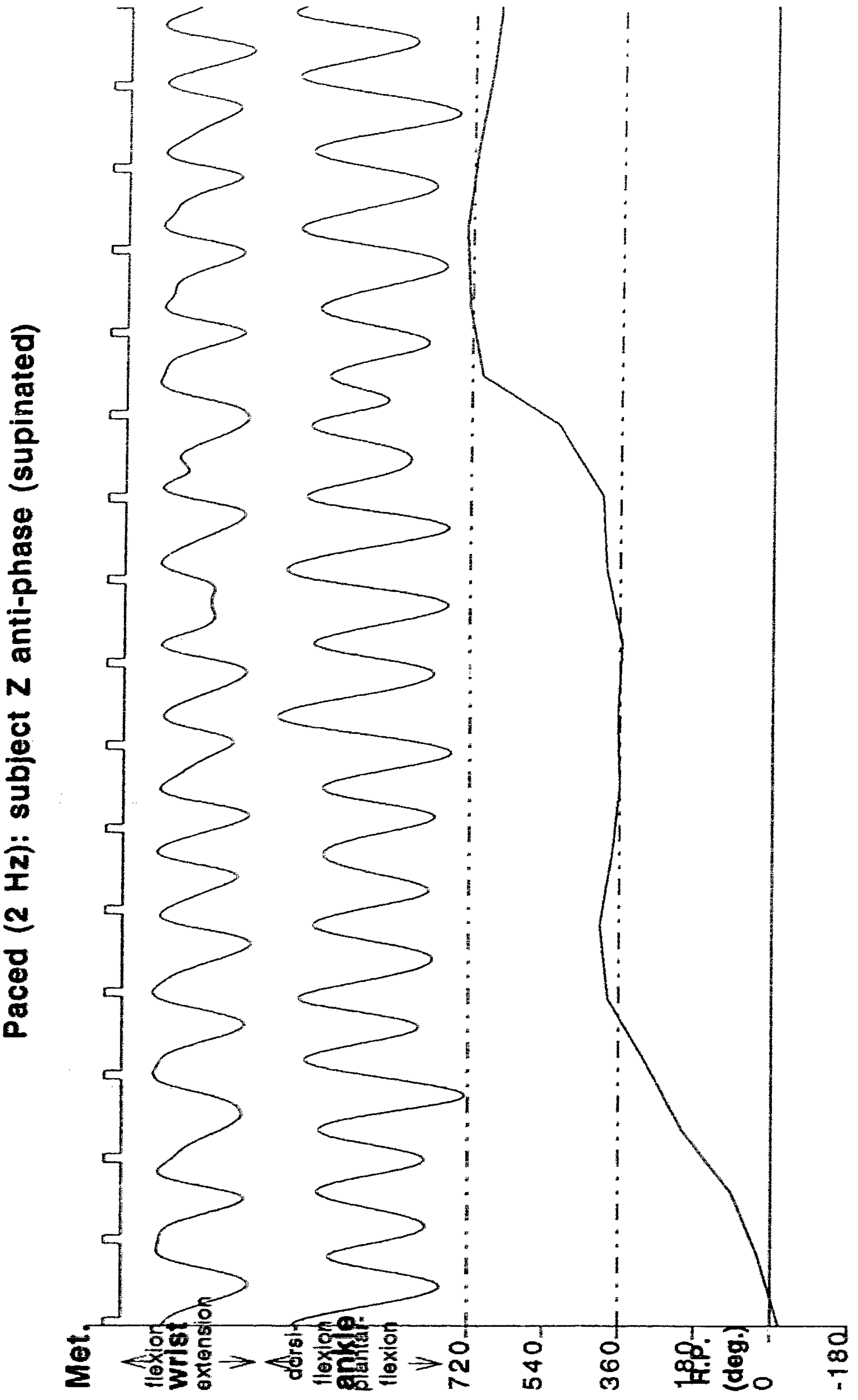

Fig. 4.3 Sample time series of a movement prepared in the anti-phase mode and paced at a frequency of 2 Hz with the forearm in a supinated position (subject Z).

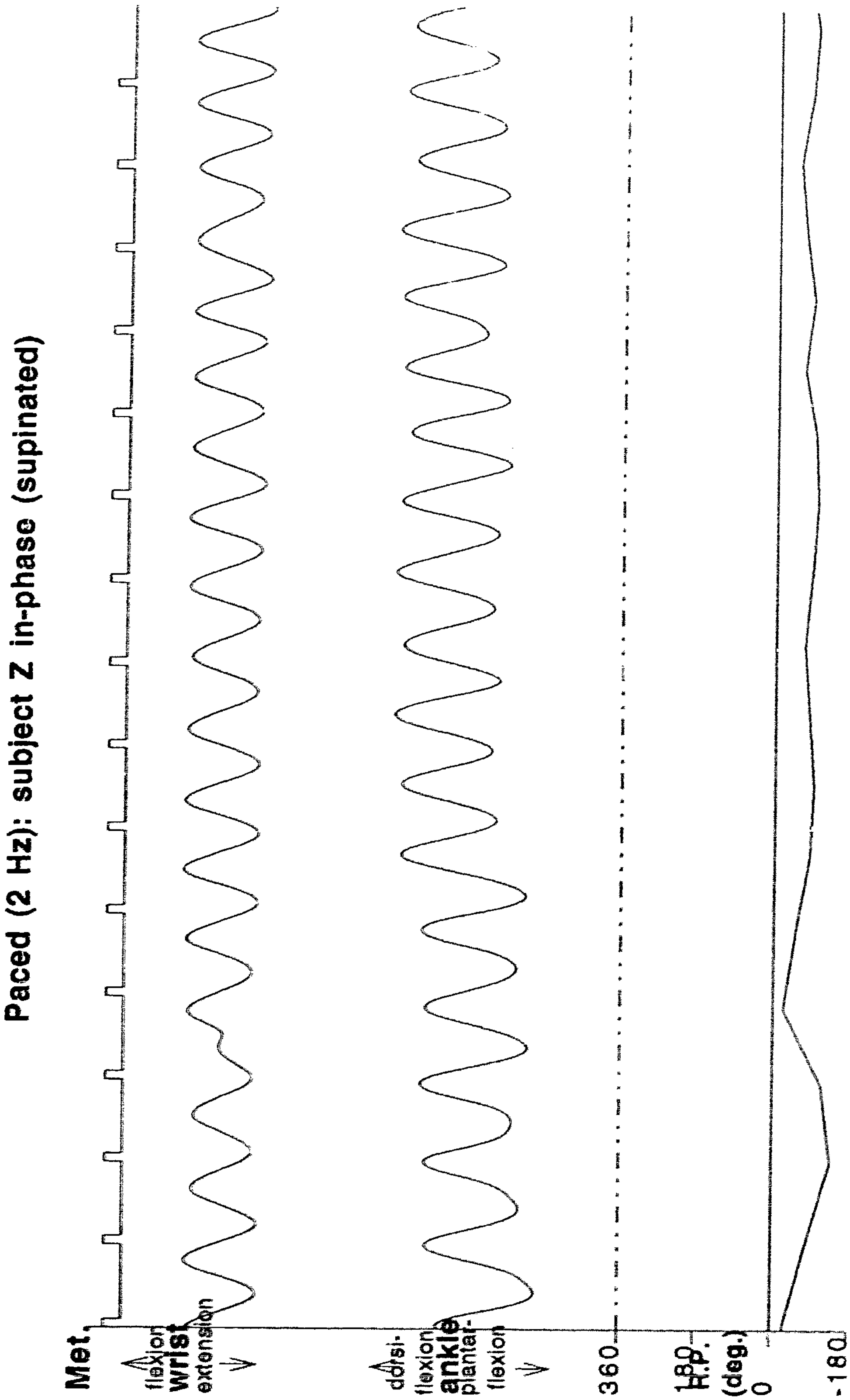

Fig. 4.4 Sample time series of a movement prepared in the in-phase mode and paced at a frequency of 2 Hz with the forearm in a supinated position (subject Z).

## 4.3 Results

### 4.3.1 Metronome Limb Relations

As a preliminary means of estimating the extent to which subjects maintained the required frequency relation, Pearson product-moment correlations between individual limb frequencies and metronome frequencies were calculated. Data from each joint and from trials in each forearm position were pooled for the purposes of these analyses. Thus measures of association were available for each side in each mode of coordination and at each metronome frequency. It was noted that in all instances (all subjects in all conditions) the degree of correlation exceeded 0.99. Although these data indicate that within conditions there was a high degree of consistency, inspection of the mean frequencies suggested that between conditions there existed systematic differences in the degree of deviation from the metronome frequency. In order to examine these tendencies in greater detail, a frequency deviation score was calculated for each trial. This score reflected the absolute difference between the mean frequency for that trial and the metronome frequency, expressed as a function of the metronome frequency. The resulting percentage deviation scores were treated to promote homogeneity of variance using an arc sine transformation (Myers, 1979) and analysed using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 2 frequency (1 Hz, 2 Hz) by 2 forearm position (pronated, supinated) by 2 joint (wrist, ankle) design. Each trial was treated as a single case. Side, mode of coordination, frequency and forearm position were grouping factors, joint was a within case factor. Planned orthogonal comparisons of means were performed to highlight a limited number of preselected contrasts. Mean values reported in the text correspond to untransformed percentage scores.

Subject: W

Overall, deviation scores were equivalent for movements paced at 1 Hz (0.25%) and those paced at 2 Hz (0.81%) ($F(1, 48) = 2.38$, $p > 0.10$). Further contrasts were performed to examine possible interactions between the factors of side, mode of coordination and pacing frequency. It was determined that movements paced at 1 Hz did not differ from those paced at 2 Hz in terms of deviation from the metronome when executed by the right side and prepared in either the anti-phase ($F < 1$) or in-phase ($F < 1$) mode of coordination. In comparison, movements of the left side which were paced at 1 Hz (0.23%) deviated less from the metronome frequency than those paced at 2 Hz (2.61%) ($F(1, 48) = 14.59$, $p < 0.001$) in the anti-phase mode of coordination. For left side movements in the in-phase mode, the degree of deviation was essentially the same when movements were paced at 1 Hz and 2 Hz ($F < 1$).

Subject: X

It was noted that the degree of deviation from the metronome frequency was larger when movements were paced at 2 Hz (4.25%) relative to when movements were paced at 1 Hz (0.50%) ($F(1, 47) = 91.58$, $p < 0.0001$). This effect was present for movements of the left side prepared in both the anti-phase ($F(1, 47) = 36.81$, $p < 0.0001$) and in-phase ($F(1, 47) = 6.67$, $p < 0.02$) modes of coordination. When movements of the right side were prepared in the anti-phase mode, devation from the metronome frequency was larger when movements were paced at 2 Hz (8.66%) compared to when paced at 1 Hz (0.40%). In contrast when prepared in the in-phase mode, movements of the right side deviated from the metronome frequency to an equivalent degree when paced at 1 Hz and 2 Hz ($p > 0.15$).

Subject: Y

When paced at 2 Hz (4.60%) deviations from the metronome frequency were greater than when movements were paced at 1 Hz (0.56%) ($F(1, 48) = 207.63$, $p < 0.0001$). This effect was evident for the left side ($F(1, 48) = 266.82$, $p < 0.0001$) and the right side ($F(1, 48) = 217.64$, $p < 0.0001$) when these movements were prepared in the anti-phase mode of coordination. When movements of both the left and the right side were prepared in-phase the effect of pacing frequency was not present to a statistically significant degree ($p > 0.05$, and $F < 1$ respectively).

Subject: Z

The degree of deviation from the metronome frequency was larger when movements were paced at 2 Hz (12.00%) relative to when movements were paced at 1 Hz (1.21%) ($F(1, 48) = 139.34$, $p < 0.0001$). This effect was evident for the left side ($F(1, 48) = 25.23$, $p < 0.0001$) and the right side ($F(1, 48) = 59.23$, $p < 0.0001$) when these movements were prepared in the anti-phase mode, and for the left side ($F(1, 48) = 17.89$, $p < 0.0001$) and the right side ($F(1, 48) = 44.34$, $p < 0.0001$) when these movements were prepared in the in-phase mode of coordination.

### 4.3.2 Discrete Frequency:

Independent analyses of variance for mean preferred frequency and coefficient of variation (CV) were performed for each subject using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 2 frequency (1 Hz, 2 Hz) by 2 forearm position (pronated, supinated) by 2 joint (wrist, ankle) design. Each trial was treated as a single case. Side, mode of coordination, frequency and forearm position were grouping factors, joint was a within case factor. Planned orthogonal comparisons of means were performed to highlight a limited number of preselected contrasts.

Subject: W

Mean frequency:

The average mean frequency adopted was equivalent for the left (1.00 Hz) and right side (1.00 Hz) when movements were paced at a frequency of 1 Hz ($F < 1$). However when movements were paced at 2 Hz, the mean frequency exhibited by movements of the right side (2.00 Hz) was distinguished from the frequency of movements of the left side (1.98 Hz) ($F(1, 48) = 5.44$, $p < 0.05$). For movements paced at 1 Hz, the average frequency was equivalent for movements prepared in the anti-phase (1.00 Hz) and in-phase (1.00 Hz) modes of coordination ($F < 1$). In contrast when paced at 2 Hz movements prepared in the anti-phase mode (1.98 Hz) exhibited lower mean frequencies than those prepared in the in-phase mode (2.00 Hz) ($F(1, 48) =$

5.00, $p < 0.05$). It was noted that when movements were paced at 1 Hz the frequency of movements made by the left side did not differ from the frequency of those made by the right side when prepared in either the anti-phase or in-phase mode of coordination ($F < 1$). When paced at 2 Hz and prepared anti-phase, movements of the left side (1.96 Hz) were characterised by lower mean frequencies than movements of the right side (2.00 Hz) ($F(1, 48) = 10.54$, $p < 0.01$). When paced at 2 Hz and prepared in-phase movements of the left side (2.00 Hz) and of the right side (2.00 Hz) were indistinguishable in terms of mean frequency ($F < 1$).

Coefficients of Variation:

Coefficients of variation were larger for the left side (4.69) than the right side (3.61) ($F(1, 48) = 5.28$, $p < 0.05$). Greater variability was also exhibited in the anti-phase mode (4.91) relative to the in-phase mode (3.39) ($F(1, 48) = 10.40$, $p < 0.01$). As is apparent from inspection of Figure 4.5A the extent of the difference in variability between the left and right side was dependent on the mode of coordination in which the system was prepared. In the anti-phase mode, larger coefficients were exhibited by the left side (5.90) than by the right side (3.92) ($F(1, 48) = 8.88$, $p < 0.01$). However in the in-phase mode the left (3.48) and right side (3.30) were essentially equivalent ($F < 1$). Discrete frequencies were more variable when movements were paced at 2 Hz (4.65) compared to when paced at 1 Hz (3.64) ($F(1, 48) = 4.61$, $p < 0.05$). As is also revealed by Figure 4.5 (panel A), the magnitude of the difference in variability between the left and right side was also dependent on the frequency of pacing. When movements were paced at 2 Hz, greater variability was exhibited by movements of the left side (5.78) than of the right side (3.53) ($F(1, 48) = 11.40$, $p < 0.01$). In contrast, when movements were paced at 1 Hz there were no differences in variability between the left (3.60) and right (3.68) side ($F < 1$). It was of interest to determine whether, the differences in period variability between those movements paced at 1 Hz and those paced at 2 Hz were differentially expressed depending on the mode of coordination. For movements prepared in the in-phase mode, movements paced at 1 Hz (3.73) and at 2 Hz (3.04) modes were not distinguished on the basis of variability of frequency ($p > 0.20$). In contrast, in conditions in which movements were conducted in the anti-phase preparation, greater variability was exhibited when movements were paced at 2 Hz (6.27) relative to those at 1 Hz (3.55) ($F(1, 48) = 16.59$, $p < 0.001$). Further contrasts were performed to examine possible interactions between the factors of side, mode of coordination and pacing frequency. It was determined that greater variability was present for movements of the left side compared to movements of the right side when these were prepared in the anti-phase mode of coordination and paced at 2 Hz ($F(1, 48) = 18.65$, $p < 0.0001$). In comparison movements of the left side were no more variable than those of the right side in the anti-phase preparation when paced at 1 Hz, or in the in-phase preparation when movements were paced at either 1 Hz or 2 Hz ($F < 1$).

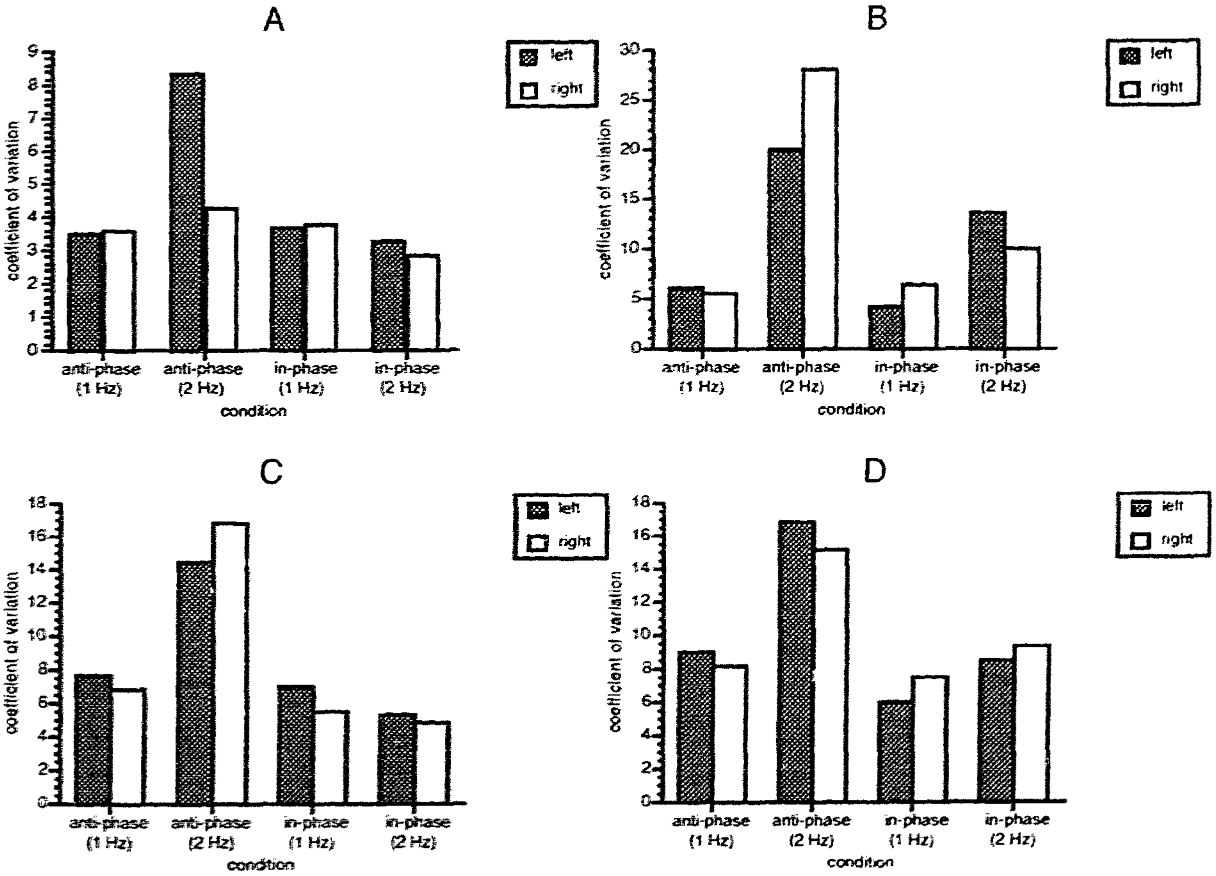

Fig. 4.5. Coefficient of variation discrete frequency for subject W (A), X (B), Y (C), Z (D) as a function of side, mode and pacing frequency.

Subject: X

Mean frequency:

The average mean frequency adopted was equivalent for the left (1.00 Hz) and right side (1.00 Hz) when movements were paced at a frequency of 1 Hz ($F < 1$). However when movements were paced at 2 Hz, the mean frequency exhibited by movements of the right side (2.09 Hz) was distinguished from the frequency of movements of the left side (1.99 Hz) ($F(1, 47) = 36.15$, $p < 0.0001$). For movements paced at 1 Hz, the average frequency was equivalent for movements prepared in the anti-phase (1.00 Hz) and in-phase (1.01 Hz) modes of coordination ($F < 1$). Similarly when paced at 2 Hz movements prepared in the anti-phase mode (2.04 Hz) and in-phase mode (2.03 Hz) ($F < 1$) were essentially identical. It was observed that when movements were paced at 1 Hz the frequency of movements made by the left side did not differ from the frequency of those made by the right side when prepared in either the anti-phase or in-phase mode of coordination ($F < 1$). When paced at 2 Hz and prepared anti-phase, movements of the left side (1.93 Hz) exhibited lower mean frequencies than movements of the right side (2.15 Hz) ($F(1, 47) = 78.69$, $p < 0.0001$). When paced at 2 Hz and prepared in-phase movements of the left side (2.03 Hz) and of the right side (2.02 Hz) were indistinguishable in terms of mean frequency ($F < 1$).

Coefficients of Variation:

Coefficients of variation although on the average larger for the right side (12.55) than the left side (11.05) did not distinguish side to a statistically significant degree ($p > 0.05$). Greater variability was exhibited in the anti-phase mode (14.98) relative to the in-phase mode (8.62) ($F(1, 47) = 67.88$, $p < 0.0001$). The left (9.00) and right (8.23) side were essentially equivalent in terms of variability when prepared in the in-phase mode ($F < 1$), whereas in the anti-phase mode movements of the right side (16.87) exhibited greater variability than equivalent movements of the left side (13.09) ($F(1, 47) = 12.16$, $p < 0.01$). As is suggested by inspection of Figure 4.5 (panel B), discrete frequencies were more variable when movements were paced at 2 Hz (17.95) than when paced at 1 Hz (5.65) ($F(1, 47) = 252.90$, $p < 0.0001$). As is also revealed by Figure 4.5, the magnitude of the difference in variability between the left and right side was sensitive to the frequency of pacing.

When movements were paced at 1 Hz there were no differences in variability between the left (5.24) and right (6.07) side ($F < 1$). In contrast, when movements were paced at 2 Hz, greater variability was exhibited by movements of the right side (19.04) than of the left side (16.85) ($F(1, 48) = 4.07$, $p < 0.05$). The differences in period variability between those movements paced at 1 Hz and those paced at 2 Hz were expressed in both the anti-phase (mean difference = 18.10, ($F(1, 47) = 278.49$, $p < 0.0001$)) and in-phase (mean difference = 6.49, ($F(1, 47) = 34.64$, $p < 0.0001$)) modes of coordination.

Additional contrasts decomposing possible interactions between the factors of side, mode of coordination and pacing frequency were also performed. It was evident that the right side exhibited greater variability than the left side when movements were prepared in the anti-phase mode ($F(1, 47) = 28.32$, $p < 0.0001$) in the in-phase mode ($F(1, 47) = 6.09$, $p < 0.02$) and paced at a frequency of 2 Hz. Movements of the left side were no more variable than those of the right side in either preparation when paced at 1 Hz ($p > 0.15$).

Subject: Y

Mean frequency:

The average mean frequency adopted was equivalent for the left (1.01 Hz) and right side (1.00 Hz) when movements were paced at a frequency of 1 Hz ($F < 1$). When movements were paced at 2 Hz, mean frequencies for movements of the left (1.91 Hz) and right side (1.92 Hz) were not distinguished to a statistically significant degree ($p > 0.05$). When movements were paced at 1 Hz, the average frequency was equivalent for movements prepared in the anti-phase (1.01 Hz) and in-phase (1.00 Hz) modes of coordination ($F < 1$). However when paced at 2 Hz movements prepared in the anti-phase mode (1.82 Hz) were associated with lower mean frequencies than those movements prepared in the in-phase mode (2.00 Hz) ($F(1, 48) = 473.53$, $p < 0.0001$). Movements paced at 1 Hz exhibited similar mean frequencies when made by the left side and right side and prepared in either the anti-phase or in-phase mode of coordination ($F < 1$). When paced at 2 Hz and prepared anti-phase, movements of the left side (1.81 Hz) exhibited lower mean frequencies than movements of the right side (1.84 Hz) ($F(1, 48) = 7.37$, $p < 0.01$). This was not the case when movements paced at this frequency were prepared in-phase, frequencies for the left (2.01 Hz) and right side (2.00 Hz) were equivalent ($F < 1$).

Coefficients of Variation:

Coefficients of variation for the left side (8.62) and the right side (8.50) were essentially equivalent ($F < 1$). Movements prepared in the anti-phase mode (11.34) were more variable with respect to frequency than those prepared in the in-phase mode (5.68) ($F(1, 48) = 147.33$, $p < 0.0001$). The left and right side were not distinguished in terms of variability in either the in-phase or anti-phase modes of coordination ($p > 0.10$) or when paced at either 1 Hz or 2 Hz ($p > 0.10$). Discrete frequencies were more variable when movements were paced at 2 Hz (10.34) compared to when paced at 1 Hz (6.77) ($F(1, 48) = 56.72$, $p < 0.0001$). However the expression of this difference was dependent upon the mode of coordination in which the system was prepared. When movements were conducted in the in-phase mode, movements paced at 1 Hz (6.31) were more variable than those paced at 2 Hz (5.05) to a degree that approached conventional levels of statistical significance ($p = 0.07$). In contrast, when movements were prepared in the anti-phase mode, movements paced at 2 Hz (15.63) were appreciably more variable than those paced at 1 Hz (7.23) ($F(1, 48) = 157.16$, $p < 0.0001$). While movements made by the left and right side were not generally distinguished in terms of variability, when conducted in the anti-phase mode of coordination and paced at 2 Hz, right side movements (16.77) were more variable than right side equivalents (14.48) ($F(1, 48) = 5.81$, $p < 0.02$). In all other combinations of mode and pacing frequency movements of the left and right side were essentially equivalent ($p > 0.10$).

Subject: Z

Mean frequency:

The average mean frequencies of movement for the left (1.01 Hz) and the right side (1.01 Hz) were indistinguishable when movements were paced at a frequency of 1 Hz ($F < 1$). When movements were paced at 2 Hz, mean frequencies for movements of the left (2.17 Hz) and right side (2.31 Hz) differed from each other to a degree which was statistically significant ($F(1, 48) = 28.00$, $p < 0.0001$). When movements were paced at both 1 Hz and 2 Hz the average frequency was equivalent for movements prepared in the anti-phase and in-phase modes of coordination ($F < 1$). Movements paced at 1 Hz exhibited similar mean frequencies when made by the left side and right side and prepared in either the anti-phase or in-phase mode of coordination ($F < 1$). When paced at 2 Hz and prepared anti-phase, movements of the left side (2.18 Hz) exhibited lower mean frequencies than movements of the right side (2.32 Hz) ($F(1, 48) = 14.06$, $p < 0.001$). This was also the case when movements paced at this frequency were prepared in-phase, frequencies for the left (2.16 Hz) were lower than those of the right side (2.30 Hz) ($F(1, 48) = 13.94$, $p < 0.001$).

