

Patterns of Human Interlimb Coordination Emerge from the Properties of Non-Linear, Limit Cycle Oscillatory Processes: Theory and Data

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ABSTRACT. The present article represents an initial attempt to offer a principled solution to a fundamental problem of movement identified by Bernstein (1967), namely, how the degrees of freedom of the motor system are regulated. Conventional views of movement control focus on motor programs or closed-loop devices and have little or nothing to say on this matter. As an appropriate conceptual framework we offer Iberall and his colleagues' physical theory of homeokinetics first elaborated for movement by Kugler, Kelso, and Turvey (1980). Homeokinetic theory characterizes biological systems as ensembles of non-linear, limit cycle oscillatory processes coupled and mutually entrained at all levels of organization. Patterns of interlimb coordination may be predicted from the properties of non-linear, limit cycle oscillators. In a set of experiments and formal demonstrations we show that cyclical, two-handed movements maintain fixed amplitude and frequency (a stable limit cycle organization) under the following conditions: (a) when brief and constantly applied load perturbations are imposed on one hand or the other, (b) regardless of the presence or absence of fixed mechanical constraints, and (c) in the face of a range of external driving frequencies from a visual source. In addition, we observe a tight phasic relationship between the hands before and after perturbations (quantified by cross-correlation techniques), a tendency of one limb to entrain the other (mutual entrainment) and that limbs cycling at different frequencies reveal non-arbitrary, sub-harmonic relationships (small integer, subharmonic entrainment). In short, all the above patterns of interlimb coordination fall out of a non-linear oscillatory design. Discussion focuses on the compatibility of these results with past and present neurobiological work, and the theoretical insights into problems of movement offered by homeokinetic physics. Among these are, we think, the beginnings of a principled solution to the degrees of freedom problem, and the tentative claim that coordination and control are emergent consequences of dynamical interactions among non-linear, limit cycle oscillatory processes.

1. Introduction

THE BEGINNING of the 1970s brought about a remarkable change in the approach of psychology and related disciplines to the area of movement behavior. This so-called "product to process" shift that many have remarked on (e.g., Pew, 1974; Schmidt, 1975) evolved from emerging models of human information processing and empirical attempts to discover the nature of a myriad of hypothetical processes—stimulus detection, memory retrieval, response selection (to name but a few)—thought to be involved in behavioral action. Even more significant was the embracing by psychologists of control-theoretic and cybernetic concepts; a move that led to models of motor skill learning (Adams, 1971; Schmidt, 1975) and memory (cf. Laabs, 1973; Stelmach, 1974) and a great deal of laboratory activity (for updates and developments of closed-loop theory, see Adams, 1977; for updates on schema theory, see Shapiro & Schmidt, 1982).

At the beginning of the 1980s it seems timely to remark that our theories and models (like many of the theories and models in biology and the social sciences) are flawed by a deep-seated anthropomorphism that extends back to the time of Descartes: acting humans are compared to machines (computers and servomechanisms) provided with means of control and self-regulation. Motor control theories are peppered with anthropomorphic concepts—perceptual traces, reference mechanisms, comparators, schemas, programs, and so forth—created to "explain" data. Although these concepts have been, and probably will remain, useful for developing an intuitive idea of the way motor systems work we believe it is now time to consider a *dynamical* account of movement behavior—one that is consonant with the newly emerging physics of living systems (cf. Kelso, 1981; Kelso, Holt, Kugler, & Turvey, 1980; Kugler, Kelso, & Turvey, 1980, 1982; Turvey, 1980)—even if it is at the expense of some abstraction. The theoretical approach offered here is in its infancy, but the need for it and the types of experiments motivated by it (some of which we report here) can be clarified when we consider further some of the shortcomings of existing theory.