Coefficients of Variation:

Overall, coefficients of variation for the left side (10.14) and the right side (10.03) were essentially equivalent ($F < 1$), and were not different in either the in-phase or anti-phase modes of coordination ($p > 0.20$) or when paced at either 1 Hz or 2 Hz, or in any combination thereof ($p > 0.20$). Movements prepared in the anti-phase mode (12.34) were more variable with respect to frequency than those prepared in the in-phase mode (7.83) ($F(1, 48) = 30.59$, $p < 0.0001$). In addition, discrete frequencies were more variable when movements were paced at 2 Hz (12.49) than when paced at 1 Hz (7.68) ($F(1, 48) = 34.87$, $p < 0.0001$). The magnitude of this difference was observed to be sensitive to the prevailing mode of coordiantion. When prepared in the in-phase mode movements paced at 2 Hz (8.91) were more variable than those paced at 1 Hz (6.75) to a degree that approached statistical significance ($p = 0.07$). When prepared anti-phase, movements paced at 2 Hz (16.07) were evidently more variable than those paced at 1 Hz (8.60) ($F(1, 48) = 42.01$, $p < 0.0001$).

### 4.3.3 Discrete Relative Phase

Preliminary inspection of relative phase time series suggested that for a number of subjects there were trials for which relative phase values failed to exhibit stationarity. Therefore as a precursor to the derivation of test statistics for discrete relative phase, a number of measures were employed to appraise stationarity. The relative phase values obtained for each trial were tested for uniformity using the Rayleigh test (Mardia, 1972). Each trial was also classified on the basis of whether phase wandering was exhibited. Phase wandering was considered to have occured when discrete relative phase deviated by more than 180° from the target value for that trial. Data from trials in each forearm position condition were pooled and the number of trials exhibiting phase wandering expressed as a percentage of the total number of trials in each combination of side, mode of coordination and pacing frequency. In addition a quasi-continuous measure of relative phase was obtained by performing a linear interpolation between the discrete relative phase values at the original sampling frequency. These data were transformed such that values expressed the "distance" from the in-phase and the anti-phase mode in the range 0 to 0.5. A value of 0 expressed perfect in-phase coordination, whereas a value of 0.5 expressed perfect anti-phase coordination. These data were rectified and histograms constructed of the proportion of the total trial time accounted for by values of the transformed relative phase series in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50. These data are reported independently for each subject.

#### Relative Phase Stationarity

#### Subject: W

The hypothesis of uniformity was supported ($p < 0.01$) for all trials. In every instance there existed a predominant direction of relative phase. In addition phase wandering was present in only two trials (one for each side), prepared in the anti-phase mode and paced at a frequency of 2 Hz.

This tendency is also evident in Figure 4.6. which illustrates the proportion of trial duration accounted for by values in each relative phase range bin.

TABLE 4.1 Summary table of proportion of trials exhibiting phase wandering for .subject W

| | anti-phase | | in-phase | |
|---|---|---|---|---|
| | 1 Hz | 2 Hz | 1 Hz | 2 Hz |
| left side | 0% | 12.5% | 0% | 0% |
| right side | 0% | 12.5% | 0% | 0% |

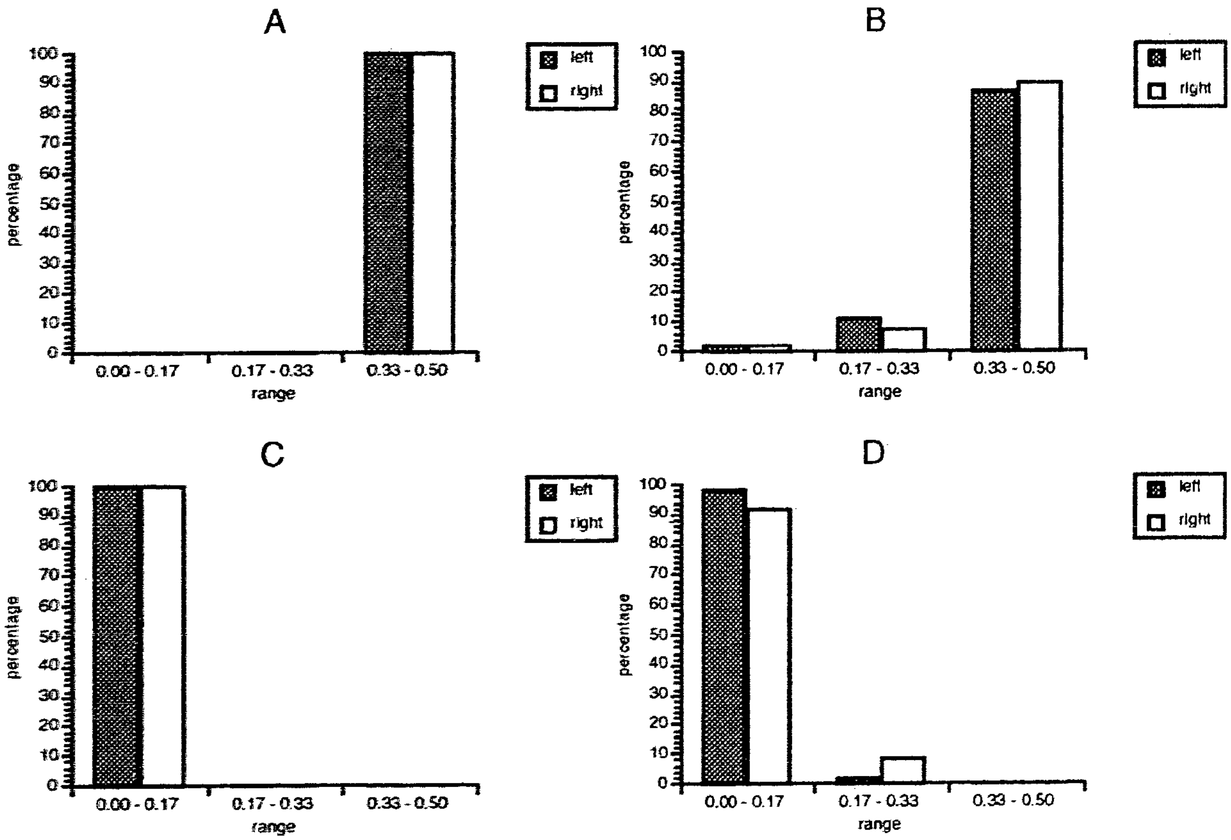

Fig. 4.6. Subject: W, proportion of total time accounted for by transformed relative phase values in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50, 1 Hz (anti-phase) (A), 2 Hz (anti-phase) (B), 1 Hz (in-phase) (C), 2 Hz (in-phase) (D).

Subject: X

The hypothesis of uniformity was supported ($p < 0.01$) for all trials prepared in the in-phase mode of coordination. However, it was noted that in six of eight trials performed by the left side, prepared in the anti-phase mode of coordination and paced at 2 Hz hypothesis of uniformity was not supported. In addition, two of eight trials executed by the right side, prepared in the anti-phase mode of coordination and paced at 2 Hz similarly failed to exhibit uniformity in the direction of relative phase. These tendencies toward phase wandering in movements prepared anti-phase and paced at 2 Hz are further supported by inspection of Table 4.2 and by examination of Figure 4.7. It was also noted (Table 4.2) that for the left side, movements prepared in-phase and paced at 2 Hz also exhibited phase wandering on 37.5% of trials.

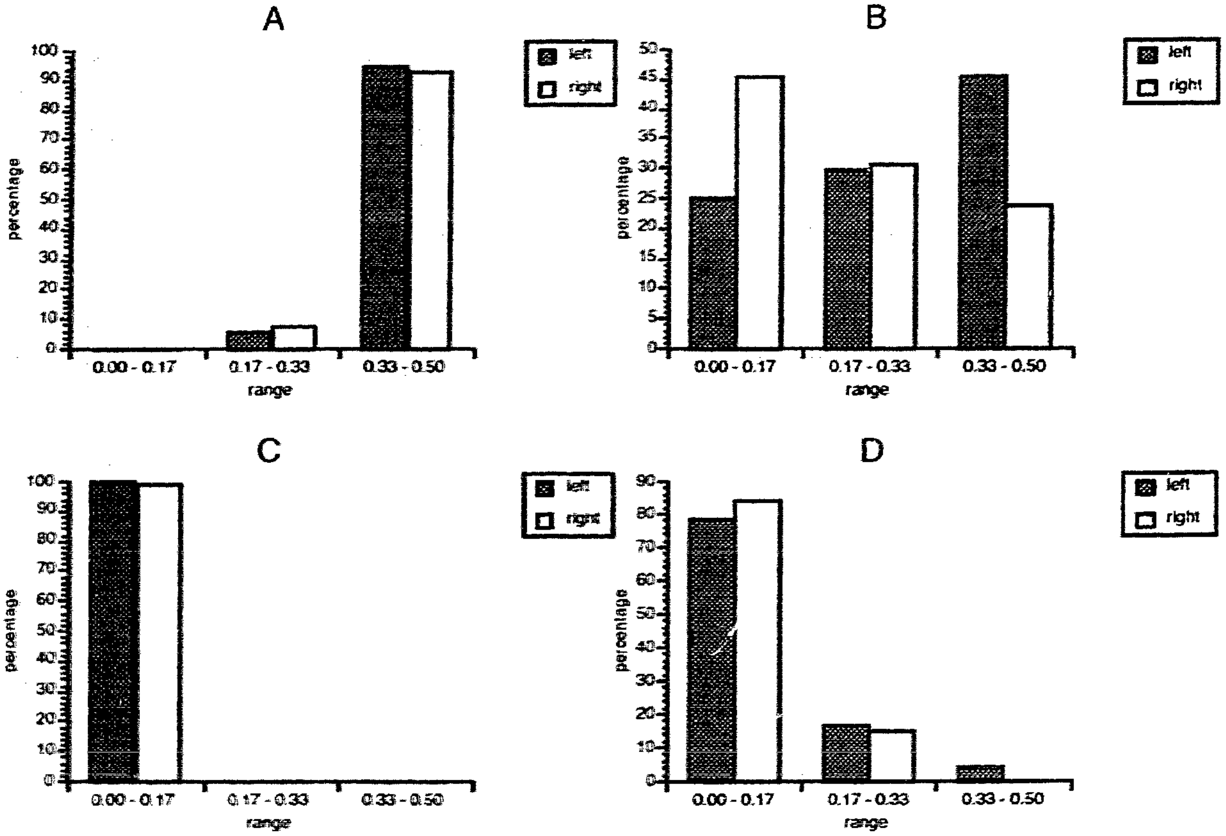

Fig. 4.7. Subject: X, proportion of total time accounted for by transformed relative phase values in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50, 1 Hz (anti-phase) (A), 2 Hz (anti-phase) (B), 1 Hz (in-phase) (C), 2 Hz (in-phase) (D).

TABLE 4.2 Summary table of proportion of trials exhibiting phase wandering for .subject X

| | anti-phase<br>1 Hz | <br>2 Hz | in-phase<br>1 Hz | <br>2 Hz |
|---|---|---|---|---|
| left side | 0% | 100% | 0% | 37.5% |
| right side | 0% | 100% | 0% | 0% |

Subject: Y

The hypothesis of uniformity was supported ($p < 0.01$) for in-phase and anti-phase trials. In addition phase wandering was absent in all trials prepared in the in-phase mode of coordination. However, phase wandering was evident in 75% of trials of the left side and 100% of trials of the right side prepared in the anti-phase mode and paced at a frequency of 2 Hz.

TABLE 4.3 Summary table of proportion of trials exhibiting phase wandering for subject Y

| | anti-phase<br>1 Hz | <br>2 Hz | in-phase<br>1 Hz | <br>2 Hz |
|---|---|---|---|---|
| left side | 0% | 75% | 0% | 0% |
| right side | 12.5% | 100% | 0% | 0% |

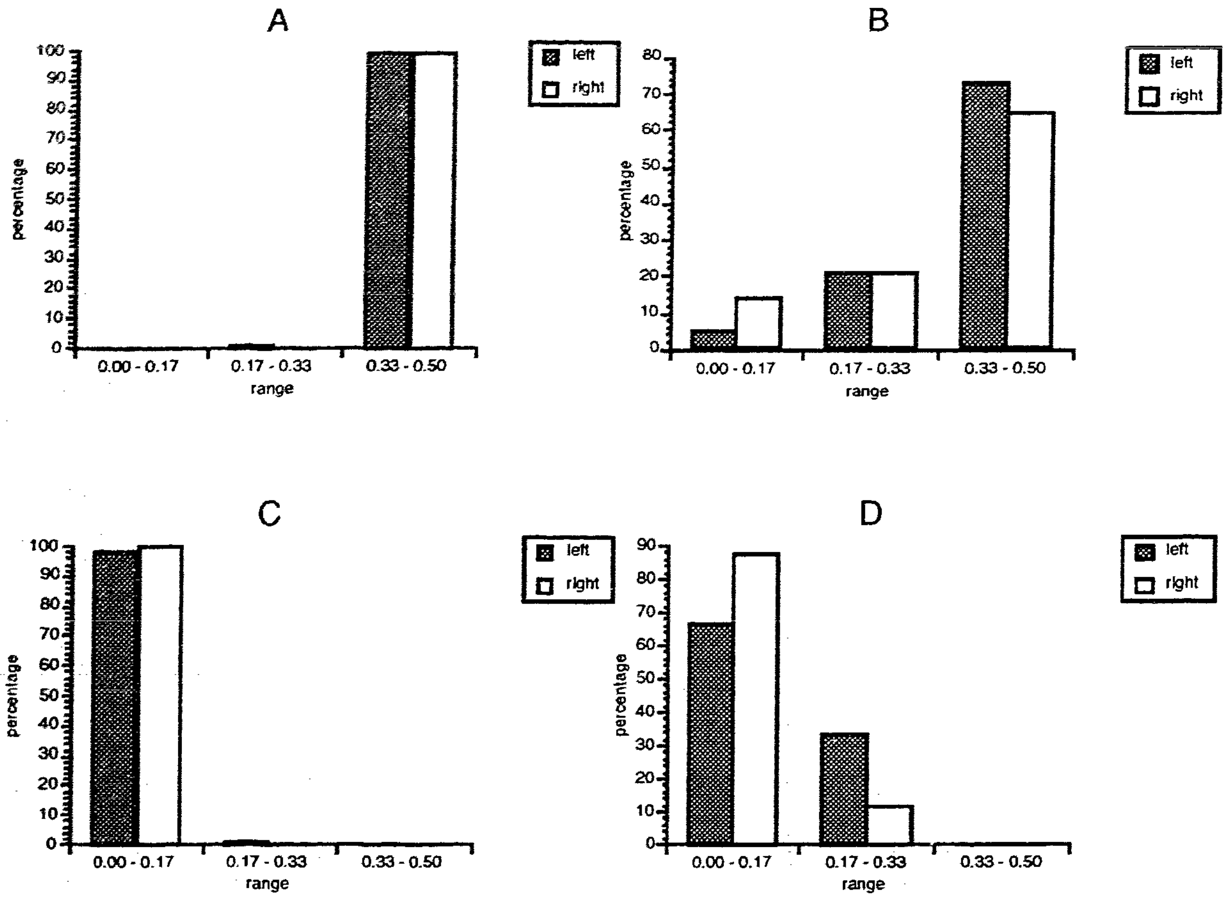

Fig. 4.8. Subject: Y, proportion of total time accounted for by transformed relative phase values in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50, 1 Hz (anti-phase) (A), 2 Hz (anti-phase) (B), 1 Hz (in-phase) (C), 2 Hz (in-phase) (D).

## Subject: Z

It was noted that for subject Z the hypothesis of uniformity was not supported (p > 0.01) for a single trial paced at a frequency of 2 Hz in which movements of left side were initially prepared in the anti-phase mode of coordination with the forearm paced in a supinated position. Thus it was generally the case that there existed a dominant direction of relative phase. As is evident from inspection of Table 4.4 however, phase wandering was prevalent for movements of both the left and right side particularly when prepared initially in the anti-phase mode of coordination and paced at 2 Hz. It was also notable that for this subject, phase wandering was also evident for movements prepared in-phase and paced at a frequency of 2 Hz.

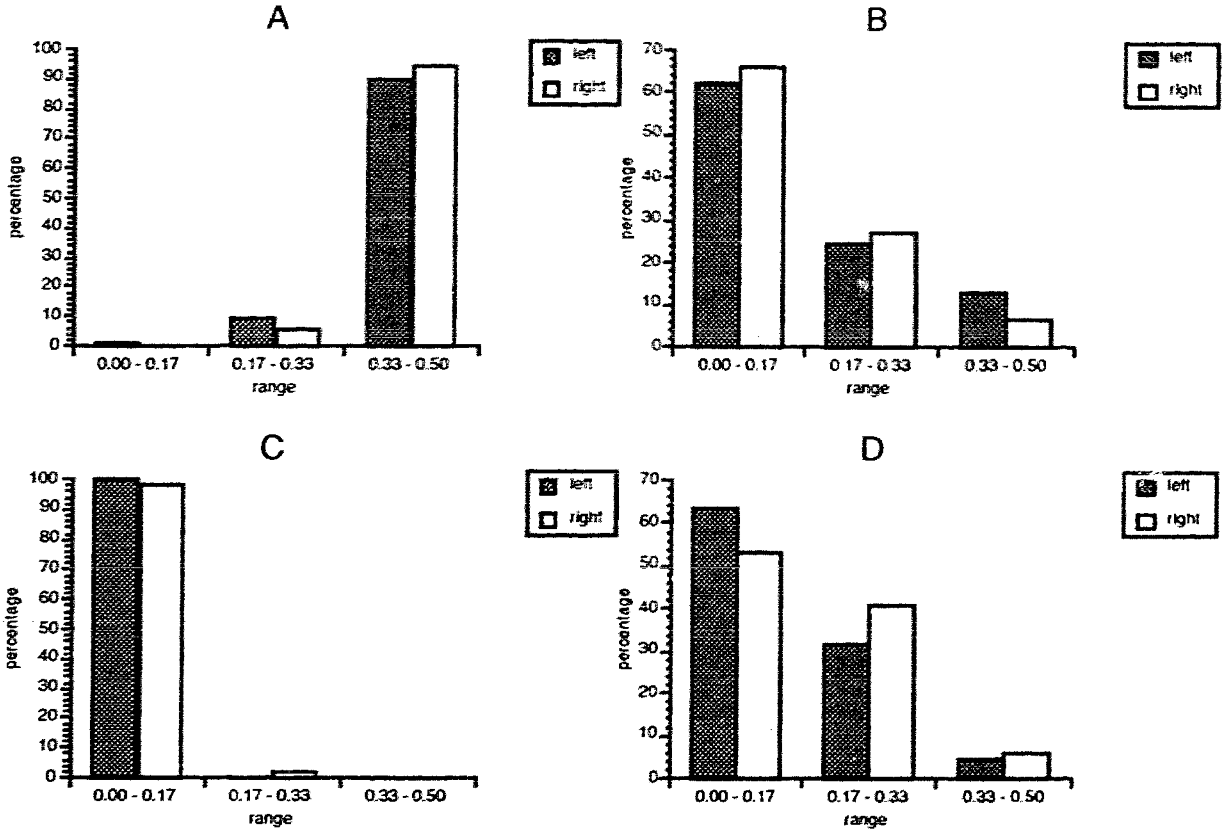

Fig. 4.9. Subject: Z, proportion of total time accounted for by transformed relative phase values in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50, 1 Hz (anti-phase) (A), 2 Hz (anti-phase) (B), 1 Hz (in-phase) (C), 2 Hz (in-phase) (D).

TABLE 4.4 Summary table of proportion of trials exhibiting phase wandering for subject Z

| | anti-phase | | in-phase | |
|---|---|---|---|---|
| | 1 Hz | 2 Hz | 1 Hz | 2 Hz |
| left side | 12.5% | 87.5% | 0% | 25% |
| right side | 12.5% | 87.5% | 0% | 50% |

In light of the observation that non-stationarity was present in the majority of trials prepared in the anti-phase mode of coordination and paced at 2 Hz for subjects X, Y, and Z, it was concluded that no meaningful analysis of mean relative phase and uniformity of relative phase could be performed. These analyses were however performed for subject W following removal of the two trials which failed to exhibit stationarity. Test statistics for mean relative phase were calculated separately for anti-phase and in-phase trials. In the first instance, in order to compare left side to right side conditions, data were collapsed over metronome frequency and forearm position. In the second instance, in order to compare metronome frequency conditions, data were collapsed over side and forearm position. In order to control for the potential inflation of Type I errors resulting from multiple comparisons, alpha was assigned as $p = 0.01$. In addition mean relative phase values were also assessed with respect to the target relative phase value for each mode of coordination. In performing these analyses, data were in the first instance pooled by collapsing over metronome frequency and forearm position, and in the second instance by collapsing over side and forearm position. Confidence intervals (99%) were calculated following Mardia (1972) (see also Batschelet. 1981). Analyses of variance for transformed uniformity scores were performed for each subject using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 2 frequency (1 Hz, 2 Hz) by 2 forearm position (pronated, supinated) design. Each trial was treated as a single case. Planned orthogonal comparisons of means were performed to highlight a limited number of preselected contrasts.

### Subject: W

### Mean Relative Phase

In the anti-phase mode of coordination the mean value of relative phase exhibited by movements of the left side (184.0°) was not different from the target value of 180° ($p > 0.01$). Whereas, for movements of the right side (195.5°) mean relative phase values were different to a statistically significant degree from 180° ($p < 0.01$). When prepared in the in-phase mode of coordination the mean relative phase adopted for movements of the left side (350.6°) was not reliably less than 0° ($p > 0.01$). The corresponding mean value for right side movements (346.5°) was also not different from 0° ($p > 0.01$). Movements paced at 1 Hz (194.3°) exhibited mean relative phase values different from 180° when prepared in the anti-phase mode ($p < 0.01$). This was not the case when movements were paced at 2 Hz (184.3°) ($p > 0.01$). When prepared in the in-phase mode, movements paced at 1 Hz (6.6°) and at 2 Hz (330.7°) were characterised by mean relative phase values which were reliably different from 0° ($p < 0.01$).

Mean relative phase values were essentially equivalent for movements of the left side and the right side both when movements were prepared in the anti-phase ($F(1, 28) = 2.23$, $p > 0.01$) and in the in-phase modes of coordination ($F < 1$). When movements were prepared in the anti-phase mode, the mean relative phase relation adopted at a metronome frequency of 1 Hz was equivalent to that adopted at a metronome frequency of 2 Hz ($F(1, 28) = 1.67$, $p > 0.01$). However, when prepared in the in-phase mode the mean phase relation exhibited at a metronome frequency of 1 Hz differed to a statistically significant degree from the mean phase relation exhibited at a metronome frequency of 2 Hz ($F(1, 30) = 67.49$, $p < 0.01$).

### Uniformity of Relative Phase

Overall uniformity of relative phase was equivalent for movements of the left (2.63) and right side (2.67) ($F < 1$). Movements made in the in-phase (2.74) mode of coordination exhibited greater uniformity of relative phase than those prepared in the anti-phase mode (2.56) ($F(1, 46) = 14.05$, $p < 0.001$). Movements executed when the metronome frequency was 1 Hz (2.86) revealed greater uniformity than those completed when the metronome frequency was 2 Hz (2.44) ($F(1, 46) = 81.04$, $p < 0.0001$). The left and right side were essentially equivalent in terms of uniformity when prepared in the anti-phase mode ($F < 1$), and in the in-phase mode ($F < 1$). When movements were paced at 1 Hz there were no differences in uniformity between the left (2.85) and right (2.87) side ($F < 1$). Similarly, when movements were paced at 2 Hz, movements of the left side (2.41) were equivalent to those of the right side (2.47) ($F < 1$). The greater uniformity associated with movements paced at 1 Hz relative to 2 Hz was evident both when movements were prepared in the anti-phase ($F(1, 46) = 92.42$, $p < 0.0001$) and the in-phase ($F(1, 46) = 8.94$, $p < 0.01$) modes of coordination. Further contrasts were performed to examine possible interactions between the factors of side, mode of coordination and pacing frequency. However these analyses failed to indicate that any comparisons were of statistical significance ($p > 0.20$).

## 4.4 Summary and Discussion

The primary objective of this experiment was to examine temporal and coordinative variability in circumstances in which oscillation frequency, a putative control parameter, was controlled via external pacing. The veracity of detailed analyses of the evolution of the intrinsic (order parameter) dynamics resulting from changes in the value of the control parameter was contingent upon the ability to demonstrate that subjects had faithfully adhered to the pacing regime. It has been customary (e.g., Jeka, 1992; Scholz & Kelso, 1990) to evaluate concurrence of the limb and metronome frequencies through measures of correlation. However it can be demonstrated that two samples which exhibit large differences in absolute values may yet be highly correlated. In this experiment, the degree of correlation between individual limb frequencies and metronome frequencies was in every instance close to unity (greater than 0.99). Considered in isolation these data would suggest that subjects adhered closely to the metronome frequency. However consideration of the degree of deviation between limb frequencies and metronome frequencies (cf., Scholz & Kelso, 1989) indicated a strong sensitivity to experimental conditions. In particular, in three of the four subjects, the degree of deviation from the metronome frequency was markedly greater when the metronome frequency was 2 Hz compared to when 1 Hz. In addition, for all subjects, the mean frequency exhibited for left side movements prepared in the anti-phase mode of coordination and paced at 2 Hz was reliably different from movements of the right side in these conditions.

Upon inspection it appeared that the asymmetries expressed in terms of variability of frequency which were evident in Experiment 1 were eliminated through the imposition of external pacing. Only subject W demonstrated coefficients of variation for discrete frequency which were larger for movements of the left side. Indeed in a subset of experimental conditions two subjects (X and Y) exhibited coefficients of variation which were larger for movements of the right side. Differences in this direction were not observed in Experiment 1. However there was clearly wide variation between subjects in the extent to which task requirements were satisfied.

Consideration of the patterns of coordination, expressed in terms of the relative phase relations existing between the wrist and ankle joints manifested additional obstacles to the interpretation of measures of coordination. Cursory inspection of relative phase time series suggested that some subjects were not only failing to adhere to the pacing regime, they were also on occasion unable to maintain the prescribed mode of coordination. Central to the interpretation of measures of variability of relative phase as indices of the stability of an attractor state is the requirement that the variability observed reflects variation about a mean value corresponding to a stationary (attractor) state. The absence of stationarity suggests that stability has been lost and associatively that the system is no longer confined to the region of state space corresponding to the putative attractor. In these circumstances, standard measures of variability are rendered more problematic with respect to interpretation of the stability of an attractor state. As illustrated by Figures 4.6 to 4.9 however, it remains possible to calculate distributions of relative phase in the regions of attractor states. These distributions also provide information concerning the relative stability of attractor states.

In evaluating the stationarity of relative phase a battery of three measures was employed. This included the Rayleigh test of uniformity, the classification of deviations from the target value of relative phase which were greater than 180°, and relative phase distribution histograms. In general terms the Rayleigh test of uniformity is the most satisfactory measure of stationarity. However in an experimental context large uniformity values can be associated with trials which fail to exhibit stationarity if phase wandering is manifested only in limited portions of the period over which the system is observed. It was for this reason that additional measures of stationarity were employed. The three measures were however consistent in indicating that in three subjects the requirement of stationarity was not satisfied when movements were initially prepared in the anti-phase mode of coordination and paced at 2 Hz. These observations suggest that in these subjects the attractor located in the vicinity of 180° which was evident when the value of the control parameter was 1 Hz was no longer present when movements were paced at a frequency of 2 Hz. It should be emphasised however that while phase wandering occurred when movements were prepared anti-phase and paced at 2 Hz, remnants of the attractor previously located at 180° were evident in some subjects. This is demonstrated in Figure 4.8 (panel B) examination of which suggests that for subject Y there continued existed attraction to the anti-phase mode. In comparison, examination of Figure 4.9 (panel B) demonstrates that for subject Z the in-phase mode dominates at a pacing frequency of 2 Hz regardless of the initial preparation.

Subject W was consistent in exhibiting stationarity of relative phase in 62 of 64 trials. A complete analysis of measures of relative phase was therefore conducted for this individual. Although it was noted that in two of eight conditions examined mean values of relative phase deviated from the target values, no clear pattern of deviation could be discerned. The uniformity of relative phase was sensitive both to the mode of coordination in which the system was prepared and to the frequency of pacing. In all conditions movements of the left and right side were equivalent with repect to this measure. In this regard however it should be noted that anti-phase movements of the left side which were paced at 2 Hz deviated from the metronome to a greater degree than did those movements paced at 1 Hz. This was not the case for anti-phase movements conducted by the right side which deviated to an equivalent degree at each pacing frequency. In addition, the mean frequency of movements of the left side was lower than that of the right side only when movements were prepared in the anti-phase mode and paced at a frequency of 2 Hz. These data suggest that the degree of stability exhibited by the left side in the anti-phase mode when paced at 2 Hz, which was equivalent to that of the right side, may only have been achieved at the expense of greater deviations from the metronome frequency which thus served to reduce the effective value of the control parameter. It is conceivable that alternative methods of implementing oscillation frequencies may be necessary to equilibrate the degree of adherence across all conditions. For example, subjects could be required to learn to reproduce the desired oscillation frequencies.

Clearly three of the subjects were simply unable to maintain an anti-phase mode of coordination when movements were paced at a frequency of 2 Hz. These data suggest that the attractor corresponding to a relative phase value of 180° which was stable when the control parameter value was 1 Hz, no longer existed at a control parameter value of 2 Hz. A striking characteristic of the data was the general failure of subjects to adhere to the pacing frequency particularly when movements were prepared in the anti-phase mode of coordination and paced at 2 Hz. Note that in this experiment subjects were instructed to attempt to maintain the initial mode of coordination in circumstances in which the pattern of coordination might begin to change. Thus, although particular emphasis was placed upon the maintainence of a 1:1 frequency relation with the metronome, it is likely that subjects compromised this requirement in an attempt to maintain the prescribed mode of coordination in the face of the obliteration of the attractor corresponding to180° at a control parameter value of 2 Hz. The endeavour to maintain the prescribed mode may profitably be conceived of as the superposition of intentional dynamics upon the preexisting intrinsic dynamics (e.g., Schöner & Kelso, 1988b). As it appears that the intrinsic dynamics pertaining at 2 Hz were such as to virtually preclude the maintainence of the prescribed (180°) mode it is likely that any attempt to achieve the anti-phase mode required almost continuous intentional intervention. While consideration has been given to intentionally mediated perturbations of the intrinsic dynamics which, while continuous in terms of their dynamics, are discrete in terms of their onsets (Scholz & Kelso, 1990), little is known concerning the effect of quasi-continuously applied perturbations. In particular it is not clear how such intervention might impinge upon other aspects of the dynamics such as the actual reproduced frequency of oscillation.

# 5 Experiment 3

## 5.1 Introduction

The large number of microscopic degrees of freedom from which the coordinative system is assembled are predicted to act collectively or cooperatively at the macroscopic level. Indeed the formation of behavioural patterns may be contingent upon the interaction of multiple degrees of freedom (Schöner & Kelso, 1988a). In addition, the noise sources arising from the weak interaction of the many subsystems from which the system is composed are thought to give rise to stochastic forces which permit the exploration of otherwise inaccessible regions of state space. These properties, which have been encapsulated in formal models of bimanual coordination (e.g., Schöner et al., 1986), may play a role in determining various system time scales and the relations between them. The nature of these time scales relations may in turn account for both qualitative and quantitative characteristics of macroscopic coordination, and in particular for switching among multiple behavioural patterns (c.f., Schöner & Kelso, 1988b).

Given two dynamical systems characterized by equivalent potential topologies, differences in the levels of intrinsic noise, modelled as the strength of the stochastic force, would be expected to engender differences in equilibration time $\tau_{equ}$. This is the time required to obtain the stationary probability distribution (see Kelso, Ding, Schöner, 1991). In the bistable case the equilibration time is determined largely by the time required to traverse from one stationary state to another (Schöner & Kelso, 1988a). Estimates of $\tau_{equ}$ may be obtained from the experimentally derived measure of mean first passage time (MFPT). For the bistable case, Schöner et al., (1986) modelled the stochastic force as Gaussian white noise of unit variance, the strength of which was determined by a noise strength parameter Q. These authors also determined the Q dependence of the mean first passage time, estimating that the MFPT varied from 6.4 s to 2.4 s as Q was varied from 0.1 Hz to 1.0 Hz, for parameters of a = 2.0 Hz and b = 0.5 Hz. If the limb/flank hemisphere complexes are adequately represented as dynamical systems possessing equivalent potential topologies, yet distinguished in terms of the magnitude of stochastic forces, differences would be predicted to arise in terms of their respective equilibration times. However, there appears little basis to suggest a priori that the limb/flank hemisphere complexes are distinguished in this manner. Although some investigators have suggested that "the left hand is operated with greater noise than the right" (Roy & Elliott, 1989, p. 514), where such differences have been described, they have been expressed in terms of the system dynamics rather than in terms of subsystem specific noise (e.g., Annett et al., 1979; Roy & Elliott, 1986).

Preliminary evidence (e.g., Newell & van Emmerik, 1989; van Emmerik & Newell, 1990; van Emmerik, 1991) suggests the more beguiling possibility that the limb-hemisphere systems are distinguished on the basis of their intrinsic dynamics. If this is the case, the preferred and non-preferred limb/flank joint couples would be predicted to exhibit qualitative differences in the topology of the potential landscape for an appropriate collective variable such as relative phase, for a given control parameter regime. Such differences will be reflected by the absolute and relative stabilities of attractor states which are in turn indexed by a number of measures which can be derived experimentally. These include (a) The (local) relaxation time which is the time required for the system to return to the stationary state following an externally applied perturbation; (b) The variability of the collective variable over time under stationary conditions; (c) The time scale over which correlations of the pattern variables decay (correlation time), which is derived either from correlation functions or from the corresponding power spectra (Schöner, in press). Additional measures gauging the difference in stability between two adjacent states can be estimated from the time to the initiation of, and the length of, the transient switching process (Schöner & Kelso, 1988b).

Stability is most conveniently gauged by measures attendant upon noise sources arising from the interaction of the component subsystems. The stochastic forces on the collective dynamics (c.f., Haken, 1983) may be considered "continuously applied perturbations" of small magnitude which force the system away from the attractor state (Schöner & Kelso, 1988a). As such, the variability (e.g., standard deviation/uniformity) of the collective variable around the attractor state is a measure of the size of the fluctuations about that state, and in turn indexes the stability of the state (Schöner & Kelso, 1988a; Kelso et al., 1987). Thus, if equivalence of subsystem specific noise is assumed, experimentally derived measures of order parameter fluctuations, such as the uniformity of relative phase, permit otherwise analogous systems to be distinguished in terms of the stability of their local attractor states (c.f., Schöner & Kelso, 1988c). In addition, the average length of time before the system first changes state for a given parameter regime is a measure of the equilibration time $\tau_{equ}$ which in turn indexes the relative stability of adjacent attractor states.

These measures therefore provide means of determining whether the limb-hemisphere systems are distinguished on the basis of their intrinsic dynamics. The present experiment was conducted to determine whether asymmetries in intrinsic dynamics may be discriminated in a multijoint rhythmic coordination task.

## 5.2 Methodology

Procedure

Individuals performed paced oscillatory motions of the wrist and foot commencing in two modes modes of coordination, in-phase and anti-phase, and in one of two forearm position conditions (supine or prone). Subjects were required to produce one full cycle of movement for each beat of an auditory metronome while maintaining the prescribed mode of coordination. The frequency of the metronome was increased from an initial frequency of 1.25 Hz to a frequency of 2.75 Hz in steps (7 frequency plateaus) of 0.25 Hz. The duration of each isofrequency plateau was 8 seconds. By way of "warm-up" four pulses at 1.25 Hz preceded the eight plateaus and, to obviate anticipation of the end of the trial, three pulses at 2.75 Hz terminated the trial.

Subjects were instructed to maintain the pattern in which they were prepared as accurately as possible, but were also told that should the pattern change they were not to intervene. That is, they were not to actively resist pattern change but were to establish the most comfortable pattern compatible with the prevailing frequency. Subjects were given no direction concerning the temporal locus of the metronome pulse with respect to the movement cycle. Rather, individuals were free to establish their own metronome-movement cycle coordinative pattern, subject to the constraint of isofrequency coordination.

In the in-phase (forearm supinated) mode, flexion (extension) of the wrist was required to be coincident with dorsi-flexion (plantar-flexion) of the foot . In the anti-phase (forearm supinated) mode, flexion (extension) of the wrist was required to be coincident with plantar-flexion (dorsi-flexion) of the foot. In the in-phase (forearm prone) mode, flexion (extension) of the wrist was required to be coincident with plantar-flexion (dorsi-flexion) of the foot . In the anti-phase (forearm prone) mode, flexion (extension) of the wrist was required to be coincident with dorsi-flexion (plantar-flexion) of the foot.

In each forearm position, trials alternated between in-phase and anti-phase trials, commencing with an in-phase trial. For each side (left or right), two blocks of trials were performed. Twelve trials were performed in each block (six in each coordination mode) for a grand total of 48 trials. In all conditions, subjects were permitted one in-phase practice trial. Two subjects first performed all trials for the left side followed by all trials for the right side. For the other two subjects, the order was reversed. In each of these subgroups, one subject performed a block of trials for which the forearm was placed in a supinated position prior to a block in which the forearm was in a prone position. For the other subject this order was reversed.

Trials commenced with 2 "lead-in" metronome pulses at the base frequency (1.25 Hz) at which point the initiation of data collection was automatically triggered. Two further lead-in pulses followed. Coincident with the first pulse of each frequency plateau, a reference pulse was output to one channel of the A/D. Three "lead-out" pulses at the final frequency (2.75 Hz) followed the termination of the final frequency plateau, at which point data collection was terminated.

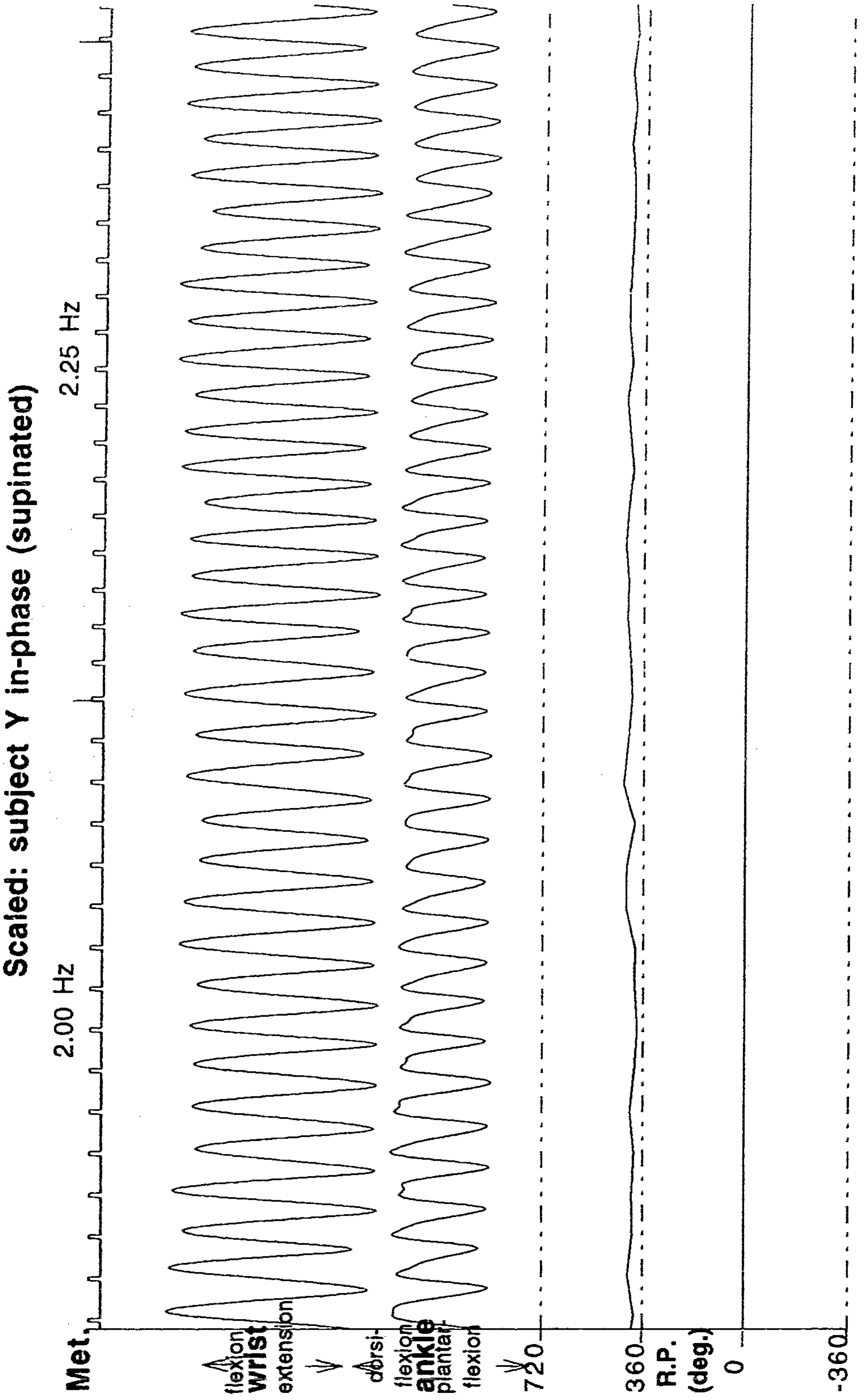

Fig. 5.1 Subsection (pacing frequency 2.00 Hz - 2.25 Hz) of a sample time series of movements prepared in the in-phase mode with the forearm in a supinated position (subject Y).

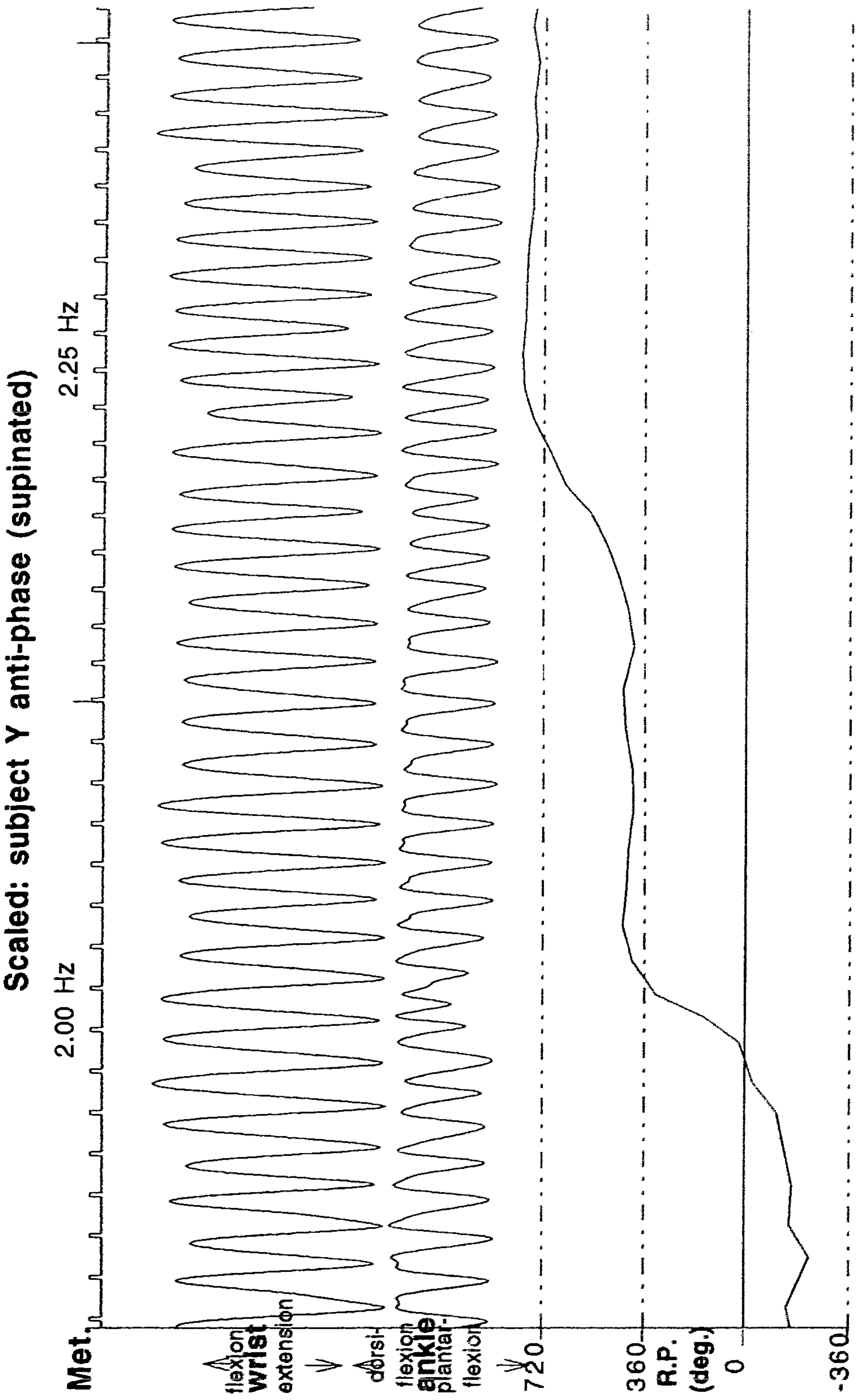

Fig. 5.2 Subsection (pacing frequency 2.00 Hz - 2.25 Hz) of a sample time series of movements prepared in the anti-phase mode with the forearm in a supinated position (subject Y).

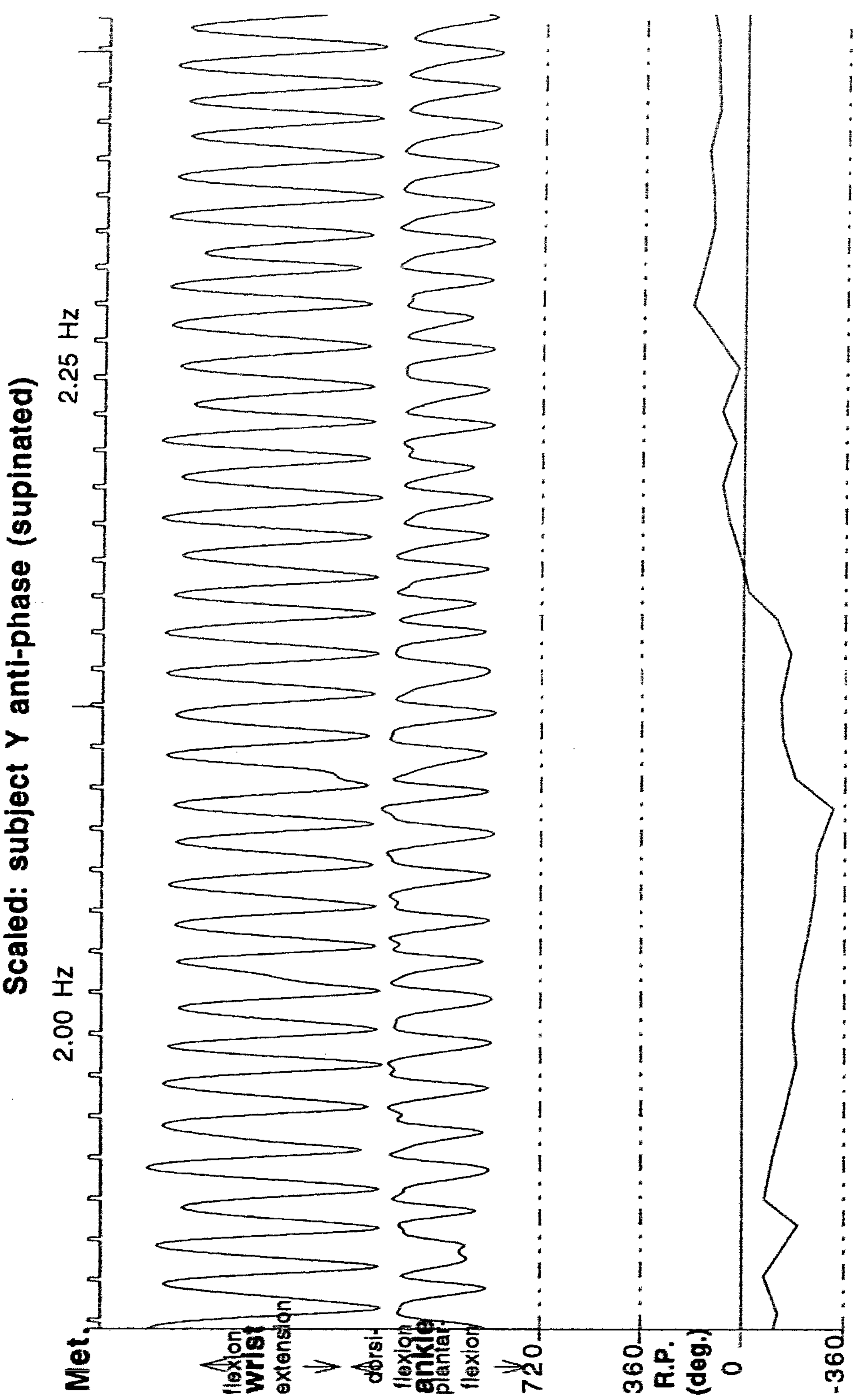

Fig. 5.3 Subsection (pacing frequency 2.00 Hz - 2.25 Hz) of a sample time series of movements prepared in the anti-phase mode with the forearm in a supinated position (subject Y).

## 5.3 Results

### 5.3.1 Metronome Limb Relations

A frequency deviation score was calculated for each trial. This score reflected the absolute difference between the mean frequency for that trial and the metronome frequency. Data were pooled for each subject by collapsing over mode of coordination and forearm position, and were analysed using a 2 side (left, right) by 2 joint (wrist, ankle) by 7 frequency design. Each trial was treated as a single case. Side was a grouping factor. Joint and frequency were within case factors. Planned orthogonal comparisons of means were performed to highlight the contrasts between movements of the left and the right side, and between movements paced at 1.25 Hz and at all other frequencies entering the analysis. Analyses of simple effects were performed to compare movements of the left and right side at each pacing frequency.

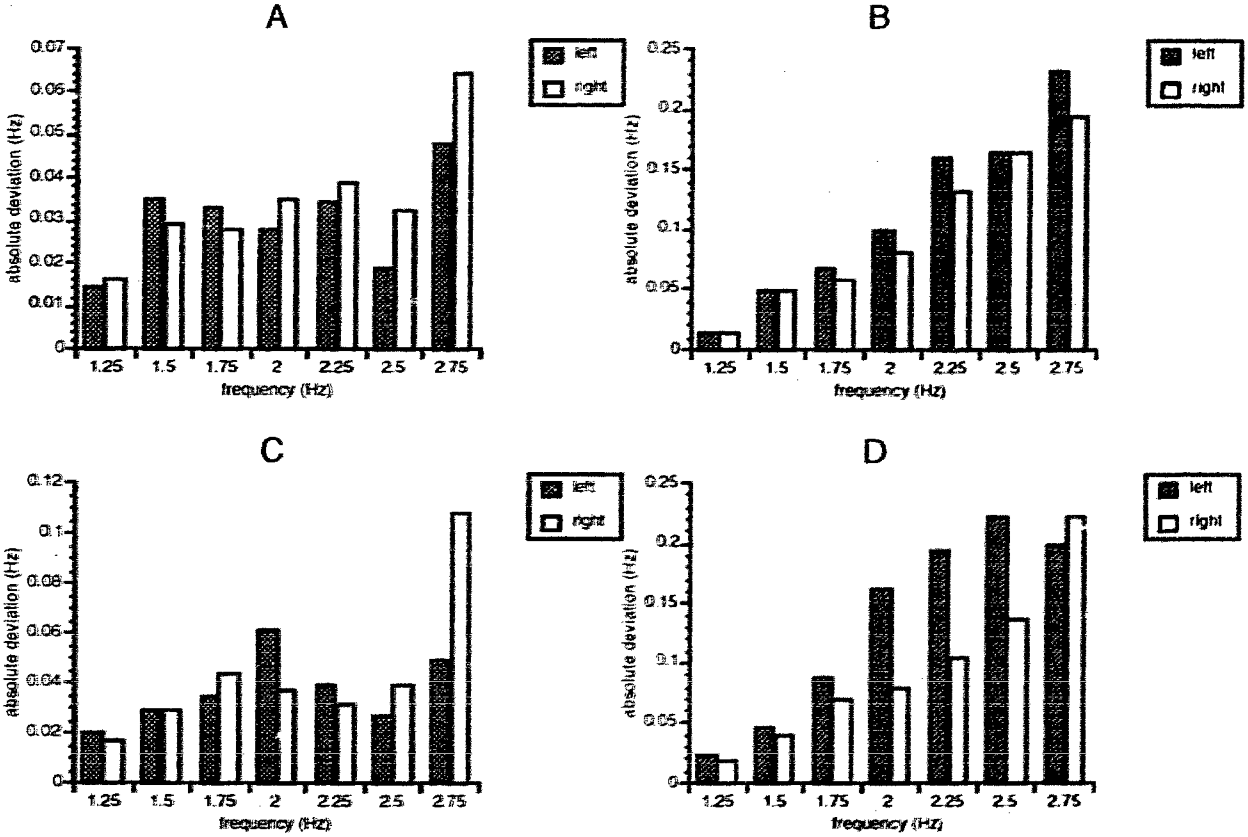

Fig. 5.4. Absolute deviation from metronome frequency as a function of side and pacing frequency for subjects W (panel A), X (panel B), Y (panel C), and Z (panel D).

As Figure 5.4 illustrates, there was a general tendency for the degree of deviation from the metronome to increase with scaling of frequency. This was confirmed by a number of the individual subject analyses.