2. Some Limitations of Current Theory.¹

The problem—aptly understated—that has not received as much theoretical attention in the movement domain as it warrants, is one

We wish to thank Katherine Harris, David Goodman, Betty Tuller, Richard Schmidt, Ronald Marteniuk, and Michael Turvey for comments on an earlier version of this paper. The research was supported by NIH Grants AM-25814, NS-13617 and Biomedical Research Support Grant RR05596.

¹All current theories of regulation and control—mathematical systems theory, automata theory, cybernetics—though different in detail are alike in likening man to a machine; it is to this issue that we address limitations.

shared by all living systems; namely, how the internal degrees of freedom of the system are regulated (cf. Bernstein, 1967; Iberall & McCulloch, 1969). Recently we and others have addressed this problem in some detail (e.g., Fowler, Rubin, Remez, & Turvey, 1980; Greene, 1972, 1978; Kelso, 1981; Kelso & Holt, 1980; Kelso et al., 1980; Kugler et al., 1980, 1982; Turvey, 1977, 1980; Turvey, Shaw, & Mace, 1978). One suspects that a main deterrent to a biologically motivated solution to the degrees of freedom problem lies in the view—shared by many—that humans, like computers, are simply information processing devices (cf. Berlinski, 1976). Theoretically, so the argument goes, computers can perform any calculable task that humans perform. Thus it should be possible to retrace the putative sequential steps that a human takes in solving a problem and instantiate them in program form. The physical realization of such a program would exhibit behavior that was artificially intelligent in the sense that such behavior would be indistinguishable from human performance. But, as Berlinski (1976) emphasizes, such a claim rests on a fundamental error. Just because computers can *simulate* certain types of human performance is hardly evidence that humans actually do *employ* such programs. Searle (1980) takes a similar stance in noting that the feature that seemed so attractive to people in artificial intelligence, namely the distinction between the program and its realization, proves fatal to the claim that simulation qualifies as *duplication*. Thus in Searle's (1980) terms:

The same program could be realized by an electronic machine, Cartesian mental substance or a Hegelian world spirit. . . . If mental operations consist of computational operations on formal symbols, then it follows that they have no interesting connection with the brain [for] the brain just happens to be one of the indefinitely many types of machine capable of instantiating the program. This form of dualism . . . is Cartesian in the sense that it insists that what is specifically mental about the mind has no intrinsic connection with the actual properties of the brain (p. 423–424).

A second and related point is that both programming and cybernetical solutions to the degrees of freedom problem underestimate the dynamics of the structure to be controlled. They fail, as Yates, Marsh, and Iberall (1972) remark, the "test of matching": in order to couple a control device to the system being controlled there must be some match between scales of energy or mass for efficient operation to ensue. In short, computational or algorithmic solutions place their emphasis on the small signal, information aspects of the system but undervalue the equally important energy-converting machinery (the power fluxes, Yates et al., 1972). A viable account of the dissipation of degrees of freedom for motor systems should recognize the mutuality between informational and power sources.

Much of current theorizing on motor behavior perpetuates a conceptual chasm between the brain as the source of signals for coordination and control and the high power, energy-converting muscular system that is the putative recipient of such messages. For example, in

neurophysiological and behavioral studies of movement, it is common for investigators to assume that the products of motor function are isomorphic with the underlying (brain) processes from which those products derived. If the movement of an animal terminates at some spatial location, within a set period of time, for example, that spatial location and duration are said to be contained or *represented* in the animal's motor program. The motor program then is viewed as causally responsible for generating the spatial position of a limb and metering out the time it takes for the limb to get there.

However, in real biological systems we suspect—unlike formal systems—there may be no need to represent explicitly every detail in the behavioral sequence. Rather, sequential organization may be due primarily to dynamical laws and the existence of constraints that serve to guide those dynamics (cf. Pattee, 1977). If this view is correct then the order and regularity in movement behavior that we observe will not be due to an *a priori* prescription—in terms of programs or reference levels—that is independent of and causally antecedent to the motor activity in question. Nor will it be an isomorphic representation of the behavior to be explained. Rather spatiotemporal organization—the dissipation of degrees of freedom—will arise as an *a posteriori* fact, an emergent property that is a consequence of, and concomitant with the dynamical behavior of the system (cf. Fowler, 1977).