Subject: W

Although deviation scores for the left and right side were overall equivalent (F(1, 46) = 2.43, $p > 0.10$), it was noted that when paced at a frequency of 2.75 Hz movements of the right side deviated to a greater degree from the frequency of the metronome than movements of the left side. Deviations were also less when movements were paced at 1.25 Hz than when paced at all other frequencies.

TABLE 5.1 Summary table of absolute deviations from metronome frequency, F values for pairwise comparisons between 1.25 Hz and all other frequencies, and left side versus right side comparisons (simple effects)for each frequency: subject W

| | | | | Frequency Hz | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| left | 0.014 | 0.035 | 0.033 | 0.028 | 0.034 | 0.019 | 0.048 |
| right | 0.016 | 0.030 | 0.028 | 0.035 | 0.039 | 0.033 | 0.064 |
| vs. 1.25 | - | **32.46 | **39.54 | **30.83 | **68.38 | **12.62 | **22.16 |
| L. vs. R. | F < 1 | F < 1 | F < 1 | F < 1 | F < 1 | 3.47 | *4.78 |

**$p < 0.01$, *$p < 0.05$, d.f. (1, 46)

Subject: X

The degree of deviation from the metronome frequency was equivalent for movements of the left and the right side (F(1, 46) = 1.37, $p > 0.20$). Deviations from the metronome frequency were smaller when movements were paced at 1.25 Hz than when paced at all other frequencies.

TABLE 5.2 Summary table of absolute deviations from metronome frequency, F values for pairwise comparisons between 1.25 Hz and all other frequencies, and left side versus right side comparisons (simple effects)for each frequency: subject X

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| left | 0.015 | 0.048 | 0.068 | 0.100 | 0.159 | 0.165 | 0.233 |
| right | 0.014 | 0.050 | 0.059 | 0.082 | 0.133 | 0.164 | 0.195 |
| vs. 1.25 | - | **39.92 | **41.33 | **52.67 | **105.05 | **88.00 | **122.44 |
| L. vs. R. | F < 1 | F < 1 | F < 1 | F < 1 | 1.36 | F < 1 | 2.78 |

**p < 0.01, d.f. (1, 46)

Subject: Y

Movements of the left and right side were not distinguished in terms of their deviation from the metronome frequency ($F(1, 46) = 2.92$, $p > 0.05$). However decomposition of this contrast revealed that when movements were paced at 2.00 Hz, those of the left side deviated from the metronome to a greater degree than those of the right side, while when paced at 2.75 Hz this difference was reversed. Deviations from the metronome frequency were present in smaller degree when movements were paced at 1.25 Hz than when paced at all other frequencies.

TABLE 5.3 Summary table of absolute deviations from metronome frequency, F values for pairwise comparisons between 1.25 Hz and all other frequencies, and left side versus right side comparisons (simple effects)for each frequency: subject Y

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| left | 0.020 | 0.029 | 0.034 | 0.061 | 0.039 | 0.027 | 0.049 |
| right | 0.016 | 0.029 | 0.043 | 0.036 | 0.031 | 0.039 | 0.108 |
| vs. 1.25 | - | **11.64 | **59.24 | **29.57 | **16.87 | **9.19 | **57.60 |
| L. vs. R. | F < 1 | F < 1 | F < 1 | **6.98 | F < 1 | 1.79 | **40.42 |

**p < 0.01, d.f. (1, 46)

Subject: Z

The degree of deviation from the metronome frequency was greater for movements of the left side (0.133 Hz) than for movements of the right side (0.096 Hz) (F(1, 46) = 6.12, $p < 0.05$). This effect was evident when movements were paced at 2.00 Hz, 2.25 Hz, and 2.50 Hz. Deviations from the metronome frequency were of lesser magnitude when movements were paced at 1.25 Hz than when paced at all other frequencies.

TABLE 5.4 Summary table of absolute deviations from metronome frequency, F values for pairwise comparisons between 1.25 Hz and all other frequencies, and left side versus right side comparisons (simple effects)for each frequency: subject Z

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| left | 0.022 | 0.046 | 0.088 | 0.163 | 0.194 | 0.223 | 0.199 |
| right | 0.020 | 0.039 | 0.071 | 0.080 | 0.104 | 0.136 | 0.223 |
| vs. 1.25 | - | **11.66 | **24.98 | **44.59 | **66.28 | **94.66 | **84.20 |
| L. vs. R. | F < 1 | F < 1 | F < 1 | **9.26 | **10.53 | **10.01 | F < 1 |

**$p < 0.01$, d.f. (1, 46)

5.3.2 Stationarity of Discrete Relative Phase

Discrete relative phase values obtained for each frequency plateau were tested for uniformity using the Rayleigh test (Mardia, 1972). Data from trials in each forearm position condition were pooled and the number of trials exhibiting phase wandering was expressed as a percentage of the total number of trials in each combination of side, mode of coordination and pacing frequency. In addition a quasi-continuous measure of relative phase was obtained by performing a linear interpolation between the discrete relative phase values at the original sampling frequency. These data were transformed such that values expressed the "distance" from the in-phase and the anti-phase mode in the range 0 to 0.5. A value of 0 expressed perfect in-phase coordination, whereas a value of 0.5 expressed perfect anti-phase coordination. These data were rectified and histograms constructed of the proportion of the total trial time accounted for by values of the transformed relative phase series in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50 (Figures 5.2 - 5.5). These data are reported independently for each subject.

Phase transitions were examined using a partially interactive procedure which allowed the experimenter to view relative phase profiles via a graphical interface. The procedure was developed in-house and requires that the operator broadly delineate pre and post-transition regions. The specification of critical points is essentially "automatic". Details of the procedure and estimates of reliability and validity have been reported elsewhere (Byblow, Carson, Goodman, & Storlund, 1992). For trials exhibiting phase transitions, this procedure reported the time of the onset of a transition.

### Enumeration of phase transitions

Subject: W

When prepared in the anti-phase mode of coordination, phase transitions were observed for movements of the left side and of the right side in 6 of 12 (50%) trials in each case ($\chi^2$ (1) = 0.17, $p > 0.05$). When prepared in the in-phase mode, 1 of 12 (8%) trials for movements of both the left and right side side exhibited transitions to phase wandering ($\chi^2$ (1) = 0.55, $p > 0.05$).

TABLE 5.5 Summary table showing the proportion of trials for which the hypothesis of uniformity was supported ($p < 0.01$).subject W

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left side | 100% | 100% | 100% | 100% | 100% | 100% | 75% |
| right side | 100% | 100% | 100% | 100% | 91.7% | 100% | 66.7% |
| in-phase | | | | | | | |
| left side | 100% | 100% | 100% | 100% | 100% | 100% | 100% |
| right side | 100% | 100% | 100% | 100% | 100% | 100% | 91.7 |

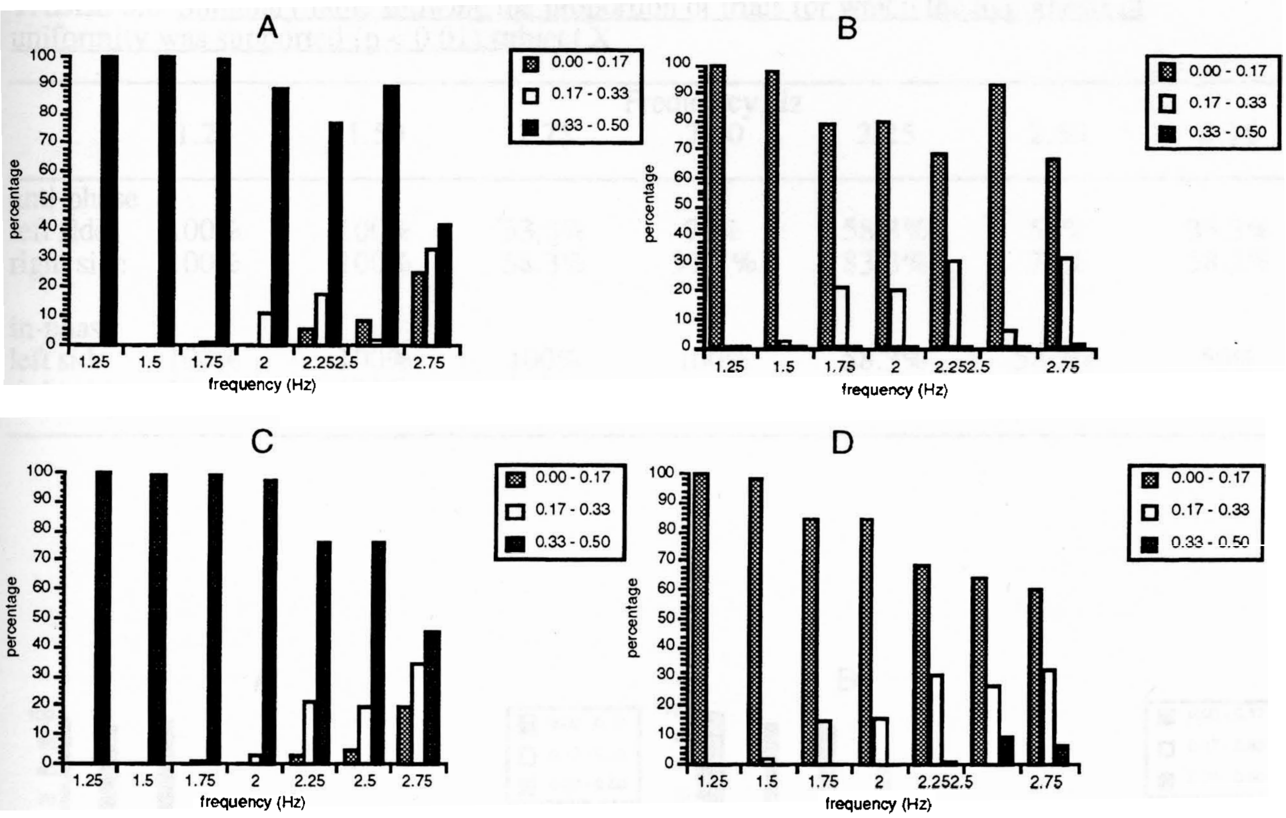

Fig. 5.5. Subject: W, proportion of total time accounted for by transformed relative phase values in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50, left side (anti-phase) (A), left side (in-phase) (B), right side (anti-phase) (C), right side (anti-phase) (D).

Subject: X

For movements conducted by both the left and right side, 12 of 12 (100%) trials prepared in the anti-phase mode of cordination exhibited phase transitions in each case ($\chi^2$ (1) = 0.00, p > 0.05). When prepared in the in-phase mode of coordination, phase transitions were observed for movements of the left side, in 10 of 12 trials (83%) and in 7 of 12 trials (58%) for movements of the right side ($\chi^2$ (1) = 0.81, p > 0.05).

TABLE 5.6 Summary table showing the proportion of trials for which the hypothesis of uniformity was supported ($p < 0.01$).subject X

|  | Frequency Hz |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase |  |  |  |  |  |  |  |
| left side | 100% | 100% | 33.3% | 75% | 58.3% | 50% | 33.3% |
| right side | 100% | 100% | 58.3% | 91.7% | 83.3% | 75% | 58.3% |
| in-phase |  |  |  |  |  |  |  |
| left side | 100% | 100% | 100% | 100% | 58.3% | 58.3% | 50% |
| right side | 100% | 100% | 100% | 100% | 91.7% | 75% | 75% |

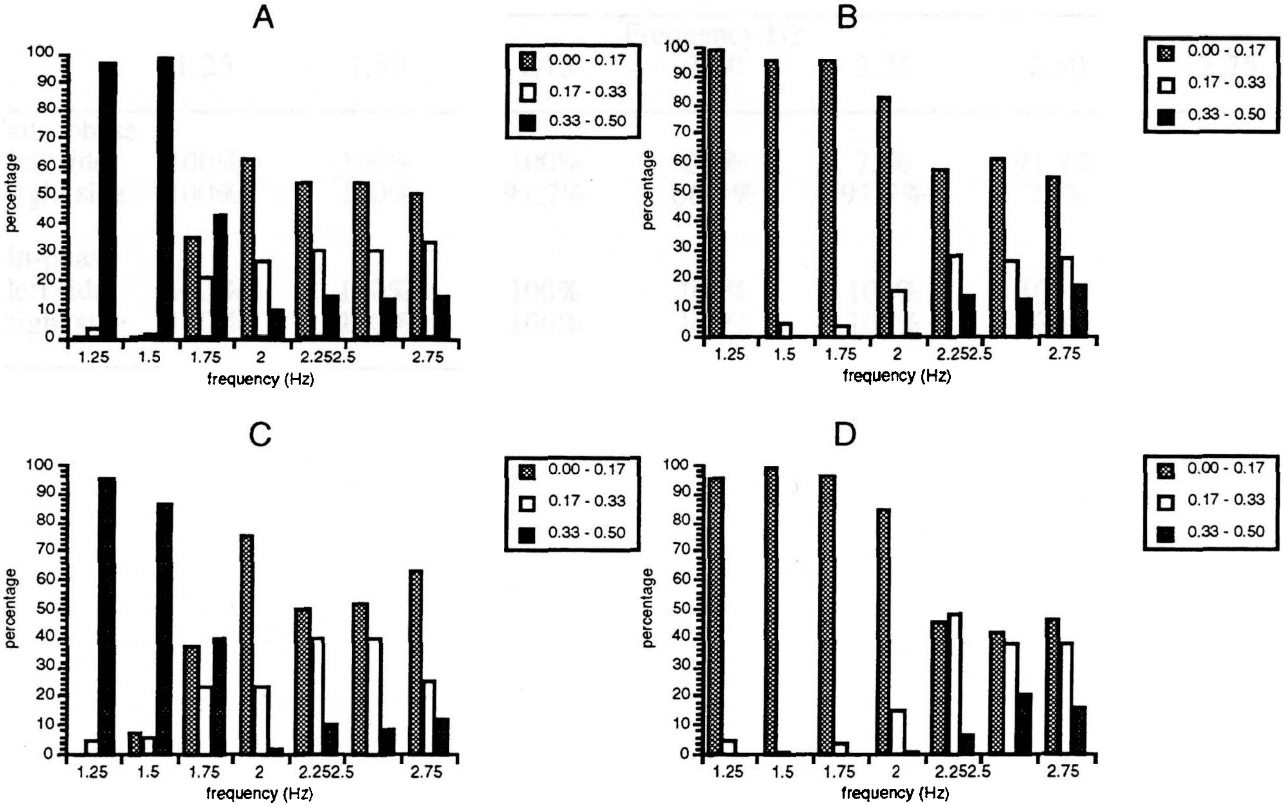

Fig. 5.6. Subject: X, proportion of total time accounted for by transformed relative phase values in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50, left side (anti-phase) (A), left side (in-phase) (B), right side (anti-phase) (C), right side (anti-phase) (D).

Subject: Y

For movements conducted by both the left and right side, 12 of 12 (100%) trials prepared in the anti-phase mode of coordination in each case exhibited phase transitions ($\chi^2$ (1) = 0.00, $p > 0.05$). Movements of the left side prepared in the in-phase mode revealed phase transitions in 6 of 12 (50%) trials. Corresponding movements of the right side revealed phase transitions in 1 of 12 (8%) trials ($\chi^2$ (1) = 3.23, $p > 0.05$).

TABLE 5.7 Summary table showing the proportion of trials for which the hypothesis of uniformity was supported ($p < 0.01$).subject Y

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left side | 100% | 100% | 100% | 50% | 75% | 91.7% | 100% |
| right side | 100% | 100% | 91.7% | 66.7% | 91.7% | 75% | 66.7% |
| in-phase | | | | | | | |
| left side | 100% | 100% | 100% | 100% | 100% | 100% | 75% |
| right side | 100% | 100% | 100% | 100% | 100% | 100% | 100% |

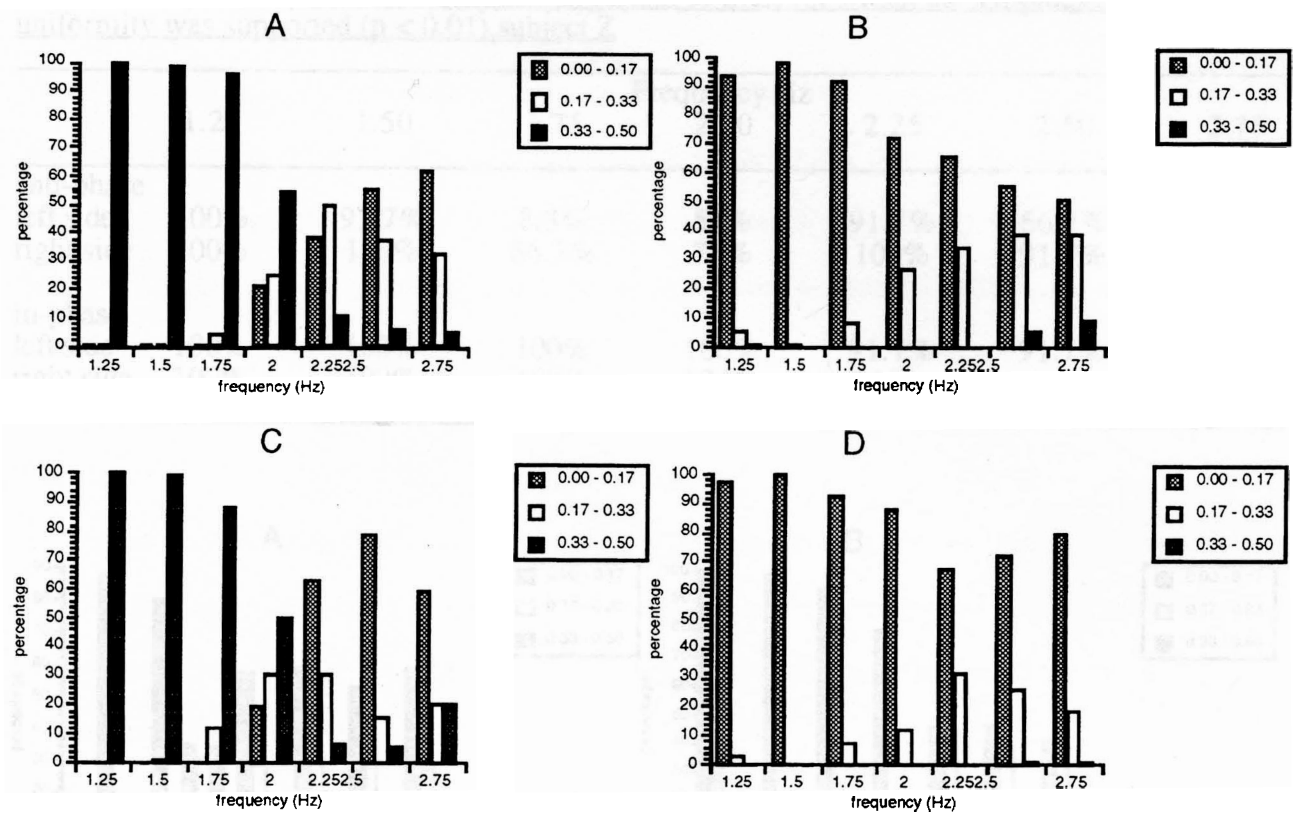

Fig. 5.7. Subject: Y, proportion of total time accounted for by transformed relative phase values in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50, left side (anti-phase) (A), left side (in-phase) (B), right side (anti-phase) (C), right side (anti-phase) (D).

Subject: Z

Movements of both the left and right side exhibited phase transitions in 12 of 12 (100%) trials prepared in the anti-phase mode of coordination ($\chi^2$ (1) = 0.00, p > 0.05). When prepared in-phase, 10 of 12 (83%) movements of the left side, and 7 of 12 (58%) movements of the right side were associated with phase transitions ($\chi^2$ (1) = 0.81, p > 0.05).

TABLE 5.8 Summary table showing the proportion of trials for which the hypothesis of uniformity was supported ($p < 0.01$).subject Z

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left side | 100% | 91.7% | 8.3% | 50% | 91.7% | 66.7% | 83.3% |
| right side | 100% | 100% | 66.7% | 75% | 100% | 91.7% | 25% |
| in-phase | | | | | | | |
| left side | 100% | 100% | 100% | 100% | 91.7% | 91.7% | 75% |
| right side | 100% | 100% | 100% | 100% | 100% | 100% | 91.7% |

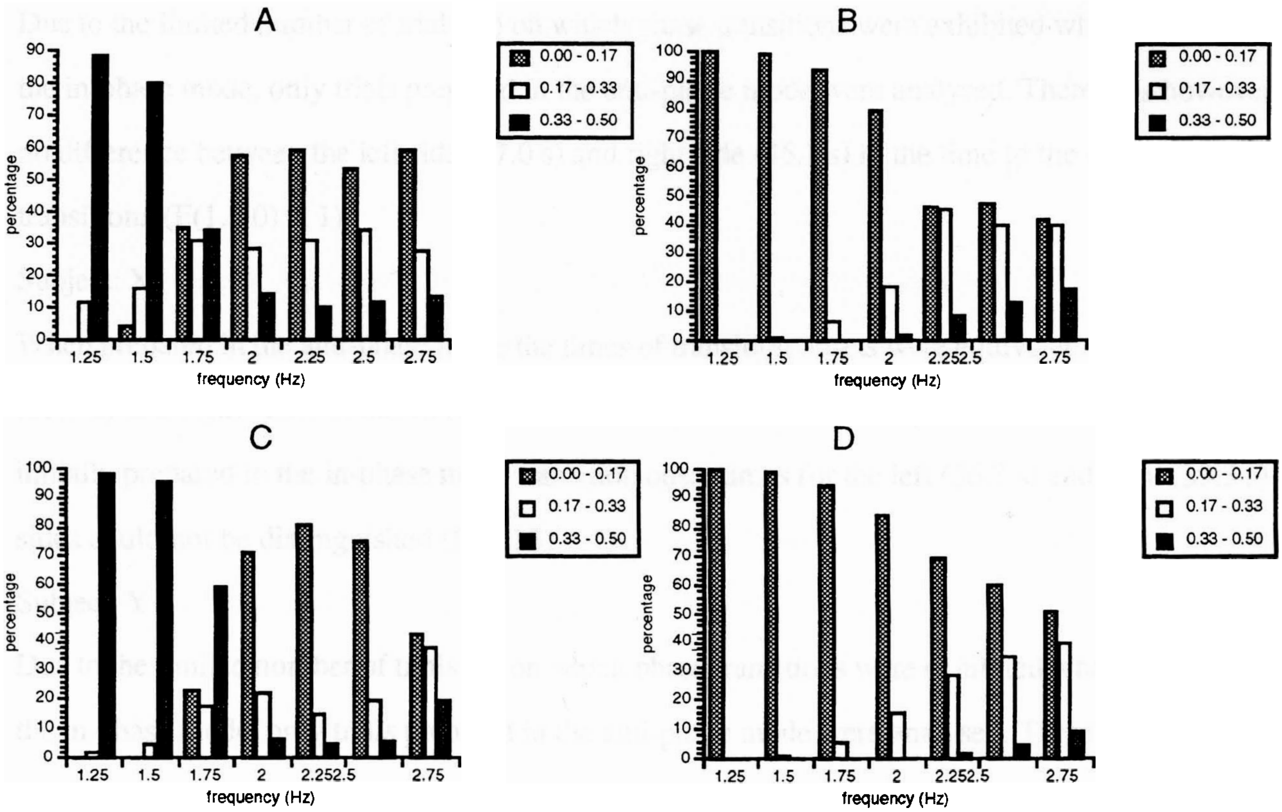

Fig. 5.8 Subject: Z, proportion of total time accounted for by transformed relative phase values in the ranges 0.00 - 0.17, 0.17 - 0.33, and 0.33 - 0.50, left side (anti-phase) (A), left side (in-phase) (B), right side (anti-phase) (C), right side (anti-phase) (D).

### 5.3.3 Transition Onset Times

As the number of transitions observed differed appreciably between modes, anti-phase and in-phase trials were treated independently. For each subject, these data were analysed using a 2 side (left, right) by 2 forearm position (pronated, supinated) design. Each trial was treated as a single case. Planned orthogonal comparisons of means were performed to highlight the contrast between movements of the left and of the right side.

Subject: W

Due to the limited number of trials (2) on which phase transitions were exhibited when prepared in the in-phase mode, only trials prepared in the anti-phase mode were analysed. There was however no difference between the left side (47.0 s) and right side (46.1 s) in the time to the onset of transitions (F(1, 10) < 1).

Subject: X

When prepared in the anti-phase mode the times of transition onsets were equivalent for the left (20.7 s) and right (18.9 s) hands (F(1, 20) = 1.52, p > 0.20). Similarly, when movements were initially prepared in the in-phase mode transition onset times for the left (36.7 s) and right (39.3 s) sides could not be distinguished (F(1, 13) < 1).

Subject: Y

Due to the limited number of trials (7) on which phase transitions were exhibited when prepared in the in-phase mode, only trials prepared in the anti-phase mode were analysed. There was however no difference between the left side (30.5 s) and right side (30.4 s) in the time to the onset of transitions (F(1, 20) < 1).

Subject: Z

When prepared in the anti-phase mode the times of transition onsets were equivalent for the left (18.9 s) and right (21.0 s) hands (F(1, 20) = 1.96, p > 0.15). Similarly, when movements were initially prepared in the in-phase mode transition onset times for the left (40.0 s) and right (44.3 s) sides were not different (F(1, 13) < 1).

### 5.3.4 Pre Transition Behaviour

In order to probe for one of the signature features of transitional behaviour, the presence of critical fluctuations, the uniformity of relative phase was assessed in the regions prior to the onset of transitions. Analyses of variance for transformed uniformity scores were performed for each subject using a single factor (normalized pretransition isofrequency plateau (t - n)) repeated measures design. As a consequence of wide differences in the transition frequency, the number of pretransition plateaus entering into analyses were not equivalent for all subjects. Anti-phase and in-phase trials were also treated independently. In performing these analyses, data were pooled for each subject by collapsing over side and by forearm position. Each trial was treated as a single case.

Subject: W

Anti-phase trials were analysed using four levels of pretransition plateau. As is evident from Figure 5.9A, the degree of consistency exhibited on the plateau immediately prior to transition was less than on preceding plateaus ($F(3, 33) = 4.69$, $p < 0.01$). Pairwise comparison of means using the Tukey HSD procedure confirmed that the consistencies of relative phase on the t - 1 plateau were distinguished from those associated with all other plateaus ($p < 0.01$). As only two transitions were observed on in-phase trials it was not possible to conduct a meaningful analysis of pretransition plateaus for these data.

Subject: X

In pooling all anti-phase data, two trials on which transitions were exhibited on the second (1.50 Hz) plateau were excluded. This step enabled two levels of pretransition plateau to be used in analysis of the remaining (22) trials. Figure 5.9B illustrates that the consistency of relative phase on the t -1 plateau was less than on the t - 2 plateau. This was confirmed by the analysis of variance ($F(1, 21) = 4.98$, $p < 0.05$). In-phase trials were analysed using three levels of pretransition plateau. It was again noted that consistency values on the immediate pretransition plateau (t - 1) were lower than on plateaus t - 2 and t -3 (F(2, 32) = 8.62, $p < 0.01$). Consistency values for plateau t -1 were different to a statistically significant degree from those for plateau t -3 ($p < 0.01$, Tukey HSD).