3. The Dynamic Alternative.

The answer to what Bellman (1961) called “the curse of dimensionality”—the problem of understanding the relationship between informational and power processes—is offered in a recourse to dynamics defined as the physics of motion and change. If, as we assume, living systems obey the laws of physics (though they are not readily reducible to them) then, given that formal machine concepts may provide an inadequate basis for complex behavior, what can a dynamical explanation offer in their place? To provide a reasonable answer to this question we have to be armed with certain physical concepts that apply to active living systems.

In the past, a physical description of biological processes has been deemed inappropriate because dynamics has dealt almost exclusively with the behavior of closed, entropic systems (i.e., systems tending towards randomness and disorder). Thermodynamic law states that in a closed system the tendency towards entropy will increase to a maximal value, and that the process is irreversible. In contrast to closed, physical systems, living systems are “open,” by virtue of their ability to capture, degrade, and dissipate free energy. As Schroedinger (1945) remarked, living systems “accumulate negentropy” and in so doing maintain their structure and function.

It is only recently that an adequate physics has developed to accommodate the facts of biological systems. Morowitz (1979), following the lead of Prigogine (1976; Prigogine & Nicolis, 1971) and Katchalsky and

Curran (1967) has provided argument that continuous energy flow through a living system constitutes its chief distinguishing feature. In order to prevent the drift towards static equilibrium, biological systems must perform work. Since an isolated, closed system cannot do steady work it must be connected with a source and a sink; and it is the flow of energy from the source to the sink that constitutes work. *Energy flow, per se, is the chief organizing factor of living systems* (cf. Morowitz, 1979).

All this may seem far removed from a theory of movement, but it leads us to one fundamentally important principle that follows from Morowitz's (1979) main Theorem (p. 33): *the flow of energy through the system from a source to a sink will lead to at least one cycle in the system.* It is the notion that cyclicity provides a dynamic basis for investigating (and understanding) motor systems that we turn our attention to next.

4. Cyclicity—with Special Reference to Homeokinetic Physics (Iberall, 1977, 1978; Iberall, Soodak, & Hassler, 1978; Soodak & Iberall, 1978; Yates, 1980; Yates & Iberall, 1973)

Persistent cyclicity in biological systems is a non-linear phenomenon; if it were not, the strictures of thermodynamics would ensure a steadily decaying function. Consider, for example, simple mechanical systems such as a mass-spring, in which the equation of motion describes a trajectory towards an equilibrium state. Such systems may be described by a second order differential equation as follows:

$$m\ddot{x} + c\dot{x} + kx = 0. \quad (1)$$

In Equation 1, oscillatory motion will decay at a rate proportional to the magnitude of the viscous (frictional) term c . This fact is predicated upon the second law of thermodynamics—time flows in the direction of entropy. Yet as we have noted above, living systems are characterized by sustained motion and persistence; they are not statically stable; rather they maintain their form and function by virtue of their dynamic stability. How then can we ensure sustained motion without violating thermodynamic law?

Consider again the familiar mass-spring equation, but this time with a forcing function, $F(\Theta)$:

$$m\ddot{x} + c\dot{x} + kx = F(\Theta) \quad (2)$$

It is not enough to supply energy to the system described in Equation 2, it must also be supplied at the right place and time in the oscillation. Moreover, the forcing function must exactly offset the energy lost in each cycle for sustained performance to occur (i.e., to satisfy thermodynamic strictures). Many real systems meet this requirement by employing a mechanism—called an escapement—which releases exactly the energy needed to compensate for dissipative losses.² The escape-

²Examples of biological escapements can be found in numerous

ment consists of a non-linear element that taps energy from a high potential source—as long as it lasts—to overcome local thermodynamic losses. Thus a pulse or “squirt” of energy is released into the system via the escapement such that, averaged over cycles, the left hand side of Equation 2 equals the right hand side, thereby ensuring sustained motion. Such cycles are called *limit cycles* because they are capable of returning to a stable mode regardless of disturbances that may speed up or slow down the cycle (see below for further details of limit cycle properties).

Real clocks are non-linear, limit cycle oscillators that, once started, have self-sustaining properties (cf. Andranow & Chaiken, 1949). Many investigators of movement have hypothesized the existence of “clocks” or “metronomes” for purposes of timing (see Keele, 1981, for most recent review) and the rhythmic structure of many biological systems is beyond question (cf. Oatley & Goodwin, 1971; Aschoff, 1979) as is the existence of social-cultural rhythms (e.g., Brazleton, Koslowski, & Main, 1974). However, neither in the field of chronobiology nor in the motor systems area are such hypotheses based firmly in thermodynamic physical theory. Cyclicity (clock-like behavior) in a system arises as a consequence of the transfer of energy from a high potential source to a low potential sink. Cyclicity is ubiquitous in all complex systems, as Yates (1980) has emphatically remarked, because it is an “obligatory manifestation of a universal design principle for autonomous systems.”

What does a physically-based theory of periodic phenomena buy us in terms of a principled approach to the coordination and control of movement? The historical antecedent to modern models of the regulation of behavior is the Barnard-Cannon principle of homeostasis. That is, the internal states of an organism are preserved at equilibrium despite changes in the external environment. Modern feedback theories (modeled on quasi-linear servomechanisms) extend the notion of a reference-signal-as-goal state to one that can be achieved and adjusted through processes of detection, comparison, and error correction³ (cf. Adams, 1971, 1977; Schmidt, 1975). In sharp contrast, the physical scheme that we outline here is *homeokinetic* (Iberall, 1970): It is the operating conditions of a configuration of interacting, non-linear, limit cycle oscillatory processes that determine the stability (or regulated state) of the organism. According to Iberall and his colleagues (Iberall, 1977, 1978; Iberall et al., 1978; Yates & Iberall, 1973) stability in self-organizing, autonomous systems (the living kind) arises when many cyclical processes become entrained. Thus we can conceive of systemic

Footnote Continued

metabolic processes such as the Krebs cycle where release of ATP is triggered by the metabolic demands of the cell.

³*Strictly speaking, regulators and servomechanisms are different concepts even though it is common in the motor control area to hear them used synonymously. In the former, the reference value remains constant; in the latter the reference value varies continually.*

behavior as being established by an ensemble of non-linear components that are entrained into a coherent configuration.

Elsewhere we have reviewed and presented evidence for the notion—stemming from Bernstein's (1947) initial insights—that a group of muscles, functioning as a unit exhibits properties qualitatively like that of a non-linear oscillatory system (cf. Asatryan & Fel'dman, 1965; Fowler et al., 1980; Kelso, 1977; Kelso & Holt, 1980; Kelso, Holt, & Flatt, 1980; Kelso et al., 1980, for review). Briefly, we have shown that limb movements may be terminated accurately despite unexpected changes in initial conditions, unpredictable load disturbances during the movement trajectory, functional deafferentation, and all of these in combination. These results have been widely accepted both in animal and human work (e.g., Cooke, 1980; Polit & Bizzi, 1978; Schmidt, 1980) and are interpreted—to a first approximation—as evidence for a mass-spring system (see also Hollerbach, 1980, for expansion of this view to cursive handwriting). But linear mass-spring systems cannot exhibit homeokinetic properties even though they are capable of displaying periodicity. That is to say, the only cycles that meet the non-linear and self-sustaining criteria of biological systems are limit cycles (cf. Goodwin, 1970; Yates & Iberall, 1973; Yates, 1980). A brief discussion of limit cycle properties is thus in order, since it is these that provide a deductive framework for the present experiments.