Subject: Y

Anti-phase trials were analysed using three levels of pretransition plateau (Figure 5.9C). An effect for plateau was evident (F(2, 46) = 20.02, $p < 0.0001$). Pairwise comparison of means using the Tukey HSD procedure indicated that consistency values on plateau t -1 were lower than on both the t - 2 and t - 3 plateaus ($p < 0.01$). In-phase trials were analysed using five levels of pretransition plateau. There was no indication of an overall effect for plateau (F(4, 24) = 1.85, $p > 0.15$).

Subject: Z

In pooling all anti-phase data, one trial on which a transition was exhibited on the second (1.50 Hz) plateau was excluded. This step enabled two levels of pretransition plateau to be used in analysis of the remaining (23) trials. As inspection of Figure 5.9D reveals, consistency of relative phase was less on the t -1 plateau than on the t - 2 plateau (F(1, 22) = 8.92, $p < 0.01$). Three levels of plateau were employed in the analysis of in-phase trials. An effect of plateau was noted (F(2, 30) = 6.66) $p < 0.01$). Pairwise comparison of means (Tukey HSD) indicated that consistency values were lower for the t -1 plateau than for both the t - 2 and t - 3 plateau ($p < 0.05$).

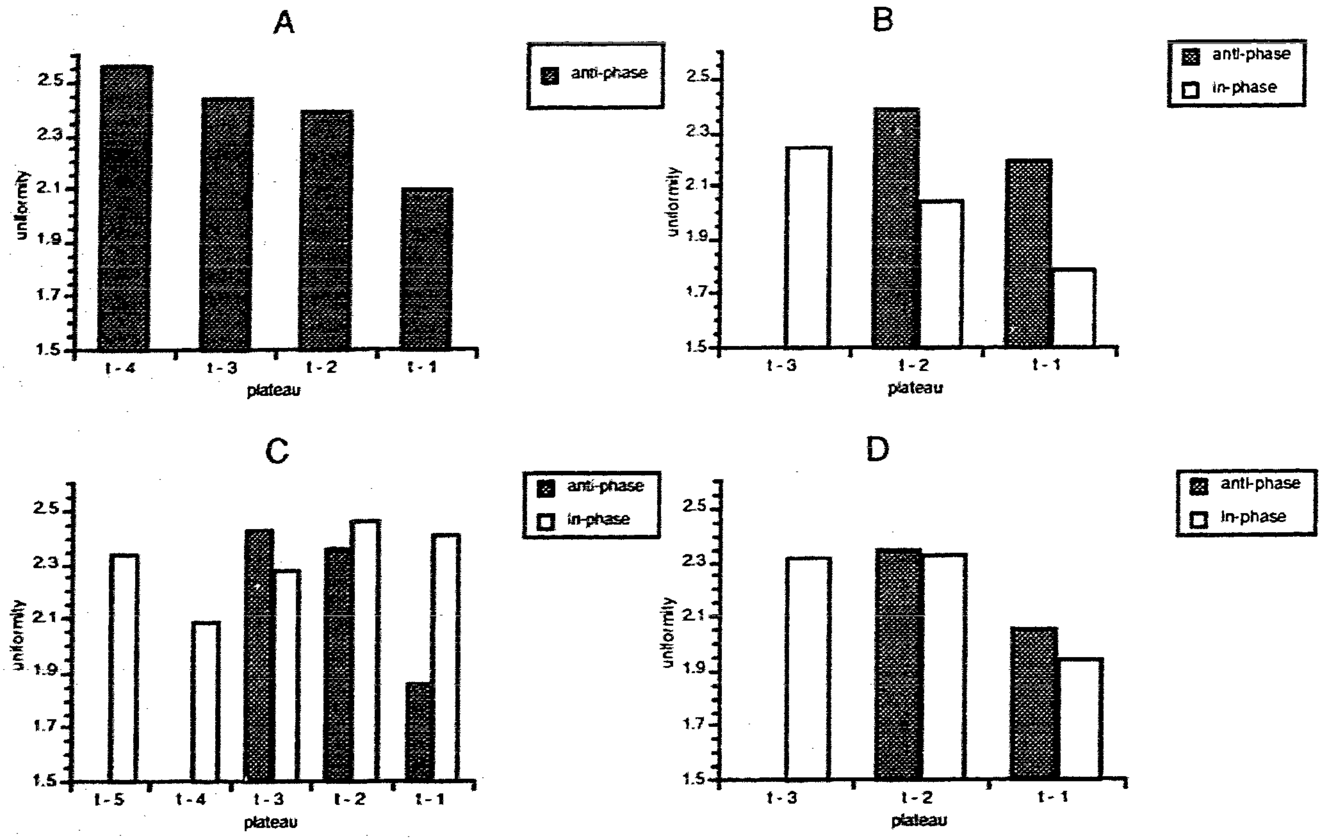

Fig. 5.9. Mean consistency for subject W (A), X (B), Y (C), Z (D) in coupled conditions, as a function of mode and pretransition frequency plateau.

### 5.3.5 Transition Pathways

All transitions were classified with respect to the direction in which relative phase "moved" during the transition. Positive values reflected an increasing value of relative phase at transition corresponding to the ankle gaining at least one half cycle relative to the wrist. Whereas negative values indicate the ankle has lost at least one half cycle relative to the wrist. For the purposes of these classifications, data were pooled for each subject by collapsing over side and by forearm position. Analyses (binomial expansions) were conducted to determine the probability of obtaining through chance the observed distributions of transition pathways (Ferguson, 1971). In order to control for the potential inflation of Type I errors resulting from multiple comparisons, alpha was assigned as $p = 0.01$.

Subject: W

For movements initially prepared in the anti-phase mode, 58% (7/12) exhibited negative transition pathways ($p > 0.15$). Only two trials prepared in the in-phase mode exhibited transitions. One transition pathway was positive, the other was negative.

Subject: X

Of movements initiated in the anti-phase mode of coordination, 71% (17/24) exhibited negative transition pathways ($p < 0.01$). Of those prepared in the in-phase mode, 65% (11/17) showed negative transition pathways ($p > 0.05$).

Subject: Y

Of movements initiated in the anti-phase mode of coordination, 75% (18/24) exhibited negative transition pathways ($p < 0.01$). Only seven trials prepared in the in-phase mode exhibited transitions. Three transition pathways were negative, the remaining four were positive.

Subject: Z

Of movements initiated in the anti-phase mode of coordination, 96% (23/24) exhibited negative transition pathways ($p < 0.01$). Of those prepared in the in-phase mode, 12% (2/17) showed negative transition pathways ($p < 0.01$).

### 5.3.6 Relative Phase Relations

Estimates of mean relative phase and of the uniformity of relative phase were obtained for all frequency plateaus prior to the onset of phase transitions. As a consequence of wide differences in the transition frequencies, the number of pretransition plateaus entering into these analyses were not equivalent for all subjects. Anti-phase and in-phase trials were also treated independently. For a level of frequency to be entered into an analysis, it was necessary that all trials in a given mode of coordination were stable at that frequency. Data were pooled for each subject by collapsing over forearm position. In calculating test statistics for mean relative phase, in order to control for the potential inflation of Type I errors resulting from multiple comparisons, alpha was assigned as $p = 0.01$. Mean relative phase values were also assessed with respect to the target relative phase value for each mode of coordination. Confidence intervals (99%) were calculated following Mardia (1972) (see also Batschelet 1981). Analyses of variance for transformed uniformity scores were performed for each subject using a 2 side (left, right) by pacing frequency design. Each trial was treated as a single case. Side was a grouping factor and frequency was a within case factor. Mean values reported in the text correspond to transformed uniformity scores.

Subject: W

Mean Relative Phase

Movements of the left and right side were observed to differ in terms of mean relative phase only when movements were conducted in the anti-phase mode and paced at 1.75 Hz. It was notable that in both modes of coordination there was a consistent trend towards increasing values of relative phase with increases in pacing frequency (Table 3.2.1). This was reflected in statistically significant differences between these values and those obtained at 1.25 Hz. At higher pacing frequencies (above 1.50 Hz) relative phase values also tended to deviate from target values to a substantial degree.

TABLE 5.9 Summary table of mean relative phase, 99% confidence intervals, and F values for pairwise comparisons between the left and right side for each frequency, and between 1.25 Hz and all other stable frequencies for each side: subject W

|  |  |  |  | Frequency Hz |  |  |  |
|---|---|---|---|---|---|---|---|
|  | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase |  |  |  |  |  |  |  |
| left | 175.5 | 167.7 | †197.5 | †208.5 | N.A. | N.A. | N.A. |
| 99% c.i. | ±8° | ±14° | ±8° | ±14° | N.A. | N.A. | N.A. |
| vs. 1.25 | - | 2.28 | *31.56 | *39.13 | N.A. | N.A. | N.A. |
| right | †164.9 | †157.4 | 174.1 | †195.5 | N.A. | N.A. | N.A. |
| 99% c.i. | ±10° | ±8° | ±16° | ±10° | N.A. | N.A. | N.A. |
| vs. 1.25 | - | 3.46 | 2.45 | *46.77 | N.A. | N.A. | N.A. |
| L. vs. R. | 7.14 | 3.91 | *16.02 | 5.21 | N.A. | N.A. | N.A. |
| in-phase |  |  |  |  |  |  |  |
| left | 358.7 | 5.7 | †46.8 | †48.0 | †48.2 | N.A. | N.A. |
| 99% c.i. | ±10° | ±15° | ±10° | ±10° | ±18° | N.A. | N.A. |
| vs. 1.25 | - | 1.44 | *102.36 | *108.40 | *53.43 | N.A. | N.A. |
| right | 7.1 | †11.5 | †41.0 | †41.0 | †49.3 | N.A. | N.A. |
| 99% c.i. | ±8° | ±8° | ±11.5° | ±8° | ±17° | N.A. | N.A. |
| vs. 1.25 | - | 1.22 | *55.05 | *80.35 | *48.81 | N.A. | N.A. |
| L. vs. R. | 3.86 | 1.08 | 1.36 | 2.71 | < 1 | N.A. | N.A. |

†different from target relative phase value ($p < 0.01$, $n = 12$)
*$p < 0.01$, d.f. (1, 22)

### Uniformity of Relative Phase

For movements prepared in the anti-phase mode, the measure of uniformity failed to distinguish movements made by the left and the right sides ($F(1, 22) < 1$). A main effect for frequency was noted ($F(3, 66) = 24.63$, $p < 0.0001$). Movements paced at a frequency of 1.25 Hz were more uniform with respect to relative phase than those paced at all other frequencies ($p < 0.01$, Tukey HSD). It was also the case that when prepared in the in-phase mode, movements of the left and right side were equivalent with respect to uniformity ($F(1, 22) < 1$). A main effect for frequency was noted ($F(4, 88) = 6.73$, $p < 0.001$). Decomposition of this effect using the Tukey HSD procedure indicated that movements paced at 1.25 Hz exhibited greater uniformity of relative phase than those paced at 1.50 Hz, 1.75 Hz, and 2.25 Hz ($p < 0.05$). In addition, movements paced at

2.00 Hz were more uniform with respect to relative phase than those paced at 1.50 Hz ($p < 0.05$). An interaction of side and pacing frequency was also present ($F(4, 88) = 5.11$, $p < 0.001$). Decomposition of this interaction using simple effects (Winer, 1962) indicated that uniformity values for the left side were greater than those of the right side when movements were paced at 2.25 Hz ($F(1, 108) = 8.89$, $p < 0.01$). In contrast, when movements were paced at 1.50 Hz, uniformity values for the right side were greater than those of the left side ($F(1, 108) = 4.87$, $p < 0.05$). At all other pacing frequencies, uniformity values for movements of the left and right sides were equivalent ($p > 0.05$).

TABLE 5.10 Summary table showing the uniformity of relative phase subject W

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left side | 3.03 | 2.43 | 2.41 | 2.48 | N.A. | N.A. | N.A. |
| right side | 2.99 | 2.53 | 2.35 | 2.34 | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left side | 2.73 | 2.31 | 2.60 | 2.76 | 2.72 | N.A. | N.A. |
| right side | 2.90 | 2.56 | 2.52 | 2.55 | 2.38 | N.A. | N.A. |

Subject: X

Mean Relative Phase

Movements of the left and right side were not distinguished in terms of mean relative phase. Due to the limited number of levels entering into the analysis, it was impossible to gauge any trends across frequencies when movements were conducted in the anti-phase mode (Table 3.2.3). In the in-phase mode, when movements were made by the right side, values of relative phase increased with increases in pacing frequency. It was also generally the case that mean values deviated to a statistically significant degree from target values when movements were prepared in the in-phase mode.

TABLE 5.11 Summary table of mean relative phase, 99% confidence intervals, and F values for pairwise comparisons between the left and right side for each frequency, and between 1.25 Hz and all other stable frequencies for each side: subject X

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left | †162.8 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ± 11.5° | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| right | †154.3 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ± 13° | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | 2.23 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left | †339.6 | †340.2 | †347.0 | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ± 10° | ± 4.5° | ± 10° | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | < 1 | 2.50 | N.A. | N.A. | N.A. | N.A. |
| right | †328.7 | †345.5 | 351.2 | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ± 10° | ± 4.5° | ± 14° | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | *18.41 | *16.27 | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | 5.55 | 2.74 | F < 1 | N.A. | N.A. | N.A. | N.A. |

†different from target relative phase value ($p < 0.01$, $n = 12$)
*$p < 0.01$, d.f. (1, 22)

Uniformity of Relative Phase

When movements were conducted in the anti-phase mode, the left and right side were equivalent with respect to uniformity ($F(1, 22) = 1.74$, $p > 0.20$). This was also the case for movements prepared in the in-phase mode ($F(1, 22) < 1$). However, in the latter case there was a main effect for frequency ($F(2, 44) = 11.16$, $p < 0.001$). Movements paced at a frequency of 1.25 Hz were more uniform with respect to relative phase than those paced at both 1.50 Hz and 1.75 Hz ($p < 0.05$, Tukey HSD). An interaction of side and pacing frequency was also present ($F(2, 44) = 6.43$, $p < 0.01$). Decomposition of this interaction indicated that uniformity values for the left side were greater than those of the right side when movements were paced at 1.25 Hz ($F(1, 66) = 6.47$,

$p < 0.02$). In contrast, when movements were paced at 1.75 Hz, uniformity values for the right side were greater than those of the left side ($F(1, 66) = 5.25$, $p < 0.05$). At 1.50 Hz, uniformity values for movements of the left and right sides were equivalent ($F < 1$).

TABLE 5.12 Summary table showing the uniformity of relative phase subject X

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left side | 2.55 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| right side | 2.36 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left side | 2.67 | 2.27 | 2.04 | N.A. | N.A. | N.A. | N.A. |
| right side | 2.39 | 2.35 | 2.30 | N.A. | N.A. | N.A. | N.A. |

Subject: Y

Mean Relative Phase

Movements of the left and right side differed in terms of mean relative phase only when movements were conducted in the anti-phase mode and paced at 1.75 Hz.

In the in-phase mode there was a tendency towards increasing values of relative phase with increases in pacing frequency (Table 3.2.5). In this mode, mean relative phase values most closely approached target values at a pacing frequency of 1.75 Hz. At lower and higher pacing frequencies mean values tended to be less than and greater than target values respectively. In the anti-phase mode it was more difficult to resolve trends due to the limited number of levels of pacing frequency. However, when movements were conducted by the right side there was an apparent tendency toward increases in relative phase which paralleled increases in frequency.

TABLE 5.13 Summary table of mean relative phase, 99% confidence intervals, and F values for pairwise comparisons between the left and right side for each frequency, and between 1.25 Hz and all other stable frequencies for each side: subject Y

| | | | | Frequency Hz | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left | 179.1 | 177.4 | 172.4 | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | < 1 | 1.91 | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ± 11.5° | ± 8° | ± 10° | N.A. | N.A. | N.A. | N.A. |
| right | 173.3 | 180.8 | †197.7 | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | 4.92 | *32.98 | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ± 8° | ± 4.5° | ± 10° | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | 1.64 | 1.04 | *30.44 | N.A. | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left | 344.5 | 353.8 | 12.7 | †48.0 | †50.4 | N.A. | N.A. |
| vs. 1.25 | - | 1.81 | *12.04 | *90.19 | *66.81 | N.A. | N.A. |
| 99% c.i. | ± 19° | ± 11.5° | ± 17° | ± 8° | ± 16° | N.A. | N.A. |
| right | †331.9 | †347.3 | 10.2 | †40.8 | †43.6 | N.A. | N.A. |
| vs. 1.25 | - | *16.59 | *32.16 | *231.54 | *65.95 | N.A. | N.A. |
| 99% c.i. | ± 10° | ± 4.5° | ± 19° | ± 10° | ± 24.5° | N.A. | N.A. |
| L. vs. R. | 3.46 | 2.53 | F < 1 | 2.84 | F < 1 | N.A. | N.A. |

†different from target relative phase value ($p < 0.01$, $n = 12$)
*$p < 0.01$, d.f. (1, 22)

### Uniformity of Relative Phase

When movements were prepared in the anti-phase mode, the left side and right side were equivalent in terms of the uniformity of relative phase ($F(1, 22) = 1.69$, $p > 0.20$). A main effect for frequency was present ($F(2, 44) = 22.50$, $p < 0.0001$). Movements paced at a frequency of 1.75 Hz were less uniform than those paced at 1.50 Hz and 1.25 Hz ($p < 0.01$, Tukey HSD). When prepared in the in-phase mode, movements of the left and right side were equivalent with respect to this measure ($F(1, 22) < 1$). There was however a main effect for frequency ($F(4, 88) = 14.84$, $p < 0.0001$). Decomposition of this effect using the Tukey HSD procedure indicated that movements paced at 1.75 Hz were less uniform than movements paced at all other frequencies ($p < 0.01$).

TABLE 5.14 Summary table showing the uniformity of relative phase subject Y

| | Frequency Hz<br>1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
|---|---|---|---|---|---|---|---|
| anti-phase | | | | | | | |
| left side | 2.44 | 2.51 | 2.06 | N.A. | N.A. | N.A. | N.A. |
| right side | 2.52 | 2.44 | 1.82 | N.A. | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left side | 2.25 | 2.49 | 1.96 | 2.22 | 2.54 | N.A. | N.A. |
| right side | 2.37 | 2.47 | 1.92 | 2.43 | 2.42 | N.A. | N.A. |

Subject: Z

Mean Relative Phase

Movements of the left and right side were not distinguished in terms of mean relative phase (Table 3.2.4). There was also no evidence to suggest the presence of differences in mean relative phase between movements paced at 1.25 Hz and 1.50 Hz in the in-phase mode. In both modes of coordination, mean relative phase values were not distinguishable from target values.

TABLE 5.15 Summary table of mean relative phase, 99% confidence intervals, and F values for pairwise comparisons between the left and right side for each frequency, and between 1.25 Hz and all other stable frequencies for each side: subject Z

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left | 158.9 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ±23° | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| right | 171.4 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ±16° | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | 1.85 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left | 359.1 | 10.0 | N.A. | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ±13° | ±14° | N.A. | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | 3.18 | N.A. | N.A. | N.A. | N.A. | N.A. |
| right | 8.5 | 12.1 | N.A. | N.A. | N.A. | N.A. | N.A. |
| 99% c.i. | ±13° | ±14° | N.A. | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | < 1 | N.A. | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | 2.53 | F < 1 | N.A. | N.A. | N.A. | N.A. | N.A. |

†different from target relative phase value ($p < 0.01$, $n = 12$)
*$p < 0.01$, d.f. (1, 22)

Uniformity of Relative Phase

When movements were conducted in the anti-phase mode, the left and right side were equivalent with respect to uniformity ($F(1, 22) < 1$). For movements prepared in the in-phase mode there was a tendency for movements of the right side to exhibit larger uniformity values than movements of the left side, however this trend failed to meet conventional levels of statistical significance ($F(1, 22) = 3.54$, $p = 0.07$). A tendency for movements paced at 1.25 Hz to exhibit larger uniformity values than those paced at 1.50 Hz also failed to attain statistical significance ($F(1, 22) = 3.91$, $p = 0.06$).

TABLE 5.16 Summary table showing the uniformity of relative phase subject Z

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left side | 2.39 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| right side | 2.31 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left side | 2.47 | 2.30 | N.A. | N.A. | N.A. | N.A. | N.A. |
| right side | 2.61 | 2.50 | N.A. | N.A. | N.A. | N.A. | N.A. |

### 5.3.7 Discrete Frequency:

Coefficients of variation and discrete frequencies were obtained for all frequency plateaus prior to the onset of phase transitions. As a consequence of wide differences in the transition frequencies, the number of pretransition plateaus entering into these analyses were not equivalent for all subjects. Anti-phase and in-phase trials were also treated independently. For a level of frequency to be entered into an analysis, it was necessary that all trials in a given mode of coordination were stable at that frequency. Data were pooled for each subject by collapsing over forearm position. Analyses of variance for these measures were performed for each subject using a 2 side (left, right) by 2 joint (wrist, ankle) by 7 pacing frequency design. Each trial was treated as a single case. Side was a grouping factor, and joint and metronome frequency were within case factors. In the case of coefficients of variation, planned orthogonal comparisons of means were performed to highlight the contrasts between movements of the left and the right side, and between movements paced at 1.25 Hz and all other frequencies entering the analysis. Analyses of simple effects (Winer, 1962) were performed to compare movements of the left and right side at each pacing frequency. Discrete frequencies for movements of the left and the right side were examined at each pacing frequency using analyses of simple effects.

Subject: W

For movements prepared in the anti-phase mode of coordination, mean frequencies were equivalent for movements of the left and right side ($p > 0.20$) at pacing frequencies of 1.25, 1.50, and 1.75 Hz. However, when movements were paced at 2.00 Hz, movements of the left side (2.01 Hz) exhibited mean frequencies which were lower than those exhibited by movements of the right side (2.04 Hz) ($F(1, 87) = 9.95$, $p < 0.01$). When movements were prepared in the in-phase mode, elicited frequencies were essentially identical for the left and right side at all pacing frequencies ($p > 0.05$). Movements of the left and right side were not distinguished overall in terms of coefficients of variation ($F(1, 22) < 1$) when prepared in either the in-phase or anti-phase mode. However, it was noted that for movements prepared in-phase and paced at 1.50 Hz, movements of the left side exhibited larger coefficients than those of the right side. In both modes, larger coefficients of variation were present for movements paced at 1.50 Hz and 1.75 Hz, and in the anti-phase mode for movements paced at 2.00 Hz, than for movements paced at 1.25 Hz.

TABLE 5.17 <u>Summary table of coefficients of variation, F values for pairwise comparisons between 1.25 Hz and all other frequencies, and left side versus right side comparisons (simple effects)for each frequency: subject W</u>

| | | | | Frequency Hz | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left | 3.55 | 6.01 | 5.67 | 5.03 | N.A. | N.A. | N.A. |
| right | 3.87 | 5.78 | 5.66 | 5.29 | N.A. | N.A. | N.A. |
| vs. 1.25 | - | **27.17 | **25.84 | **12.78 | N.A. | N.A. | N.A. |
| L. vs. R. | F < 1 | F < 1 | F < 1 | F < 1 | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left | 3.93 | 6.72 | 4.62 | 3.53 | 3.20 | N.A. | N.A. |
| right | 3.37 | 5.42 | 4.85 | 3.96 | 3.90 | N.A. | N.A. |
| vs. 1.25 | - | **37.09 | *7.52 | F < 1 | F < 1 | N.A. | N.A. |
| L. vs. R. | 1.24 | †6.59 | F < 1 | F < 1 | 1.92 | N.A. | N.A. |

*$p < 0.05$, d.f. (1, 22)
**$p < 0.01$, d.f. (1, 22)
†$p < 0.05$, d.f. (1, 110)

Subject: X

For movements prepared in the anti-phase mode of coordination, mean frequencies were equivalent for movements of the left and right side ($F < 1$). This was also the case for all pacing frequencies when movements were prepared in the in-phase mode ($F < 1$).

Movements of the left and right side were not distinguished overall in terms of coefficients of variation ($p > 0.05$) when prepared in either the in-phase or anti-phase mode. However, it was noted that for movements prepared in-phase, larger coefficients of variation were present for movements paced at 1.50 Hz and 1.75 Hz than for movements paced at 1.25 Hz.

TABLE 5.18 Summary table of coefficients of variation, F values for pairwise comparisons between 1.25 Hz and all other frequencies, and left side versus right side comparisons (simple effects)for each frequency: subject X

| | | | | Frequency Hz | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left | 5.57 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| right | 6.74 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | 2.28 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left | 5.62 | 7.25 | 7.42 | N.A. | N.A. | N.A. | N.A. |
| right | 6.56 | 8.37 | 8.50 | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | **14.95 | **9.91 | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | 1.19 | 1.72 | 1.59 | N.A. | N.A. | N.A. | N.A. |

**p < 0.01, d.f. (1, 22)

Subject: Y

Elicited frequencies were equivalent for movements of the left and right side in both modes of coordination and at all pacing frequencies ($p > 0.05$).

Movements of the left and right side were not distinguished overall in terms of coefficients of variation ($p > 0.05$) when prepared in either the in-phase or anti-phase mode. However, when movements were prepared in the anti-phase mode, larger coefficients of variation were present for movements of the right side when paced at 1.75 Hz. In contrast, when movements were prepared in-phase, movements of the left side were associated with larger coefficients of variation than those of the right side when paced at 1.25 Hz. Movements prepared in both modes of coordination exhibited larger coefficients of variation when paced at 1.75 Hz than when paced at 1.25 Hz. In addition, when prepared in-phase and paced at 2.25 Hz smaller coefficients of variation were present than when movements were paced at 1.25 Hz.

TABLE 5.19 Summary table of coefficients of variation, F values for pairwise comparisons between 1.25 Hz and all other frequencies, and left side versus right side comparisons (simple effects)for each frequency: subject Y

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left | 6.29 | 6.79 | 8.36 | N.A. | N.A. | N.A. | N.A. |
| right | 6.04 | 6.92 | 10.15 | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | F < 1 | **38.11 | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | F < 1 | F < 1 | ‡4.61 | N.A. | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left | 7.31 | 6.24 | 9.02 | 6.82 | 4.83 | N.A. | N.A. |
| right | 5.92 | 7.34 | 9.55 | 5.84 | 4.41 | N.A. | N.A. |
| vs. 1.25 | - | F < 1 | **39.55 | F < 1 | **18.26 | N.A. | N.A. |
| L. vs. R. | †4.25 | 2.72 | F < 1 | 2.16 | F < 1 | N.A. | N.A. |

**$p < 0.01$, d.f. (1, 22)
‡$p < 0.05$, d.f. (1, 66)
†$p < 0.05$, d.f. (1, 110)

Subject: Z

The discrete frequencies produced by this subject were equivalent for movements of the left and right side in both modes of coordination and at all pacing frequencies ($p > 0.05$).