5. Properties of Limit Cycle (Non-Linear) Oscillators (cf. Minorsky, 1962; Sollberger, 1965; Pavlidis, 1973)

To reiterate briefly, the central feature of homeokinetic physics is the dynamic regulation of a system's internal degrees of freedom by means of coupled ensembles of limit cycle oscillatory processes. In contrast to program and cybernetical conceptions, homeokinetic physics views the existence of active, interacting components and large numbers of degrees of freedom as a necessary and desirable attribute of complex systems. Homeokinetics predicts the discovery of numerous cyclicities and evidence for their interaction. But what is the nature of these cyclicities and what form does their interaction take?

An important caveat at the outset (though it shall not deter us here; instead it is the impetus for the present work) is that the mathematical analysis of non-linear oscillators has hardly begun (cf. Pavlidis, 1973). In contrast, for linear systems, motion in time is relatively easily described, even though the formula describing motion, $x = f(t)$, can be quite complicated. Such functions are conceived of as a system of derivatives, from zero order (the position itself, x) to high order, expressed by a differential equation whose degree is given by the exponential number of the highest differential. In linear systems, motion is regarded as a linearly additive system of first degree differentials whose coefficients may be constants or functions of t , but not functions of x . The family of functions described by linear differential equations are open to solution by various methods of integration (cf. Sollberger, 1965).

In sharp contrast, there are no general solutions for *non-linear* differential equations of motion. For example, in the famous van der Pol equation:

$$m\ddot{x} + K(1-x^2)\dot{x} + Bx = 0 \quad (3)$$

where x = displacement
 k = stiffness,
 B = damping,
 m = mass,

the stiffness coefficient k , is itself a function of the dependent variable x , giving rise to the non-linearity and thus negating a unique solution. Fruitful insights into non-linear systems are obtained by graphical methods called phase plane techniques which plot the first differential, velocity \dot{x} against displacement x . A set of simple examples is given in Figure 1. Consider a linear differential equation, $\ddot{x} + \omega^2x = 0$. When integrated, the equation yields a set of phase ellipses of the form $(\dot{x})^2 + (\omega x)^2 = c$. One such ellipse is shown in Figure 1A and represents the relation between velocity and position in a simple oscillation. The curves themselves are called phase plane trajectories; it is clear in Figure 1A that the phase plane represents a stable, periodic motion since velocity and position repeatedly return to a certain value (for further details, see figure caption). The spiral trajectory shown in Figure 1B represents an oscillation with continuously decreasing amplitude until it reaches a standstill. A spiral inwards constitutes a damped oscillation; if the direction were outwards (not shown), the oscillation would be unstable with increasing amplitude.

The important point to realize about the phase trajectories illustrated in Figure 1A and 1B is that they are based on linear systems. A change in any parameter, such as the damping coefficient, drastically changes the form of the solution (and thus the phase trajectory). There is then, no *preferred* solution or set of solutions in a linear system. This is not the case in non-linear systems in which all trajectories tend asymptotically toward a single limit cycle despite quantitative changes in parameter values (see Figure 1C). Thus, a highly important property of limit cycles is their *structural stability* in the face of variations in parameter values. That is to say, limit cycles exhibit a tendency to maintain a fixed amplitude and frequency (a stable, orbital trajectory) no matter how perturbed (cf. Minorsky, 1962; Oatley & Goodwin, 1971; Pavlidis, 1973; Hanson, 1978). Furthermore, in order for non-linear oscillators to offset precisely the energy lost during each cycle (in the drift towards equilibrium) they must degrade a large amount of free energy (cf. Yates & Iberall, 1973; Hanson, 1978). Because of high energy exchange, non-linear oscillators are quickly resettable following external perturbations. As we shall see, the rapid return of limit cycles to their preferred frequency and amplitude following experimentally imposed perturbations is a predominant feature of the data in the present experiments.