Movements of the left and right side were not distinguished overall in terms of coefficients of variation ($p > 0.05$) when prepared in either the in-phase or anti-phase mode. Movements prepared in the in-phase mode and paced at 1.50 Hz exhibited larger coefficients of variation than those paced at 1.25 Hz.

TABLE 5.20 Summary table of coefficients of variation, F values for pairwise comparisons between 1.25 Hz and all other frequencies, and left side versus right side comparisons (simple effects)for each frequency: subject Z

| | Frequency Hz | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1.25 | 1.50 | 1.75 | 2.00 | 2.25 | 2.50 | 2.75 |
| anti-phase | | | | | | | |
| left | 6.95 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| right | 6.54 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | F < 1 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. |
| in-phase | | | | | | | |
| left | 6.50 | 7.88 | N.A. | N.A. | N.A. | N.A. | N.A. |
| right | 6.62 | 7.61 | N.A. | N.A. | N.A. | N.A. | N.A. |
| vs. 1.25 | - | **8.70 | N.A. | N.A. | N.A. | N.A. | N.A. |
| L. vs. R. | F < 1 | F < 1 | N.A. | N.A. | N.A. | N.A. | N.A. |

**$p < 0.01$, d.f. (1, 22)
†$p < 0.05$, d.f. (1, 110)

## 5.4 Summary and Discussion

### 5.4.1 Task Performance

As a preliminary means of determining the extent to which task requirements vis a vis metronome limb relations were satisfied, frequency deviation scores were calculated for each trial. These measures indexed the extent to which the subject had adhered to the frequency pacing regime. In all subjects it was noted that the degree of deviation from the metronome increased in parallel with increases in pacing frequency. At the maximum pacing frequencies these deviations were substantial. For example, when paced at a frequency of 2.75 Hz, subject X exhibited mean deviations of 0.23 Hz which were of approximately the same magnitude as changes in pacing frequency. These data raise the issue of whether frequency, which is nominally the control parameter, is best represented by the externally administered pacing frequency or by the instantiated oscillation frequency. However, there were no consistent differences between movements made by the left and by the right side in the extent to which oscillation frequencies deviated from pacing frequencies.

It has been suggested that the coupling of perception and action may itself be characterised as a pattern formation process (e.g., Kelso, Delcolle, & Schöner, 1990). This approach necessitates the identification of collective variables which correspond to perception-action patterns, which are in turn mapped onto attractors of the collective variable dynamics. The coordination of movements of a single limb with a pacing signal (auditory metronome) has been regarded as the prototypical example of broken symmetry. In circumstances in which the pacing frequency is increased, a number of the signature features of broken symmetry are exhibited (Kelso et al., 1991). These features include phase wandering which is indicative of a loss of synchronization between the limb and the metronome. While in the present study metronome-limb phase relations were not explicitly controlled nor examined (cf., Byblow et al., submitted; Carson et al., in press; Kelso et al., 1990), it is possible that the increases in frequency deviation scores which were noted as pacing frequency was scaled upward reflect loss of entrainment resulting from broken symmetry. The substructure of these processes and the manner in which pattern formation processes in the cortex map unto coordination dynamics at the level of the joint kinematics remain to be resolved (e.g., Kelso, Bressler, Buchanan, DeGuzman, Ding, Fuchs, & Holroyd, 1992).

### 5.4.2 Signature Features of Transitional Behaviour

All subjects exhibited considerable variability in the frequency at which transitions from the initial preparation occurred. In addition, there were striking differences in transition frequencies between subjects. These observations are consistent with data obtained using a bimanual paradigm (Byblow et al., submitted) in failing to confirm the presence of a dimensionless critical ratio of preferred to transition frequency number which delineates the boundary between coordinative states (Kelso, 1984).

A number of "basic phenomena" have been predicted in association with spontaneous transitions from initial preparations. These include critical fluctuations of the order parameter as the transition region is approached (Kelso et al., 1986). As a consequence of the wide variability in transition frequencies, analysis of the uniformity (variability) of the order parameter relative phase in the pre transition region was conducted on plateaus normalized to transition frequency. In all subjects the uniformity of relative phase was lower on the frequency plateau immediately preceding the transition when movements were initially prepared in the anti-phase mode of coordination. These trends were reproduced for movements initially prepared in the in-phase mode for two of the three subjects for whom it was possible to conduct these analyses. These data support the hypothesis that loss of stability mediates qualitative change in behavioural patterns (e.g., Scholz et al., 1987).

### 5.4.3 Symmetry Breaking Dynamics

The observation that transitions from the in-phase mode of coordination to phase wandering were present in the majority of trials for two of the four subjects (X and Z) satisfies one of the predictions of broken symmetry. When prepared in the anti-phase mode of coordination, subjects X and Z also presented shorter times to transition than subjects W and Y. An additional prediction of broken symmetry is that of isodirectional phase transitions. However, data concerning transition pathways were somewhat inconsistent. When prepared in the anti-phase mode, both subjects X and Z presented pathways which were generally negative. Whereas, for these subjects, transitions from the in-phase mode were either predominantly positive (subject Z) or inconsistent (subject X). Subject Y presented transitions from the anti-phase mode which were consistently negative in direction. Whereas subject W failed to exhibit consistent directions of transition.

It has also been predicted that, in the presence of broken symmetry, the scaling of control parameters will engender fixed point drift as stable states move away from initial values. Subject W exhibited values of relative phase which increased with pacing frequency in both modes of coordination. Subject X exhibited increasing values of relative phase in the only mode (in-phase) for which it was possible to obtain sufficient data. When prepared in the in-phase mode, subject Y exhibited values of relative phase which increased with pacing frequency. In the anti-phase mode these tendencies were less clearly expressed. The limited amount of data available for subject Z made it impossible to conduct meaningful assessments. It is notable that for all subjects transition directions were more likely to be in the negative than in the positive direction. In contrast, drift in relative phase values, where it could be resolved, was always in a positive direction. In combination these data are clearly inconsistent with the predictions of broken symmetry (cf., Jeka, 1992).

### 5.4.4 Asymmetries

The differences between movements executed by the left and right sides in terms of variability of frequency, which were evident in Experiment 1 were not exhibited under the frequency scaling regime employed in this experiment. Thus, the data are consistent with those obtained in Experiment 2. They suggest that the imposition of external pacing alters the structure of the task to a degree which is sufficient to attenuate between side differences in frequency variability. It was also evident that movements of the left and the right side were equivalent in terms of the actual oscillation frequency adopted. Movements of the left and the right side deviated from the metronome to an equivalent degree as the metronome frequency was increased.

One measure of the stability of a stationary state is the degree of variability of the order parameter about the mean value corresponding to that state. In this experiment, the measure of uniformity of relative phase failed to distinguish movements executed by the left and the right side. It was generally the case that the degree of uniformity decreased with increases in pacing frequency. However, movements of the left and the right side did not vary consistently in the degree to which this tendency was expressed. There was also generally no difference between movements of the left and right side in terms of the mean relative phase value. Where differences were present in two subjects, for movements prepared in the anti-phase mode and paced at 1.75 Hz, mean values were greater than the target for movements of the left side for subject W, and lower than the target for movements of the left side for subject Y.

The number of transitions exhibited in each preparation and the time at which those transitions occurred provide additional indications of the relative stability of the attractor states for movements of each side. However, in no instance were movements of the left and right side distinguished in terms of the number of transitions exhibited in either mode of coordination. In addition, transition onset times were equivalent for movements of the left and right side both when movements were prepared in the anti-phase and in-phase modes of coordination.

These data therefore provide little evidence to support the hypothesis that movements of the left and right side are distinguished in terms of their intrinsic dynamics. While movements of both side exhibit signature features of nonequilibrium phase transitions, there appear to exist no qualitative or quantitative differences in the manner in which these characteristics are expressed.

# 6 Experiment 4

## 6.1 Introduction

The results of Experiment 3 provided few indications that the limb hemisphere systems differ in terms of their intrinsic dynamics. While the use of a self paced protocol in Experiment 1 revealed differences in the variability of oscillation frequency and the associated variability of relative phase, it appeared that the application of an external pacing regime in Experiment 2 was sufficient to eliminate these differences.

However, the essence of human behaviour is the ability to switch between movement patterns in a purposeful fashion (cf. Kelso, Scholz & Schöner, 1988). As it is with respect to intentional behaviour that the clearest hand preferences are expressed and the greatest performance asymmetries are observed, the possibility may be admitted that there exist differences between the limbs in the manner in which intention acts to perturb the intrinsic dynamics. The concept of information is central to the extension of dynamical analyses to the realm of purposeful behaviour. Information and in particular intentional information is defined in the same space as the collective variables which characterize the behaviour under study (Jeka & Kelso, 1989; Schöner & Kelso, 1988b).

A dynamical description of intentional influences has been formulated in which intentional information is viewed as a perturbation of the pre-existing dynamics to a new (intended) behavioural pattern (Kelso, Scholz and Schöner,1988, see also Schöner & Kelso, 1988b). Characterization of intention as a perturbation contributing to the intrinsic dynamics appears to provide an acceptable account of experimental treatments of intentional switching between locally "stable" modes of coordination (Scholz & Kelso, 1990). Detailed descriptions of the modelling of intentional perturbations of the intrinsic dynamics are provided elsewhere (Jeka & Kelso, 1989; Schöner & Kelso, 1988b, 1988c, 1988d).. It is sufficient to note at this juncture that intentional change is conceived of as being mediated through the superposition of a perturbation corresponding to the desired or intended coordinative state. As is the case for spontaneous switching between coordinative modes, the dynamics which result from the application of an intentional perturbation and the temporal evolution of these dynamics are critically dependent upon the relative stability of the preexisting intrinsic dynamics. Thus an intentional transition from the less stable to the more stable of two adjacent stationary states is predicted to be on average of shorter duration than a transition from the more stable to the less stable state.

In modelling these phenomena, the intentional perturbation is itself endowed with dynamics. As is the case for the intrinsic dynamics, the intentional perturbation may be visualized in terms of the topology of a potential landscape. The magnitude of the perturbation is formally described in terms of the parameter $c_{int}$ which in turn corresponds to the strength of the intentional dynamics (see Jeka & Kelso, 1989; Schöner & Kelso, 1988b). In addition to exhibiting a sensitivity to the relative stabilty of the intrinsic dynamics, the duration of an intentional transition is thus also predicted to be dependent upon the the strength of the intentional influence upon the intrinsic dynamics. A formal statement of the hypothesis that there exist differences between the limbs in the manner in which intention acts to alter the intrinsic dynamics may therefore be expressed in terms of differences in the relative magnitudes of the intentional perturbation $c_{int}$. The results of Experiments 2 and 3 provided no evidence to suggest that the limb/flank hemisphere systems differed with respect to their intrinsic dynamics when subjected to an externally applied pacing regime. The present experiment was therefore conducted to determine whether the limb/flank-hemisphere systems may be distinguished in their expression of intentional dynamics.

A limited frequency range (1.25 Hz to 1.75 Hz) was employed in this experiment, as the primary objective was to determine whether there exist differences between the left and right sides in terms of the application of intentional perturbations of the dynamics. As such, demonstration of differences arising from the relative stability of coordinative modes was of secondary interest. It was considered more important to examine intentional changes in regions of state space in which both modes were stable and thus in which there were unlikely to be differences between movements of each side in the extent to which task requirements were satisfied.

## 6.2 Methodology

### Apparatus

A single red incandescent lamp, under microcomputer control, was mounted on the wall 1.3m in front of subjects at eye level.

### Procedure

Individuals performed paced oscillatory motions of the wrist and foot commencing in two modes modes of coordination, in-phase and anti-phase. The forearm was always placed in a prone position. Subjects were required to produce one full cycle of movement for each beat of an auditory metronome while maintaining the prescribed mode of coordination. In the in-phase mode, flexion (extension) of the wrist was required to be coincident with plantar-flexion (dorsi-flexion) of the foot . In the anti-phase mode, flexion (extension) of the wrist was coincident with dorsi-flexion (plantar-flexion) of the foot. Pacing was provided at four frequencies, 1.00 Hz, 1.25 Hz, 1.50 Hz and 1.75 Hz Hz. During each trial, illumination of the lamp provided a visual signal to subjects that they were to switch to the other mode of coordination. The experimenter emphasised that this was not a reaction time task. That is, the requirement was to expedite the switch itself, rather than react to the visual signal as rapidly as possible.

Subjects performed four blocks of 24 trials. Trial blocks alternated between the left side and the right side. Two subjects first performed a block of left side trials, the other two subjects, a block of right side trials. Each block comprised 6 trials at each pacing frequency (12 in-phase trials and 12 anti-phase trials). In addition, for each mode of coordination, on 4 trials the signal to switch occurred 12 seconds after the beginning of the trial, on 4 trials at 16 seconds and on 4 trials at 20 seconds. Within a block, the order of trial presentation was completely randomized.

Subjects were given no direction concerning the temporal locus of the metronome pulse with respect to the movement cycle. Rather, individuals were free to establish their own metronome-movement cycle coordinative pattern, subject to the constraint of isofrequency coordination.

The initiation of data collection was automatically triggered at the start of a trial. In the first delay condition, following 12 seconds of metronome pulses, the incandescent lamp was illuminated. Coincident with this event, a reference pulse was output to one channel of the A/D. In the remaining delay conditions, the lamp was illuminated following 16 seconds and 20 seconds respectively. In all cases, the duration of data collection was 29 seconds.

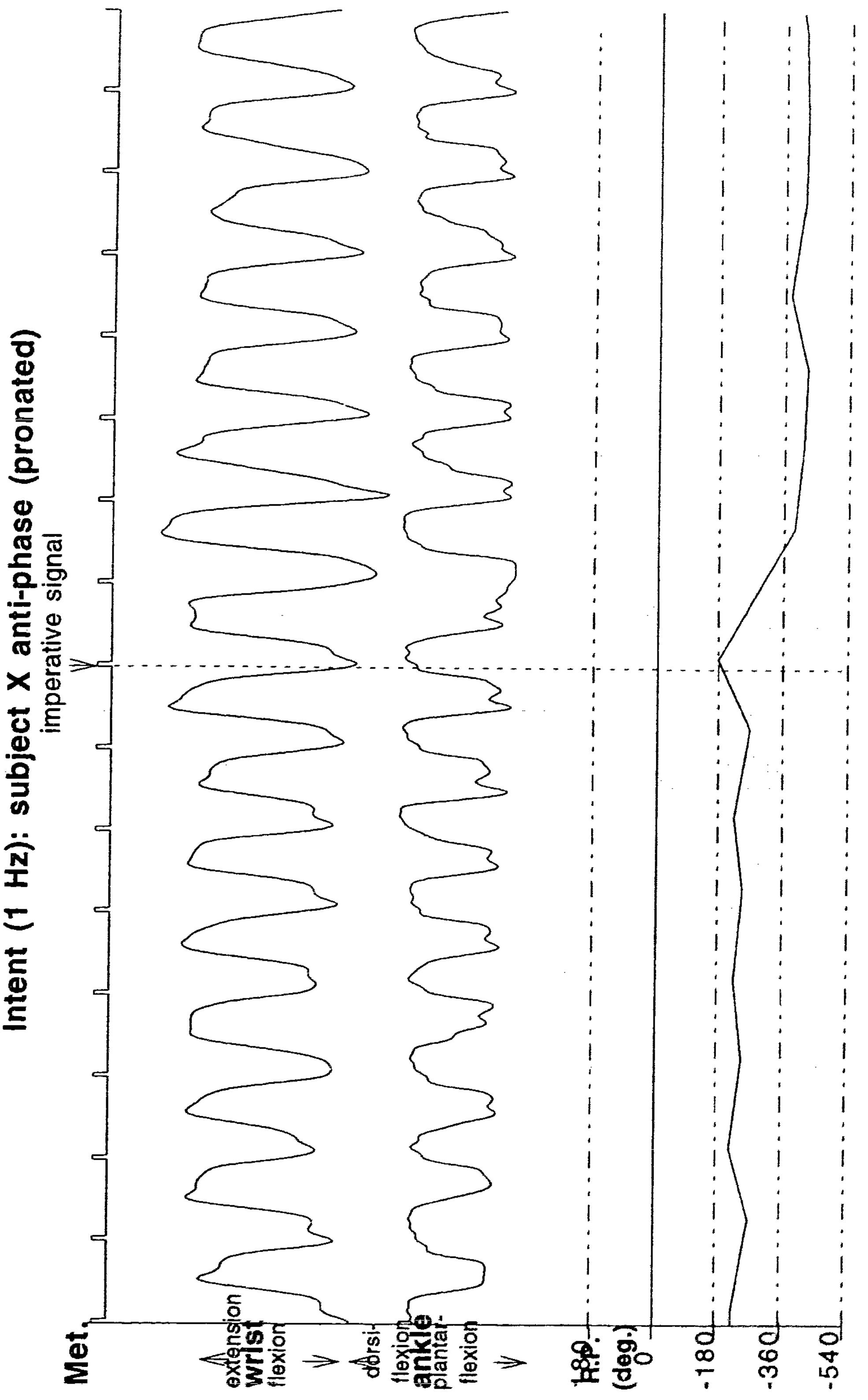

Fig. 6.1 Sample time series comprising an intentional transition from the anti-phase mode to the in-phase mode when paced at a frequency of 1 Hz (subject X).

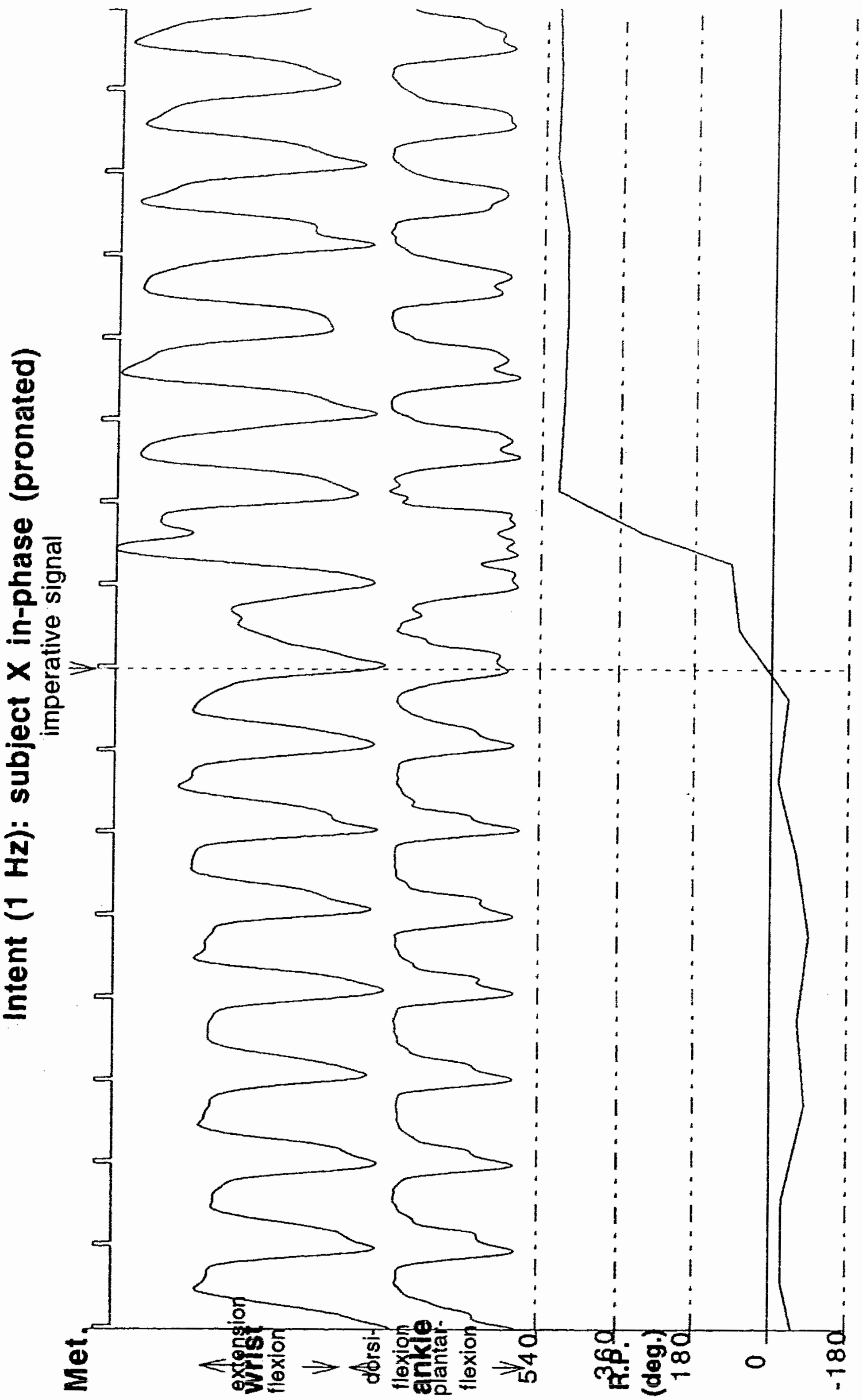

Fig. 6.2 Sample time series comprising an intentional transition from the in-phase mode to the anti-phase mode when paced at a frequency of 1 Hz (subject X).

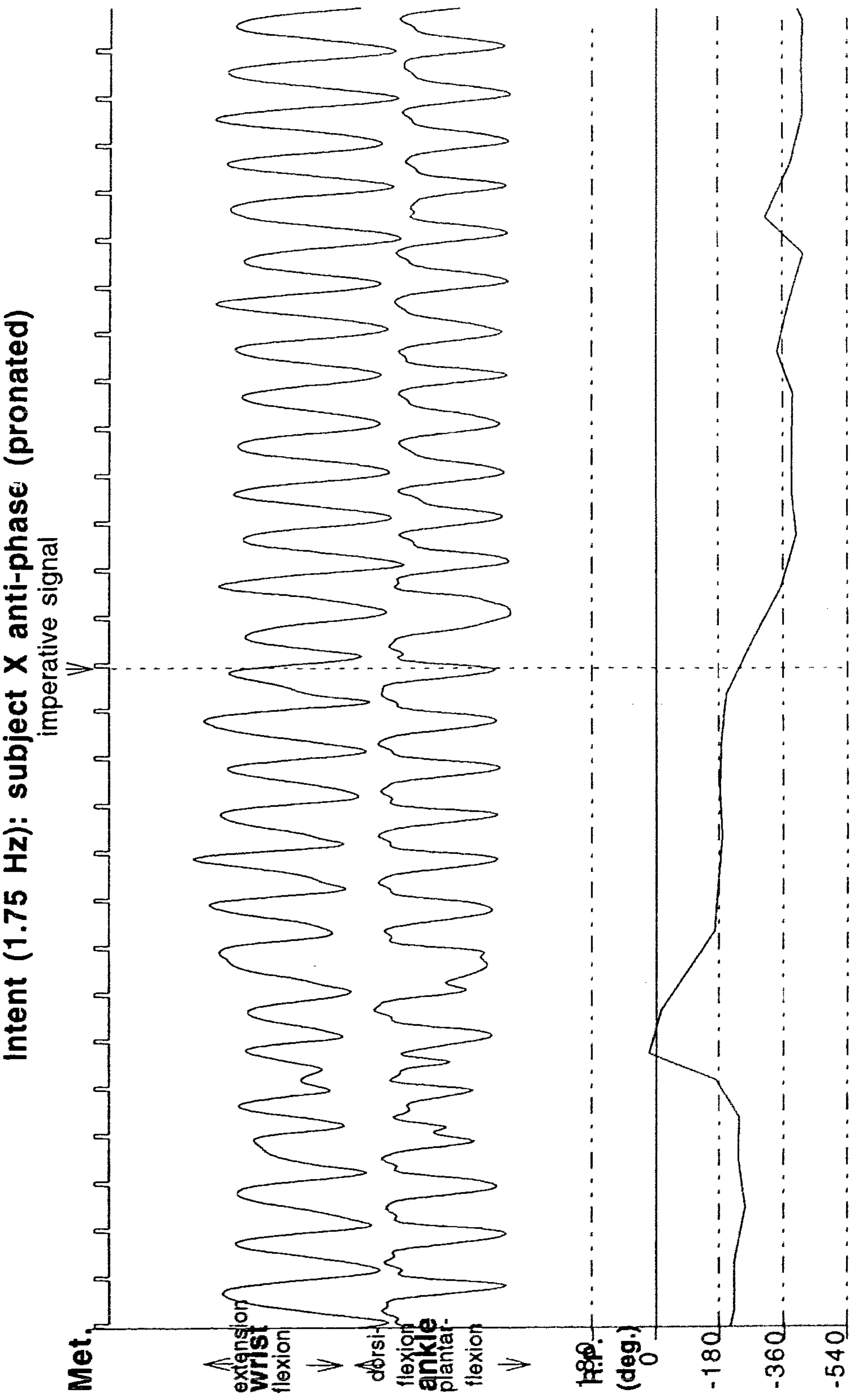

Fig. 6.3 Sample time series comprising an intentional transition from the anti-phase mode to the in-phase mode when paced at a frequency of 1.75 Hz (subject X).

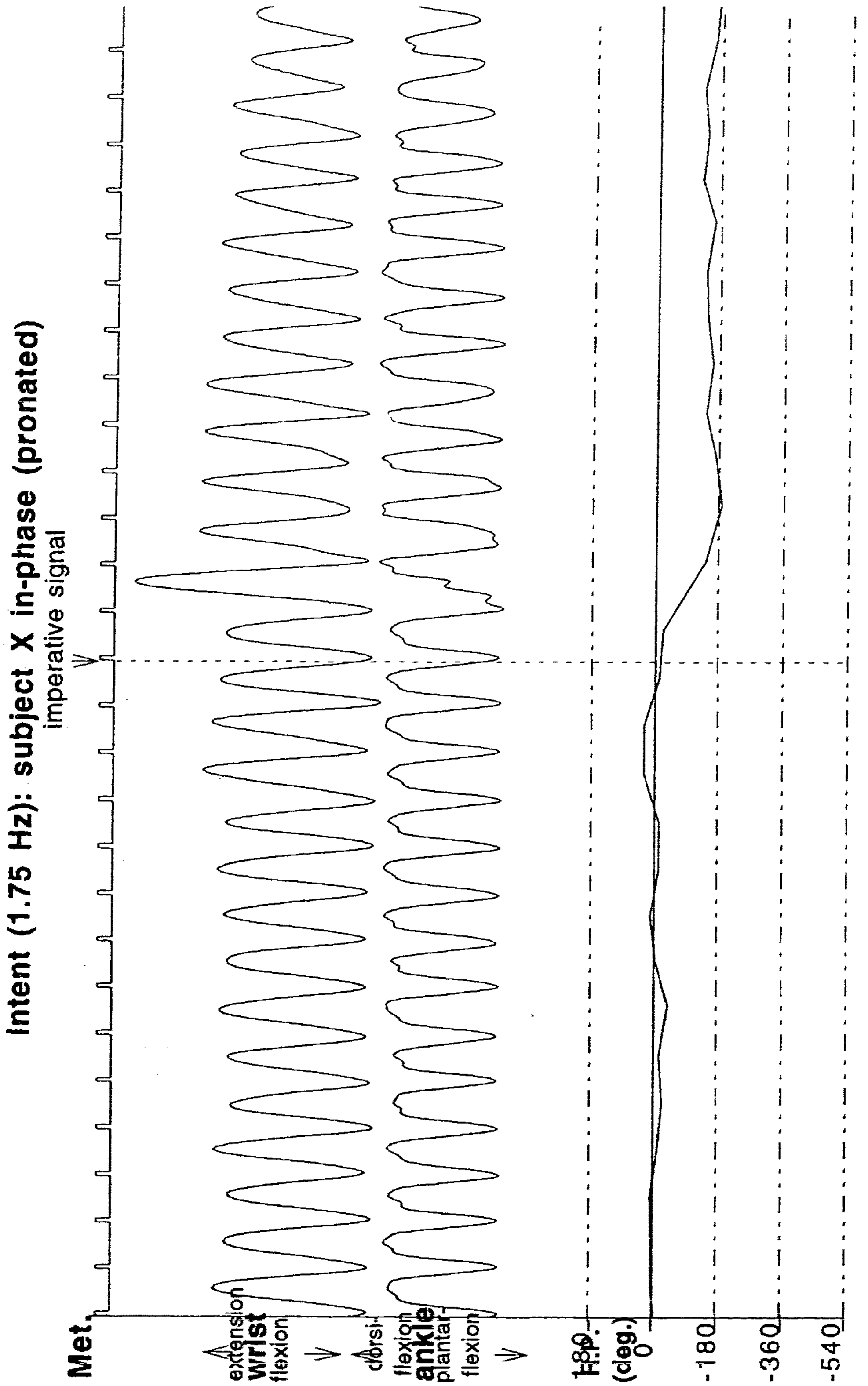

Fig. 6.4 Sample time series comprising an intentional transition from the in-phase mode to the anti-phase mode when paced at a frequency of 1.75 Hz (subject X).

## 6.3 Results

### 6.3.1 Stationarity of Discrete Relative Phase

Discrete relative phase values obtained for the 10 second period prior to the presentation of the imperative signal were tested for uniformity using the Rayleigh test (Mardia, 1972). Trials which failed satisfy the criteria of uniformity were excluded from all analyses. This procedure necessitated the removal of 6 trials for subject W, 3 trials for subject X, 0 trials for subject Y, and 1 trial for subject Z.

### 6.3.2 Metronome Limb Relations

A frequency deviation score was calculated for each trial. This score reflected the absolute difference between the mean frequency for that trial and the metronome frequency. Data were analysed using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 4 frequency (1.00 Hz, 1.25 Hz, 1.50 Hz, 1.75 Hz) by 2 joint (wrist, ankle) design. Each trial was treated as a single case. Side, mode and pacing frequency were grouping factors. Joint was a within case factor. Planned orthogonal comparisons of means were performed to highlight a number of preselected contrasts (left side versus right side, and anti-phase versus in-phase). In addition, when analyses of variance indicated the presence of a statistically significant main effect for frequency, or an interaction of side and frequency, posthoc analyses of means were conducted using the Tukey (HSD) procedure.

Subject: W

Deviation scores for the left and right side ($F(1, 74) < 1$) and the anti-phase and in-phase modes ($F(1, 74) < 1$) were equivalent. There was however a main effect for frequency ($F(3, 74) = 4.08$, $p < 0.01$). Comparison of means using the Tukey (HSD) procedure suggested that this effect comprised statistically significant pairwise differences between movements paced at 1.00 Hz and 1.25 Hz, and those paced at 1.75 Hz ($p < 0.05$).

TABLE 6.1 Summary table showing absolute deviation from the metronome frequency (Hz) for each side, and mode of coordination, as a function of pacing frequency: subject W

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 0.005 | 0.006 | 0.007 | 0.012 |
| right side | 0.006 | 0.006 | 0.007 | 0.010 |
| anti-phase | 0.005 | 0.006 | 0.007 | 0.009 |
| in-phase | 0.006 | 0.006 | 0.008 | 0.012 |

Subject: X

Deviation scores for the left and right side ($F(1, 77) = 1.21$, $p > 0.20$) and the anti-phase and in-phase modes ($F(1, 77) < 1$) were equivalent. A main effect for frequency ($F(3, 77) = 9.88$, $p < 0.001$) was noted. Comparison of means using the Tukey (HSD) procedure suggested that this effect comprised statistically significant pairwise differences between movements paced at 1.75 Hz and those paced at all other frequencies ($p < 0.01$). In addition, there was a side by frequency interaction ($F(3, 77) = 4.28$, $p < 0.01$. Movements of the right side which were paced at 1.75 Hz deviated from the metronome to a greater degree than all other combinations of side and pacing frequency ($p < 0.05$, Tukey HSD).

TABLE 6.2 Summary table showing absolute deviation from the metronome frequency (Hz) for each side, and mode of coordination, as a function of pacing frequency: subject X

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 0.012 | 0.015 | 0.009 | 0.017 |
| right side | 0.012 | 0.008 | 0.012 | 0.028 |
| anti-phase | 0.010 | 0.011 | 0.009 | 0.026 |
| in-phase | 0.015 | 0.012 | 0.012 | 0.018 |

Subject: Y

Deviation scores for the left and right side ($F(1, 80) < 1$) and the anti-phase and in-phase modes ($F(1, 80) < 1$) were equivalent. There was no consistent attributable to frequency ($F(3, 80) = 2.19$, $p > 0.10$).

TABLE 6.3 Summary table showing absolute deviation from the metronome frequency (Hz) for each side, and mode of coordination, as a function of pacing frequency: subject Y

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 0.011 | 0.007 | 0.007 | 0.008 |
| right side | 0.007 | 0.008 | 0.007 | 0.009 |
| anti-phase | 0.008 | 0.008 | 0.008 | 0.009 |
| in-phase | 0.010 | 0.007 | 0.006 | 0.008 |

Subject: Z

Deviation scores for the left and right side ($F(1, 79) < 1$) and the anti-phase and in-phase modes ($F(1, 79) < 1$) were equivalent. A main effect for frequency ($F(3, 79) = 5.40$, $p < 0.01$) was present. Comparison of means using the Tukey (HSD) procedure suggested that this effect comprised statistically significant pairwise differences between movements paced at 1.75 Hz and those paced at all other frequencies ($p < 0.05$).

TABLE 6.4 Summary table showing absolute deviation from the metronome frequency (Hz) for each side, and mode of coordination, as a function of pacing frequency: subject Z

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 0.009 | 0.008 | 0.012 | 0.016 |
| right side | 0.006 | 0.008 | 0.009 | 0.028 |
| anti-phase | 0.005 | 0.008 | 0.009 | 0.022 |
| in-phase | 0.010 | 0.009 | 0.013 | 0.023 |

### 6.3.3 Discrete Frequency:

Coefficients of variation and discrete frequencies were obtained for the 10 second period prior to the presentation of the imperative signal. Data were analysed using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 4 frequency (1.00 Hz, 1.25 Hz, 1.50 Hz, 1.75 Hz) by 2 joint (wrist, ankle) design. Each trial was treated as a single case. Side, mode and pacing frequency were grouping factors. Joint was a within case factor. Planned orthogonal comparisons of means were performed to highlight a number of preselected contrasts (left side versus right side, and anti-phase versus in-phase). In addition, when analyses of variance indicated the presence of a statistically significant main effect for frequency, or an interaction of side and frequency, posthoc analyses of means were conducted using the Tukey (HSD) procedure.

Subject: W

Coefficients of variation were greater for movements of the left side (4.17) than for movements of the right side (3.55) ($F(1, 74) = 10.28$, $p < 0.01$). Coefficients of variation for the anti-phase and in-phase modes ($F(1, 74) = 2.32$, $p > 0.10$) were equivalent. A main effect for frequency ($F(3, 74) = 6.78$, $p < 0.001$) was noted. Comparison of means using the Tukey (HSD) procedure suggested that this effect comprised statistically significant pairwise differences between movements paced at 1.00 Hz and 1.25 Hz, and those paced at 1.75 Hz ($p < 0.01$).

TABLE 6.5 Summary table showing coefficients of variation for each side, and mode of coordination, as a function of pacing frequency: subject W

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 3.55 | 3.81 | 4.38 | 4.94 |
| right side | 3.24 | 3.28 | 3.59 | 4.10 |
| anti-phase | 3.43 | 3.26 | 3.44 | 4.74 |
| in-phase | 3.37 | 3.83 | 4.53 | 4.30 |

Subject: X

Movements of the left and right side were not distinguished in terms of coefficients of variation ($F(1, 77) = 1.71$, $p > 0.15$). Coefficients of variation for the anti-phase and in-phase modes ($F(1, 77) < 1$) were also equivalent. A main effect for frequency ($F(3, 77) = 6.84$, $p < 0.001$) was observed. Comparison of means using the Tukey (HSD) procedure suggested that this effect comprised statistically significant pairwise differences between movements paced at 1.75 Hz and those paced at 1.25 Hz and 1.50 Hz ($p < 0.01$), and between those paced at 1.75 Hz and those paced at 1.00 Hz ($p < 0.05$).

TABLE 6.6 Summary table showing coefficients of variation for each side, and mode of coordination, as a function of pacing frequency: subject X

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 7.06 | 7.03 | 5.93 | 8.19 |
| right side | 7.11 | 6.26 | 7.18 | 10.07 |
| anti-phase | 6.12 | 5.88 | 5.93 | 11.06 |
| in-phase | 8.04 | 7.41 | 7.17 | 7.20 |

Subject: Y

Movements of the left and right side ($F(1, 80) < 1$), and conducted in the anti-phase and in-phase mode ($F(1, 80) < 1$) were not distinguished in terms of coefficients of variation. There was no consistent overall attributable to frequency ($F(3, 80) = 2.14$, $p > 0.10$). However an interaction of side and pacing frequency was noted ($F(3, 80) = 5.37$, $p < 0.01$). Movements of the left side which were paced at 1.50 Hz exhibited smaller coefficients of variation than movements of the right side paced at 1.75 Hz and of the left side paced at 1.00 Hz ($p < 0.05$, Tukey HSD).

TABLE 6.7 Summary table showing coefficients of variation for each side, and mode of coordination, as a function of pacing frequency: subject Y

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 5.84 | 4.67 | 3.85 | 4.38 |
| right side | 4.43 | 4.52 | 4.80 | 5.93 |
| anti-phase | 4.43 | 4.07 | 4.66 | 5.89 |
| in-phase | 5.83 | 5.12 | 3.98 | 4.42 |

Subject: Z

Although there was a tendency for movements of the right side to exhibit coefficients of variation which were larger than for movements of the left side, this trend failed to meet conventional levels of statistical significance (F(1, 79) = 3.67, $p = 0.06$). Coefficients of variation for the anti-phase mode (6.33) were larger than those for the in-phase modes (4.86) (F(1, 79) = 15.54, $p < 0.001$). A main effect for frequency (F(3, 79) = 6.36, $p < 0.001$) was noted. Comparison of means using the Tukey (HSD) procedure suggested that this effect comprised statistically significant pairwise differences between movements paced at 1.50 Hz and those paced at 1.00 Hz and 1.75 Hz ($p < 0.05$), and between those paced at 1.25 Hz and those paced at 1.75 Hz ($p < 0.05$). However, an interaction of side and frequency (F(3, 79) = 7.09, $p < 0.001$) was also present . Decomposition of this interaction (Tukey HSD) revealed that movements of the right side paced at 1.75 Hz exhibited larger coefficients of variation than all combinations other than movements of the left and right side paced at 1.00 Hz ($p < 0.01$).

TABLE 6.8 Summary table showing coefficients of variation for each side, and mode of coordination, as a function of pacing frequency: subject Z

| | Frequency Hz<br>1.00 | <br>1.25 | <br>1.50 | <br>1.75 |
|---|---|---|---|---|
| left side | 6.22 | 5.12 | 4.85 | 4.74 |
| right side | 6.15 | 4.78 | 4.43 | 8.43 |
| anti-phase | 6.43 | 5.20 | 5.00 | 8.68 |
| in-phase | 5.95 | 4.70 | 4.28 | 4.49 |

### 6.3.4 Relative Phase Relations

Estimates of mean relative phase and of the uniformity of relative phase were obtained for the 10 second period prior to the presentation of the imperative signal were tested. In calculating test statistics for mean relative phase, in order to control for the potential inflation of Type I errors resulting from multiple comparisons, alpha was assigned as $p = 0.01$. Due to the limited number of observations entering into each cell ($n = 6$) it was not possible to conduct meaningful comparisons between mean relative phase values and target relative phase values (Mardia, 1972). Analyses of variance for transformed uniformity scores were performed for each subject using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 4 frequency (1.00 Hz, 1.25 Hz, 1.50 Hz, 1.75 Hz) design. Each trial was treated as a single case. All factors were grouping. Mean values reported in the text correspond to transformed uniformity scores.

Subject: W

Mean Relative Phase

As Examination of Table 6.9 reveals, movements of the left and right side were different only in one instance in which in-phase movements were paced at 1.50 Hz. In addition for movements of the right side in both modes of coordination, and movements of the left side in the anti-phase mode, the phase difference between the wrist and the ankle was larger when movements were paced at 1.75 Hz than when paced at 1.25 Hz.

TABLE 6.9 Summary table of mean relative phase and F values for pairwise comparisons between the left and right side for each frequency, and between 1.00 Hz and 1.25 Hz, 1.50 Hz, and 1.75 Hz for each side: subject W

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| anti-phase | | | | |
| left side | 152.4 | 158.9 | 156.9 | 187.6 |
| vs. 1.25 | - | 5.28 | 1.85 | *32.20 |
| right side | 158.1 | 158.8 | 157.0 | 179.5 |
| vs. 1.25 | - | F < 1 | F < 1 | *15.08 |
| L. vs. R. | 2.37 | F < 1 | F < 1 | 1.09 |
| in-phase | | | | |
| left side | 12.7 | 13.7 | 2.6 | 29.8 |
| vs. 1.25 | - | F < 1 | 5.04 | 2.61 |
| right side | 16.1 | 23.3 | 21.0 | 39.1 |
| vs. 1.25 | - | 7.12 | F < 1 | *13.53 |
| L. vs. R. | F < 1 | 7.23 | *11.40 | F < 1 |

*$p < 0.01$, d.f. (1, 10)

### Uniformity of Relative Phase

Movements of the left and the right side were equivalent in terms of the uniformity of relative phase ($F(1, 74) < 1$). A main effect for frequency was noted ($F(3, 74) = 21.17$, $p < 0.0001$). Movements paced at 1.75 Hz exhibited smaller uniformity values than those paced at all other frequencies ($p < 0.01$, Tukey HSD). In addition movements paced at 1.50 Hz exhibited smaller uniformity values than those paced at 1.00 Hz ($p < 0.01$, Tukey HSD). When movements were prepared in the anti-phase mode (2.80) exhibited larger uniformity values than when prepared in the in-phase mode (2.65) ($F(1, 74) = 14.08$, $p < 0.001$). However, as revealed by the interaction of side, mode and pacing frequency ($F(3, 74) = 3.31$, $p < 0.05$) this effect was not consistently expressed. Movements prepared in the anti-phase mode while comprising two of the cells exhibiting the largest uniformity values (left (1.00 Hz), right (1.00 Hz)), also included two of the three cells with the lowest uniformity values (left (1.75 Hz), right (1.75 Hz)).

TABLE 6.10 Summary table showing uniformity of relative phase for each side, and mode of coordination, as a function of pacing frequency: subject W

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 2.85 | 2.77 | 2.68 | 2.55 |
| right side | 2.99 | 2.85 | 2.69 | 2.44 |
| anti-phase | 3.01 | 2.91 | 2.80 | 2.49 |
| in-phase | 2.83 | 2.71 | 2.57 | 2.50 |

Subject: X

Mean Relative Phase

Movements of the left and right side were in not observed to differ in terms of mean relative phase. There was a general tendency, expressed with varying consistency across conditions, toward increases in relative phase differences with increases in pacing frequency (Table 6.11).

TABLE 6.11 Summary table of mean relative phase and F values for pairwise comparisons between the left and right side for each frequency, and between 1.00 Hz and 1.25 Hz, 1.50 Hz, and 1.75 Hz for each side: subject X

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| anti-phase | | | | |
| left side | 149.2 | 167.2 | 180.4 | 164.4 |
| vs. 1.25 | - | 9.36 | *35.35 | 6.41 |
| right side | 148.6 | 171.6 | 189.1 | 176.3 |
| vs. 1.25 | - | *13.87 | *33.11 | 3.26 |
| L. vs. R. | F < 1 | F < 1 | 2.03 | F < 1 |
| in-phase | | | | |
| left side | 318.8 | 336.7 | 6.7 | 351.1 |
| vs. 1.25 | - | 5.29 | *54.89 | *22.78 |
| right side | 306.1 | 330.4 | 10.3 | 17.2 |
| vs. 1.25 | - | *33.66 | *10.72 | *48.61 |
| L. vs. R. | 6.46 | F < 1 | F < 1 | 5.51 |

*p < 0.01, d.f. (1, 10)

### Uniformity of Relative Phase

Movements of the left and right side were not distinguished by the measure of uniformity (F(1, 77) = 1.71, $p > 0.15$). Movements conducted in the anti-phase mode and the in-phase mode were also not differentated on this basis (F(1, 77) = 2.22, $p > 0.10$). However the interaction of side and mode was of statistical significance (F(1, 77) = 7.20, $p < 0.01$). This suggested when prepared in the anti-phase mode, movements of the left side were associated with larger uniformity values than movements of the right side. A main effect for frequency was present (F(3, 77) = 4.43, $p < 0.01$). Movements paced at 1.75 Hz exhibited smaller uniformity values than those paced at 1.00 Hz and 1.50 Hz ($p < 0.05$, Tukey HSD). An interaction of mode and pacing frequency (F(3, 77) = 4.49, $p < 0.01$ suggested that for movements prepared in the anti-phase mode, those paced at 1.75 Hz were associated with lower uniformity values than anti-phase movements paced at all other frequencies ($p < 0.01$, Tukey HSD).

TABLE 6.12 Summary table showing uniformity of relative phase for each side, and mode of coordination, as a function of pacing frequency: subject X

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 2.36 | 2.22 | 2.37 | 2.09 |
| right side | 2.23 | 2.29 | 2.23 | 1.98 |
| anti-phase | 2.40 | 2.37 | 2.40 | 1.90 |
| in-phase | 2.19 | 2.15 | 2.20 | 2.18 |

## Subject: Y

### Mean Relative Phase

Relative phase values were different for the left and right side only when prepared in the anti-phase mode of corrdnation and paced at 1.75 Hz. While relative phase values appeared to increase with increases in pacing frequency, differences were not expressed to a statistically significant degree.

TABLE 6.13 Summary table of mean relative phase and F values for pairwise comparisons between the left and right side for each frequency, and between 1.00 Hz and 1.25 Hz, 1.50 Hz, and 1.75 Hz for each side: subject Y

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| anti-phase | | | | |
| left side | 162.7 | 160.5 | 166.9 | 164.6 |
| vs. 1.25 | - | F < 1 | F < 1 | F < 1 |
| right side | 168.9 | 172.6 | 172.8 | 189.5 |
| vs. 1.25 | - | 1.27 | F < 1 | *12.86 |
| L. vs. R. | 1.84 | 6.35 | 1.21 | *24.14 |
| in-phase | | | | |
| left side | 347.7 | 336.3 | 354.8 | 358.2 |
| vs. 1.25 | - | 1.97 | 1.33 | 3.19 |
| right side | 343.8 | 344.6 | 349.7 | 1.4 |
| vs. 1.25 | - | F < 1 | F < 1 | 6.13 |
| L. vs. R. | F < 1 | 1.54 | 1.41 | F < 1 |

*p < 0.01, d.f. (1, 10)

Uniformity of Relative Phase

Movements of the left and right side were equivalent in terms of uniformity (F(1, 80) < 1). A main effect for frequency was present (F(3, 80) = 4.20, p < 0.01). Movements paced at 1.50 Hz exhibited larger uniformity values than those paced at 1.75 Hz (p < 0.01, Tukey HSD). There was also an interaction of side and pacing frequency (F(3, 80) = 5.58, p < 0.01). Decomposition of this interaction (Tukey HSD) revealed than movements of the right side paced at 1.75 Hz and movements of the left side paced at 1.00 Hz were both associated with uniformity values which were lower than for movements of the right side paced at 1.50 Hz and 1.00 Hz, and movements of the left side paced at 1.50 Hz.

Movements conducted in the anti-phase mode (2.65) and the in-phase mode (2.53) were differentated by this measure (F(1, 80) = 7.80, p < 0.01). An interaction of mode and pacing frequency (F(3, 80) = 7.01, p < 0.001 suggested that for movements prepared in the anti-phase mode and paced at 1.25 Hz, larger uniformity values were present than for in-phase movements paced at 1.00 Hz and 1.25 Hz, and anti-phase movements paced at 1.75 Hz ($p < 0.01$, Tukey HSD). The interaction of side, mode and pacing frequency was also of statistical significance ($F(3, 80) = 2.84$, $p < 0.05$). The cell exhibiting the lowest overall unifomity values was comprised of movements of the right side, prepared in the anti-phase mode and paced at 1.75 Hz.

TABLE 6.14 Summary table showing uniformity of relative phase for each side, and mode of coordination, as a function of pacing frequency: subject Y

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| left side | 2.42 | 2.60 | 2.72 | 2.58 |
| right side | 2.74 | 2.63 | 2.70 | 2.40 |
| anti-phase | 2.71 | 2.80 | 2.71 | 2.42 |
| in-phase | 2.45 | 2.43 | 2.71 | 2.56 |

Subject: Z

Mean Relative Phase

Differences between the left and right side were inconsistently expressed, being observed only when anti-phase movements were paced at a frequency of 1.50 Hz, and when in-phase movements were paced at 1.75 Hz. There was also a generally consistent tendency for relative phase to increase in parallel with increases in pacing frequency.

TABLE 6.15 Summary table of mean relative phase and F values for pairwise comparisons between the left and right side for each frequency, and between 1.00 Hz and 1.25 Hz, 1.50 Hz, and 1.75 Hz for each side: subject Z

| | Frequency Hz | | | |
|---|---|---|---|---|
| | 1.00 | 1.25 | 1.50 | 1.75 |
| anti-phase | | | | |
| left side | 163.0 | 173.1 | 195.1 | 207.2 |
| vs. 1.25 | - | 8.03 | *26.76 | *51.85 |
| right side | 166.8 | 172.2 | 172.8 | 160.8 |
| vs. 1.25 | - | F < 1 | F < 1 | F < 1 |
| L. vs. R. | F < 1 | F < 1 | *11.91 | 7.40 |
| in-phase | | | | |
| left side | 336.3 | 348.0 | 2.1 | 38.3 |
| vs. 1.25 | - | 2.10 | 8.13 | *77.03 |
| right side | 337.1 | 348.3 | 6.8 | 11.9 |
| vs. 1.25 | - | 8.71 | *16.74 | *40.93 |
| L. vs. R. | F < 1 | F < 1 | F < 1 | *16.08 |

*$p < 0.01$, d.f. (1, 10)

### Uniformity of Relative Phase

Movements of the left and the right side were equivalent in terms of the uniformity of relative phase ($F(1, 79) < 1$). Movements conducted in the anti-phase mode (2.39) exhibited smaller uniformity values than those conducted in the in-phase mode (2.50) ($F(1, 79) = 5.58$, $p < 0.05$). A main effect for frequency was present ($F(3, 79) = 8.05$, $p < 0.001$). Movements paced at 1.75 Hz exhibited smaller uniformity values than those paced at all other frequencies ($p < 0.05$, Tukey HSD). An interaction of mode and pacing frequency ($F(3, 79) = 11.82$, $p < 0.0001$) suggested that this effect was primarily accounted for by movements prepared in the anti-phase mode ($p < 0.01$, Tukey HSD).

TABLE 6.16 Summary table showing uniformity of relative phase for each side, and mode of coordination, as a function of pacing frequency: subject Z

| | Frequency Hz<br>1.00 | 1.25 | 1.50 | 1.75 |
|---|---|---|---|---|
| left side | 2.44 | 2.56 | 2.41 | 2.38 |
| right side | 2.48 | 2.59 | 2.51 | 2.17 |
| anti-phase | 2.49 | 2.63 | 2.45 | 2.00 |
| in-phase | 2.43 | 2.53 | 2.47 | 2.55 |

### 6.3.5 Transition Durations

Analyses of variance for transition durations were performed for each subject using a 2 side (left, right) by 2 mode (anti-phase, in-phase) by 4 frequency (1.00 Hz, 1.25 Hz, 1.50 Hz, 1.75 Hz) design. Each trial was treated as a single case. All factors were grouping.

Subject: W

Transitions were of longer duration for movements of the right side (1.32 s) than for movements of the left side (1.18 s) ($F(1, 74) = 8.91, p < 0.01$). Movements prepared in the anti-phase mode and the in-phase mode were equivalent in terms of transition durations ($F(1, 74) < 1$). A main effect for frequency was noted ($F(3, 74) = 34.51, p < 0.0001$). Post hoc comparison of means using the Tukey HSD procedure revealed the presence of pairwise differences between all levels of frequency other than between 1.75 Hz and 1.50 Hz, and between 1.00 Hz and 1.25 Hz ($p < 0.01$). As Figure 6.5 (Panel A) illustrates, transition durations decreased with increases in pacing frequency. The interaction of side, mode and pacing frequency was also of statistical significance ($F(3, 74) = 3.69, p < 0.05$).

Subject: X

Transitions were of equivalent duration for movements of the left and the right side ($F(1, 79) < 1$) and for movements prepared in the anti-phase and in-phase modes ($F(1, 79) < 1$). A main effect for frequency was observed ($F(3, 74) = 9.13$, $p < 0.0001$). Post hoc comparison of means using the Tukey HSD procedure revealed the presence of pairwise differences between movements paced at 1.00 Hz and those paced at all other frequencies ($p < 0.01$). As Figure 6.5 (Panel B) illustrates, on the whole there was a trend for transition durations to decrease with increases in pacing frequency.