As we have already hinted, and as Pavlidis (1973) further emphasizes, coordination in biological systems arises from cooperative relationships

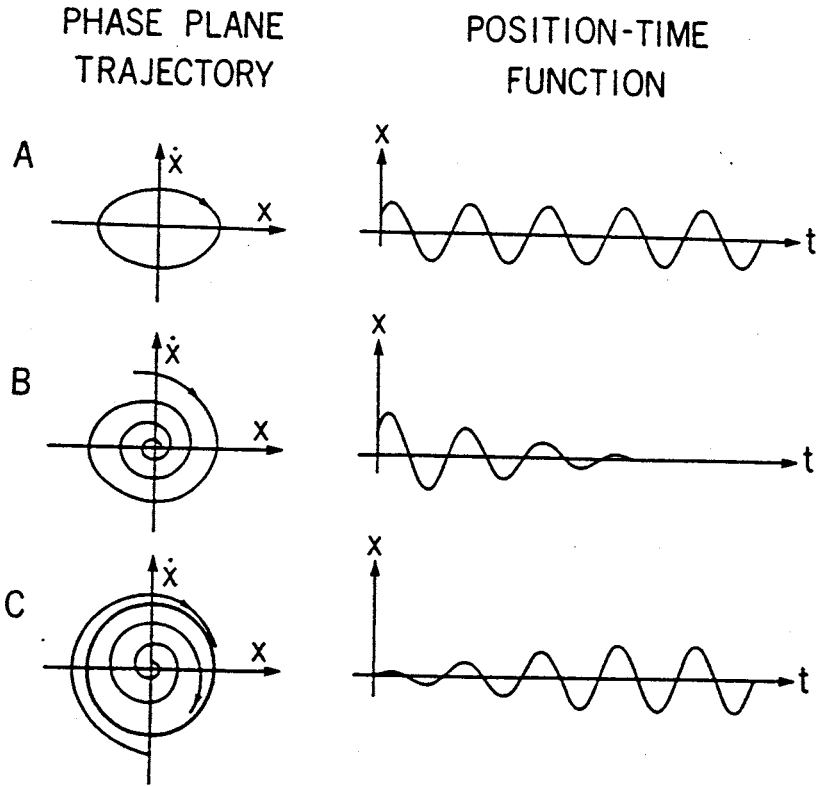


Fig. 1—Phase plane trajectories and corresponding position-time functions for three different types of oscillation.

A. Idealized harmonic motion

B. Damped harmonic motion.

C. Limit cycle oscillatory motion (see text for details)

among non-linear oscillator ensembles. In sharp contrast, linear oscillators do *not* interact among themselves—a fact that is based on the *superposition principle* in the theory of oscillations (Minorsky, 1962). As defined, the superposition principle says that oscillation in a system of several degrees of freedom consists of a number of component oscillations, each independent of the other.

An essential property of non-linear oscillatory systems, though, is that they always exhibit interaction. Perhaps the chief mode of cooperation among self-sustaining oscillators (and germane to the present experiments) is that of entrainment or synchronization.⁴ Apparently, the entrainment phenomenon was first observed by Huygens in the 17th century (cited by Minorsky, 1962). Huygens noted that two clocks

⁴Synchronization and entrainment are often used synonymously in the literature. Strictly speaking, synchronization is that state which occurs when both interval and phase of coupled oscillators are matched exactly; entrainment refers to the matching of intervals, but one oscillator may lead or lag the other.

whose "ticks" (oscillations) were out of step became synchronized when attached to a thick wooden board. Some two hundred years later, physicists studying electrical circuits and acoustics rediscovered the synchronization effect. When an electrical force of frequency W is applied to an electron-tube oscillator (frequency = W_0), the "beats" of both frequencies are apparent. As the frequencies get closer together, the beats diminish until, at a certain difference value $W - W_0$, they disappear entirely and a single frequency, W_1 , remains. Similarly when two or more oscillators interact, *mutual entrainment* occurs (the "magnet effect" of von Holst, 1973) with only a small detuning of their frequencies (Minorsky, 1962). Also, if the frequency of one oscillator is an integer multiple of another to which it is coupled, then *subharmonic entrainment*—another form of mutual interaction—takes place (also called frequency demultiplication).

In sum, entrainment is an *emergent property* of a system of non-linear oscillators; it is truly a self-organizing process in the sense that a collection of mutually entrained oscillators functions as a single unit. If, indeed, biological systems are composed of limit cycle oscillatory processes then the so-called "degrees of freedom problem"—apparent in much of the current theorizing on movement control—may be minimized by the entrainment property of non-linear systems. Moreover, entrainment ensures that the degrees of freedom may be dissipated with maximum efficiency and minimum energy cost. Let us consider how this dynamical view interfaces with behavioral experiment.

6. The Present Experiments

There is a rich empirical background in support of the present theoretical perspective. But little of the work is on human subjects (see Cohen, 1970; and Schepelmann, 1979, for exceptions), and none of it is physically (dynamically) founded. Rhythmical phenomena abound at all phylogenetic levels and in many different activities (see Stein, 1976, and Delcomyn, 1980, for reviews). Some of the early work on interlimb phase control by von Holst during the 1930's is classical in this respect, although it is not well-known (see von Holst, 1973, for English translation). In his experiments on fish fin movements for example, von Holst identified two main types of coordination. The first of these he termed *absolute coordination*—a 1:1 correspondence between cyclicities of different structures (i.e., where phase and period are the same). The second—much less common interactive state—was called *relative coordination*. Here the fins exhibited different frequencies although at least one of the phases usually corresponded to that observed during the absolute coordination state.

Relative and absolute coordination bears a close similarity to the entrainment properties of non-linear oscillators that we have addressed in the previous section. More recently, Stein (1976, 1977) has elaborated on von Holst's work using the mathematics of coupled oscillators to predict interlimb phase relationships based on the activity patterns of

"coordinating neurons" in cockroach and crayfish (see also Graham, 1977). As Stein (1977) notes, the oscillator theoretic approach to neural control is in an embryonic state. But an important first step (which we attempt to take here) is to examine the qualitative predictions of the theory.

For present purposes, there are two empirical antecedents to the following set of experiments. The first is the finding, discussed earlier, that muscles acting at a joint exhibit properties that, to a first approximation, are qualitatively like a mass-spring system. The important point to realize is that such a system is intrinsically rhythmic or cyclic even though it does not have to behave rhythmically or cyclically. Thus depending on its parameterization, a mass-spring system may or may not oscillate. *Discrete and cyclical behaviors may therefore arise as different manifestations of the same underlying organization* (cf. Fel'dman, 1966; Fowler et al., 1980; Hollerbach, 1980; Kelso & Holt, 1980). The present experiments are continuous with this theme and examine cyclical movements *per se*.

The second antecedent for the current work comes from earlier studies of human interlimb coordination (cf. Kelso, Southard, & Goodman, 1979a,b). When subjects perform movements of the two limbs to different sized targets at different distances from a home position, they do so almost simultaneously. Moreover, the limbs reach peak velocity and peak acceleration at practically the same time during the movements (but see also Marteniuk & MacKenzie, 1980). If subjects are required to move both limbs to separate targets, but one limb must hurdle an obstruction on the way, the other unobstructed hand describes a similar arc—at least on the first few trials (Kelso, Putnam, & Goodman, Note 1). When simultaneity is disrupted by instructing the subject to strike one target before the other, there is a sizeable cost (either in initiation time or movement errors) compared to temporally compatible, simultaneous conditions (Kelso et al., 1979a; Goodman & Kelso, Note 2; see also Klapp, 1979).