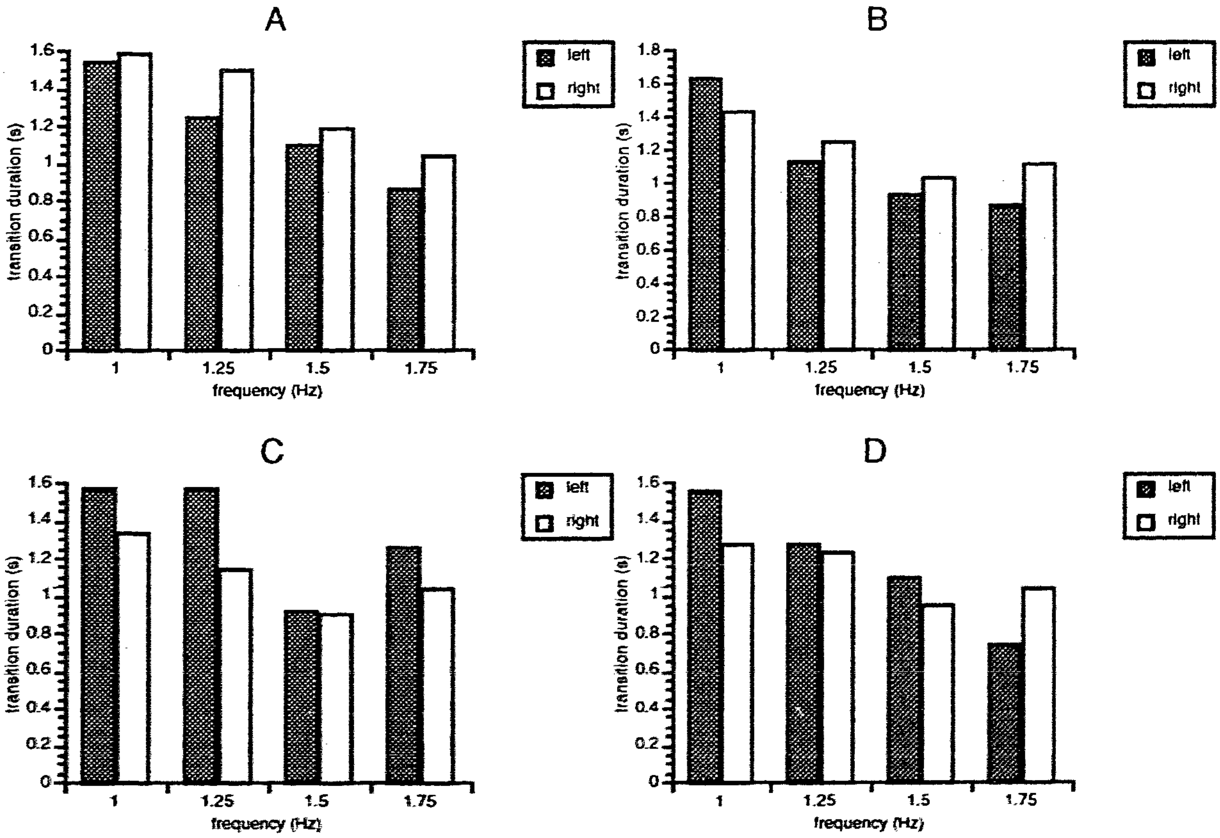

Fig. 6.5. Transition durations as a function of side and pacing frequency for subjects W (panel A), X (panel B), Y (panel C), and Z (panel D).

Subject: Y

Transitions were of longer duration for movements of the left side (1.33 s) than for movements of the right side (1.10 s) ($F(1, 80) = 3.99$, $p < 0.05$) and were of equivalent duration for movements prepared in the anti-phase and in-phase modes ($F(1, 80) < 1$). There was also present a main effect for frequency ($F(3, 80) = 4.48$, $p < 0.01$). As inspection of Figure 6.5 (Panel C) reveals, this effect was accounted for by pairwise differences between movements paced at 1.50 Hz and those paced at 1.00 Hz and 1.25 Hz ($p < 0.05$, Tukey HSD).

Subject: Z

Transitions were of equivalent duration for movements of the left and the right side ($F(1, 78) < 1$) and for movements prepared in the anti-phase and in-phase modes ($F(1, 78) = 1.44$, $p > 0.20$). A main effect for frequency was noted ($F(3, 78) = 6.77$, $p < 0.001$). Post hoc comparison of means using the Tukey HSD procedure revealed the presence of pairwise differences between movements paced at 1.00 Hz and those paced at 1.50 Hz and 1.75 Hz, and between those paced at 1.25 Hz and those paced at 1.75 Hz ($p < 0.05$). As Figure 6.5 (Panel D) illustrates, transition durations decreased with increases in pacing frequency.

### 6.3.6 Transition Pathways

All transitions were classified with respect to the direction in which relative phase "moved" during the transition. Positive values reflected an increasing value of relative phase at transition corresponding to the ankle gaining at least one half cycle relative to the wrist. Whereas negative values indicated that the ankle had lost at least one half cycle relative to the wrist. For the purposes of these classifications, data were pooled for each subject by collapsing over pacing frequency. Analyses.(binomial expansions) were conducted to determine the probability of obtaining through chance the observed distributions of transition pathways (Ferguson, 1971). In order to control for the potential inflation of Type I errors resulting from multiple comparisons, alpha was assigned as $p = 0.01$.

Subject: W

TABLE 6.17 Summary table showing proportion of trials exhibiting positive transition pathways for each side in each initial mode: subject W

| | Mode | |
|---|---|---|
| | anti-phase | in-phase |
| left side | *87.5% | *100% |
| right side | *95.65% | *100% |

*p < 0.01

Subject: X

TABLE 6.18 Summary table showing proportion of trials exhibiting positive transition pathways for each side in each initial mode: subject X

| | Mode | |
|---|---|---|
| | anti-phase | in-phase |
| left side | *4.35% | *75% |
| right side | *13.64% | *79.17% |

*p < 0.01

Subject: Y

TABLE 6.19 Summary table showing proportion of trials exhibiting positive transition pathways for each side in each initial mode: subject Y

| | Mode | |
|---|---|---|
| | anti-phase | in-phase |
| left side | 45.83% | 62.5% |
| right side | *20.83% | 33.33% |

*p < 0.01

Subject: Z

TABLE 6.20 Summary table showing proportion of trials exhibiting positive transition pathways for each side in each initial mode: subject Z

| | Mode | |
|---|---|---|
| | anti-phase | in-phase |
| left side | *16.67% | *12.5% |
| right side | *4.55% | *4.17% |

*p < 0.01

## 6.4 Summary and Discussion

### 6.4.1 Task Performance

Frequency deviation scores were used to provide a means of determining the extent to which subjects adhered to the pacing regime. Consistent with the data obtained in Experiment 3, the degree of deviation from the metronome was, for three subjects, an increasing function of the pacing frequency. Generally, deviation scores were lower in this experiment than were obtained in Experiment 3 at equivalent pacing frequencies (1.25 Hz and 1.75 Hz). This may have resulted from the single frequency per trial protocol employed in the present experiment. Nonetheless, increasing deviation from the metronome with increases in frequency appears to be a consistent effect. In all cases the degree of deviation was equivalent for movements of the left and right side, and when movements were prepared in the anti-phase and in-phase modes of coordination.

A single subject (W) presented differences between movements of the left and right sides which were expressed in terms of variability of frequency. The direction of this difference, which indicated greater variability for movements of the left side, was consistent with the data obtained in Experiment 1 when a self paced protocol was used. However, the absence of this effect in the remaining subjects is consistent with the data obtained in Experiments 2 and 3, and suggests that the imposition of external pacing protocol serves to obscure latent asymmetries.

In three of the four subjects the pacing frequency had some influence upon the variability of the oscillation frequency. In subject W, variability increased monotonically with pacing frequency. Whereas both subjects X and Z exhibited a tendency for movements to exhibit more variable oscillation frequencies at both the lowest and highest pacing frequencies. These data contrast with those obtained by Byblow et al. (submitted) who obtained *continuous* frequencies which decreased in variability with positive scaling of pacing frequencies. In the present study, a single subject (Z) exhibited coefficients of variation for discrete frequency which were larger for movements prepared in the anti-phase mode than those prepared in-phase.

Mean values of relative phase obtained for each trial were examined to determine whether any directional effect accrued from the positive scaling of pacing frequency. It was generally the case that mean values of relative phase increased with increases in pacing frequency. Although such positive drift was not consistently observed in all preparations, negative drift was not present in any instance.

Movements of the left and right sides were generally equivalent in terms of the uniformity of relative phase. Movements in the anti-phase and in-phase modes were on occasion differentiated on this basis. Subjects W and Y presented uniformity values for movements prepared in the anti-phase mode which were larger than those in the in-phase mode. These observations were somewhat contrary to expectations. Movements performed by subject Z, in the anti-phase mode, were associated with lower uniformity values than movements performed in the in-phase mode. There is at present no compelling explanation for these inconsistencies. However, the presence of higher order interactions involving side, mode and pacing frequency for subjects W and Y indicated that the main effect for mode was not consistently expressed. Uniformity of relative phase was generally observed to be inversely related to pacing frequency, suggesting that stability is compromised at higher frequencies of oscillation. In all subjects but W, this tendency was largely accounted for by movements conducted in the anti-phase mode of coordination. Similar results were obtained by Scholz and Kelso (1990) who observed that the variability of relative phase increased with frequency when subjects were moving anti-phase.

### 6.4.2 Transitional Behaviour

It has been predicted that the time required to intentionally switch from one pattern to another is dependent upon the differential stability of the pattern themselves (Scholz & Kelso, 1990). The variability (uniformity) of the order parameter relative phase for movements in each mode of coordination may be considered an index of the stability of the stationary state corresponding to each pattern. Analysis of switch durations failed to reveal differences between movements initially prepared in the anti-phase and in-phase modes of coordination. These data contrast with those obtained by Scholz and Kelso (1990) who observed that the variability of relative phase was larger in the anti-phase than in the in-phase pattern of coordination, and that switching from the in-phase to the antiphase pattern was consistently slower than switching in the opposite direction. The present data are therefore not consistent with the model, in that those subjects who exhibited differences between modes in terms of uniformity failed to present corresponding differences in switch duration. As remarked however, differences in uniformity between the coordinative modes were not reliably expressed in all conditions.

In the current experiment the duration of transitions was profoundly influenced by pacing frequency. In all subjects there was a tendency for transition durations to decrease with increases in pacing frequency. There were no differences between movements prepared in each mode of coordination in the extent to which this trend was expressed. These data reproduce those obtained by Scholz and Kelso (1990) for two of their four subjects. These effects are not predicted by the model of intentional switching posited by Schöner and Kelso (1988b). Rather, pacing frequency is anticipated to have little influence upon the slope of the potential resulting from the superposition of intrinsic and intentional dynamics. The changes in the depth of the potential minimum associated with coordinative states are predicted to have merely a weak effect upon the net switching dynamics (Scholz & Kelso, 1990). The level of influence of pacing frequency upon transition durations suggests that the model as presently formulated may be unable to encapsulate all aspects of the intentional switching process.

Scholz and Kelso (1990) employed a continuation paradigm in which metronome pacing was removed 10 cycles prior to the onset of the imperative signal. Although these authors suggested that oscillation frequencies in the induction and continuation portions were highly correlated with the metronome frequency, no inferential statistics were reported. It would have been useful to have access to indications of whether adherence to the pacing regime was equivalent in the induction and continuation phases. The likelihood that there exist systematic differences between conditions which are not adequately captured by correlation or regression measures has been discussed previously (Experiment 2). As remarked upon in detail elsewhere (Chapter 7), it is likely that the application of external pacing has significant impact upon the substructure of coordinative dynamics (Carson et al., in press). In the present experiment, the dependency upon pacing frequency and suggests transition durations were related in some fashion to the metronome period. Subjects were not instructed or constrained to commence transitions as rapidly as possible following the presentation of the imperative signal. Rather they were free to select the point in time at which to initiate a transition. It is thus possible that subjects organized their movements such that metronome pulses acted as anchors for the onsets and offsets of intentional transitions. Evidence has recently been presented which suggests that the temporal locus of a metronome pulse with respect to the movement cycle exerts a potent influence upon both individual oscillator and collective variable dynamics. In bimanual coordination these factors are sufficient to govern the discrimination of specific transition pathways (Byblow et al., submitted; Carson et al., in press).

It was suggested that if the limb/flank-hemisphere systems differ with respect to the expression of intentional dynamics, movements of the left and right sides would be distinguished by the relative magnitudes of the intentional perturbation $c_{int}$. This parameter is indexed in part by the duration of an intentional transition. Having ascertained that there existed no differences in terms of expressions of the intrinsic dynamics and in oscillation frequency, it appeared reasonable to consider any differences in transition duration between movements of the left and right sides as being attributable to differences in the application of intentional perturbations of the intrinsic dynamics. One subject (W) exhibited transitions which were of longer duration for movements of the right side. Whereas the only other subject (Y) for whom transition durations were distinguished on this basis presented slower transitions for movements of the left side. These data therefore fail to support the hypothesis that the limb/flank-hemisphere systems consistently differ with respect to the expression of intentional dynamics.

Peters (e.g., 1987, 1989, 1990b) proposed that the activity of the preferred hand thrives upon and demands focussed attention, whereas, the non-preferred hand receives a more diffuse form of attention. It has also been suggested that in bimanual movements, right handers have a propensity to direct attention preferentially to the right body half (Peters, 1987), and that it is this feature which accounts for the superiority of the right hand in producing complex rhythmic sequences such as polyrhythms. However, a clear indication of that to which attention refers has rarely been detailed (Carson, 1989b). The dynamics approach provides a principled basis with which to treat intentional, and thus presumably attended, perturbations of intrinsic dynamics. The current experiment provided no indications that movements of the limb/flank-hemisphere systems were differentiated on the basis of discrete modifications. Invocation of attention as an explanatory construct is often a posteriori, and it is not clear that attention, as invoked for example by Peters, corresponds to the application of an intentional perturbation. Currently work is being undertaken in our laboratory (Byblow, in preparation) with the aim of providing a dynamical account of asymmetries in polyrhythmic coordination. It is to be anticipated that such principled expansions of the approach will enable traditional constructs such as attention to be reconciled with the language of dynamics.

### 6.4.3 Transition Pathways

As noted above, pretranstions drift in relative phase with scaling of pacing frequency was generally positive. Classification of transition pathways indicated that one subject (W) exhibited predominantly positive transtions. Subject Z presented largely negative transitions. Whereas, subject Y exhibited a dominant direction of transition (negative) only for movements of the right side which moved from the anti-phase to the in-phase mode. The final subject (X) exhibited transitions which were of positive direction when initially prepared in the in-phase mode, and were of negative direction when initially prepared in the anti-phase mode of coordination. While these data initially appear to conflict with the predicted consequences of symmetry breaking in intrinsic dynamics, it is not necessarily the case that intentionally mediated transitions need be in the same direction as pretransition drift in relative phase. This would only be anticipated if pretransition drift is an indication of symmetry breaking in the dynamics and the perturbation was of symmetrical form. However, given that the perturbation is modelled as being endowed with dynamics, these need not be symmetrical in nature. Thus observations of transition pathways which are in a direction opposite to pretransition drift of relative phase are not necessarily inconsistent with with current dynamical models. Further work is clearly required to examine these issues.

## 7 General Discussion

It was proposed that a dynamical description of human coordination may provide a means by which to elucidate the basis of manual asymmetries. Four experiments were conducted in which the dynamics of coordinated rhythmic movements of the ankle and the wrist, on each side of the body, were examined.

In Experiment 1, a self paced protocol was employed. Subjects were required to produce movements in two modes of coordination, anti-phase and in-phase, at what they determined to be their most comfortable sustainable frequency of oscillation. The dynamics of these movements were expressed in terms of a number of variables including variability of oscillation frequency, nominally a control parameter, and the variability of discrete relative phase, the putative collective variable or order parameter. The results of the first experiment indicated that movements of the left side exhibited greater variability of oscillation frequency and of relative phase than movements of the right side.

In the second experiment, subjects attempted to execute their movements at frequencies (1 Hz or 2 Hz) specified by an external pacing regime. It was noted that when initially prepared in the anti-phase mode and paced at 2 Hz, three of the four subjects examined were unable to satisfy task requirements by reproducing the specified frequency and prescribed mode of coordination. Movements of the left and right side were not distinguished by the degree of adherence to external pacing, nor in terms of the variability with which oscillation frequencies were produced. A single subject conformed to task requirements in all conditions. Movements of the left and right side performed by this individual were distinguished from each other especially when prepared in the anti-phase mode and paced at 2 Hz. In these conditions, movements of the left side exhibited lower oscillation frequencies, and larger coefficients of variation of oscillation frequencies than movements of the right side.

The third experiment comprised a scaled frequency protocol. Pacing frequency was increased from an initial value of 1.25 Hz to 2.75 Hz in steps of 0.25 Hz. When movements were initially prepared in the anti-phase mode of coordination, spontaneous transitions to the in-phase mode or to phase wandering were observed as the pacing frequency was increased. When initially prepared in the in-phase mode, transitions to phase wandering were observed. Signature features of nonequilibrium phase transitions including loss of stability were noted. The two observed stationary coordinative states, anti-phase and in-phase, were mapped unto attractors of the collective variable dynamics. Intrinsic dynamics were assessed using measures indexing the stability of these stationary (attractor) states. These measures included the variability of the collective variable relative phase about the mean value corresponding to each stationary state. Movements of the left and right side were not distinguished with respect to this measure of stability. The number of transitions from each preparation and the time at which those transitions occurred furnished measures of the relative stability of the attractor states. Movements of the left and right sides were also not differentiated on the basis of these measures.

In a fourth experiment, coordinated movements of the left and right sides were compared with respect to the implementation of intentional perturbations of the intrinsic dynamics. Upon presentation of a visual signal, subjects were required to rapidly switch from the anti-phase to the in-phase pattern of coordination, or vice versa. The duration of transition was predicted to index the differential stability of the two patterns of coordination. However, transitions from the anti-phase to the in-phase mode were of equivalent duration to transitions from the in-phase phase to the anti-phase mode. In addition, analysis of transition durations failed to reveal differences between movements performed by the left and the right side. Transition durations were observed to scale inversely with increases in pacing frequency.

A striking feature of the data derived from the four experiments was the absence in Experiments 2 to 4 of asymmetries which were clearly expressed in Experiment 1. In the initial experiment, coupled movements of the left side exhibited larger coefficients of variation for oscillation frequency than those of the right side. Movements of the left side were also more variable with respect to relative phase. These tendencies were not consistently reproduced in any further experiments. One feature that distinguished the initial study from the later experiments was the use of a self paced frequency protocol.

Applications of the phase transition methodology to the study of human coordination have almost exclusively made use of external pacing as a means of controlling oscillation frequency. Generally pacing frequency, and thus it is assumed the oscillation frequency, is regarded as having a parametric influence upon the system dynamics. As a control parameter, frequency is considered unspecific with respect to the patterns of coordination which emerge, and as such "no specific ordering from the outside" is assumed (Jeka & Kelso, 1989, p. 8). In the current series of experiments the use of external pacing appeared sufficient to elicit basic phenomena predicted on the basis of formal models (e.g., Haken et al., 1985; Schöner et al., 1986).

Recently it has been shown that the imposition of task demands, such as those which serve to constrain the temporal locus of external pacing with respect to the movement cycle, significantly influences the dynamics when described at the level of the collective variable and at the level of the component oscillators (Byblow et al., submitted; Carson et al., in press; Kelso et al., 1990). As outlined in Chapter 2, in modelling human coordination, dynamics are not usually ascribed to the control parameter (cf., Haken & Wunderlin, 1990). Nonetheless, in an experimental preparation, the frequency of oscillation is not stationary over time. It also noteworthy that oscillation frequency varies on a time scale much slower than the variability ascribed to stochastic noise sources arising from the many degrees of freedom from which the coordinative system is assembled (cf., Wing & Kristofferson, 1973). Within a coordinative system, this variance can also be expressed differentially across the component oscillators. For example, in bimanual movements organized in absolute coordination, although paced by the same signal, coefficients of variation for the left hand are consistently larger than those for the right hand (Byblow et al., submitted; Kay et al., 1987; Riek, Carson, & Byblow, in preparation). These data suggest that oscillation frequency is more than simply parametric in biological systems in the same sense in which it is parametric in extant formal models of these systems.

In Experiments 3 and 4 of the present series it was noted that the degree to which oscillation frequency deviated from the externally furnished pacing frequency was highly dependent on the actual pacing frequency. Higher pacing frequencies engendered greater deviation from those frequencies. These data suggest that consideration be given to the manner in which an external, and ostensibly parametric, influence becomes internalized and in turn impinges upon coordinative dynamics. As outlined in discussion of Experiment 3, the coupling of perception and action may be characterised as a pattern formation process (Kelso et al., 1990). This strategy has been applied with some success in modelling these processes at the level of the joint kinematics (Kelso et al., 1990) and at the level of the neuromagnetic field patterns in the brain (Kelso et al., 1992). It is apparent that at each level of description one may describe a collective variable which encapsulates the coupling of perception and action. Significantly one may also define a variable which captures the degree of deviation from the external parametric influence. In the language of control theory this variable represents a transfer function. More useful in the present context is the concept of an "effective control parameter" which encapsulates for each level of description the degree to which an external parametric influence is internalized. Clearly each level of description uniquely defines an effective control parameter. The dynamics of the effective control parameter defined in terms of electric or electromagnetic field potentials recorded from various areas of the cortex may differ substantially from those defined at the level of the EMG which may in turn differ from those defined at the level of the joint kinematics. The extent to which these dynamics are contingent upon the task demands remains to be determined. The data obtained in Experiment 2 suggest that the degree of deviation from the pacing frequency is contingent not only upon pacing frequency but also upon the mode of coordination in which the system is prepared (cf., Kelso et al., 1990) and upon instructional variables.

The integrity of this general approach relies upon the presence of control parameters which are responsible for the emergence of patterns arising from the dynamics of the system itself (Jeka & Kelso, 1989). In experimental preparations the putative control parameter is usually explicitly defined. However, control parameters need not be externally specified. The Vector-Integration-To-

Endpoint (VITE) model proposed by Bullock and Grossberg (1991) encapsulates a GO signal which is a nonspecific control signal thought to arise at relatively high levels of the nervous system. In contrast, in giving prominence to their emergence in many natural systems, advocates of the dynamics approach maintain that nonspecific control parameters play a role in self-organization and pattern formation at many scales of observation (Kelso, 1991). However, in biological systems in general, and the human coordination system in particular, the relationships between control parameters defined at various levels of observation appear dynamic rather than static. Not unexpectedly, for a given of observation, the dynamics of the effective control parameter are contingent upon whether the parameter is externally or internally specified. Coefficients of variation for movements paced at 1.0 Hz in experiment 2, were lower than for movements of approximately the same frequency, elicited in the self paced trials in Experiment 1. These data are consistent with those obtained using two phase (induction and continuation) paradigms (e.g., Kolers & Brewster, 1985). In summary, these considerations suggest a distinction between formally defined control parameters which are strictly parametric, and effective or biologically implemented control parameters which are imbued with dynamics. Further, the external pacing, characteristic of the phase transition methodology, might plausibly be modelled as a source of information as it appears to contribute to the order parameter dynamics (cf., Byblow et al., submitted; Carson et al., in press).

What are the implications of the foregoing for the evaluation of manual asymmetries? Perhaps the most consistent findings to emerge from the extensive body of research inquiring into manual asymmetries have been the higher and less variable rates of response elicited for movements of limb segments on the right side of the body. These trends are reproduced for unimanual reciprocal movements such as tapping and for bimanual tasks. In short, the most reliable manifestations of asymmetries in motor output are expressed in terms of (oscillation) frequency and its associated variability. In the first experiment of the current series, differences in the variability of preferred frequencies, which were unevenly expressed for uncoupled movements of single joints, were consistently displayed for coupled movements involving two joints. The requirement that subjects adopt one of two patterns of coordination defined by a target relative phase relation, appeared sufficient to accentuate otherwise latent asymmetries. These features of the data were not reproduced in any of the further experiments in which an external pacing protocol was employed. It has been proposed that the processes through which an external, and ostensibly parametric, influence becomes internalized impinge upon the intrinsic dynamics which otherwise pertain when control parameters are internally specified. Byblow et al (submitted) observed that critical fluctuations, one of the signature features of non-equilibrium phase transitions, were not observed when subjects were required to maintain specific metronome-limb relations in addition to target limb-limb phase relations. Similarly, it seems likely that in Experiments 2 to 4 of the present series, the imposition of external pacing served to obscure fine structure of the dynamics. In the present context, the most salient aspects of the fine structure are those which distinguish movements conducted on the left side from those on the right side of the body.

The results of the present series of experiments do not invalidate the integrity of a dynamical account of manual asymmetries. Order parameter dynamics are always defined in terms of a coordinative task, that is, they are not context free. However these data suggest that the elicitation of asymmetries of coordination dynamics in an experimental context is highly contingent upon specific details of the task protocol. Current procedures used to elicit phase transitions may impinge upon the dynamics in a manner which serves to obscure manual asymmetries. The phase transition methodology has generally utilized external pacing regimes as a means by which to apply control parameters. It has been argued that internalization of control parameters impinges upon the coordination dynamics in a fashion which eclipses textural detail of these dynamics. There exist additional paradigms which have been used to explore the dynamics of human coordination. Prominent among these is the methodology introduced by Kugler and Turvey (1987) which has been used extensively to examine the dynamical basis of bimanual coordination (e.g., Bingham et al., 1991; Kugler et al., 1990; Rosenblum & Turvey, 1988; Schmidt, et al., 1991; Schmidt et al., 1992). There exist problems associated with this methodology, most notably those arising from the physical properties of the compound pendular system. These features may be as potent in limiting expression of the fine structure of the dynamics as the imposition of external pacing. It is possible that asymmetries in the coordination dynamics may most reliably be elucidated using protocols, such as those employed in Experiment 1, in which there is a minimal degree of intervention (e.g. Beek, 1989). Graphical and analytic techniques such as those described by Beek and Beek (1988) may be considered complimentary to this approach, and are consistent with contemporary approaches to the study of the dynamics of the CNS (see Duke & Pritchard, 1991). The phase transition methodology remains one of the most effective means of delineating collective variables at a number of levels of observation, and thus is integral to the general approach. However, in relying upon the provision of discrete external pacing as a means of applying control parameters, the current methodology may not necessarily be the most appropriate means of probing for asymmetries. Alternative procedures for effecting control parameter regimes may provide means of inducing phase transitions without inducing the alterations of the intrinsic dynamics which appear attendent upon the use of metronome based protocols.

Contemporary treatments of the neural bases of manual asymmetries have often been based upon the delineation of some population level association ("parallel") between an anatomical feature such as the size of planum temporale, and scores on undifferentiated measures of "hand skill" such as those derived from peg moving tests (e.g., Annett, 1992). These studies however, fail to provide a great deal of insight concerning "mechanisms" of asymmetry". The efficacy of a dynamical account is that any system of interest may be described simultaneously at a number of levels of observation using a unitary set of descriptive tools. The linkage between events at a "microscopic" level (for example that of the neurons and neuronal assemblies) and the "macroscopic" behavioural level is held to be by virtue of shared dynamics (Kelso, et al., 1992). To the extent that, to date, these forms of analysis have been more readily applied to perceptual-motor coordination at the level of movement kinematics, the limitation is identified as having been one of implementation rather than of principle. Recently however, multichannel neuroelectric (EEG and MEG) recordings have been employed in an attempt to determine whether patterns of coordination exhibited at the level of the neuronal ensemble and patterns revealed at the behavioural level are governed by corresponding dynamical laws (Kelso et al., 1992). These developments intimate that appraisal of the neural bases of manual asymmetries will be advanced by assessment of whether differences in coordination dynamics exhibited by the limb-hemisphere systems at the behavioural level are accountable for in terms of dynamical laws inferable at the microscopic level.

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