The ubiquity of timing constraints in movement is consistent with the clock-like behavior of mutually entrained oscillators (see Keele, 1981, for further examples, but a different interpretation), which as we have emphasized has a firm dynamic basis.⁵ It remains now for us to examine

⁵Interestingly, in *American Sign Language* (Klima & Bellugi, 1979) the constraints observed in the Kelso et al. experiments are omnipresent. According to Klima and Bellugi (1979): "If both hands move independently during a sign's articulation, then the two hands must exhibit identical hand configurations; the points of articulation are severely constrained with respect to one another (they must be in the same location or on the same horizontal or vertical plane); and the movements of the two hands must be the same (whether performed simultaneously or in alternation). The symmetry constraint thus specifies that in a two-handed sign, if both hands move and are active, they must perform roughly the same motor acts" (p. 64).

(and to illustrate) in a more direct manner some of the interlimb relationships predicted by the properties of limit cycles. One of the dominant techniques used to establish the autonomy of rhythms is to perturb the system away from its steady state behavior and observe the manner in which the system reorganizes itself (for example, this procedure is paradigmatic of circadian rhythm research, see Menaker, 1976). Only a system of non-linear oscillators will exhibit maintenance of frequency and amplitude (i.e., a bounded phase trajectory or limit cycle, see Figure 1C) despite perturbations. Thus in the first four experiments reported here (Series A), we examine the foregoing prediction in a simple way. As the fingers of the two hands perform cyclical movements, one or other is unexpectedly perturbed by the injection of a brief torque load or a constantly applied load supplied by D. C. torque motors. Our interest is to define the qualitative features of the system's response to perturbations as revealed in phase, amplitude, and frequency characteristics of each hand.

The remaining aspects of non-linear oscillatory systems that we shall pursue here focus on resonance and entrainment properties. First, non-linear oscillators (unlike linear ones) do not exhibit resonance—an amplitude increase—when driven at their preferred frequency. As noted by Iberall and McCulloch (1969), a fundamental observation about human motor behavior is that externally it does not appear to have a strong metric, but internally it must have. Complex humans operating homeokinetically are self-timed and not tied (in any stimulus-response manner) to external cue constraints. Thus the stability properties of limit cycles predict that their orbit should remain fixed over a fairly wide range of driving frequencies. Second, non-linear oscillators that are coupled together will exhibit (a) mutual entrainment if allowed to function at their preferred frequency and (b) subharmonic (small-integer) entrainment if one is driven at a different rate from the other. As we shall see, the data from the remaining experiments (Series B and C) are a testimony to the powerful entrainment feature of non-linear (limit cycle) oscillators.

GENERAL METHODS AND PROCEDURES

The apparatus used in all the experiments to be reported here consisted of a finger positioning device and associated programming electronics, the details of which are described in an earlier paper (Kelso & Holt, 1980). Essentially the apparatus consisted of two freely rotating supports which allowed flexion and extension of the index fingers about the metacarpophalangeal joint in the horizontal plane. Situated above the center of rotation of each support were programmable D.C. torque motors. An electronics control package permitted programming of torque motor output with respect to movement of the finger in either direction. Thus, in some of the experiments (1 to 4; Series A) perturbations of either digit could be applied for a short duration (termed "brief load") or for a prolonged period ("constant load"). A potentiometer

mounted over the axis of motion of each finger provided an analog signal from which a digital representation was obtained via analog-to-digital conversion at a sampling rate of 200 Hz. Additional onset and offset of load perturbation (Series A) and a metronome timing signal (Series C) were specified by analog impulses. A package of conversion routines—implemented on a PDP-11/45 computer—was used to convert the digital signals and display them as time-domain displacement tracings. Additional programs provided mean amplitude, frequency, duration and phase information (cf. Goodman, Rubin, & Kelso, Note 3).

On entering the laboratory, subjects were familiarized with the movement apparatus and seated in a dental chair so that both arms and hands could be comfortably secured in the positioning device. The procedures were described to the subject and any questions answered. The task throughout all experiments was to move the index fingers of one or both hands in a cyclical (flexion-extension) manner from the onset of an auditory start signal to a stop signal. For the two-handed task, the movements were always symmetrical, i.e., flexion (extension) of one hand was accompanied by flexion (extension) of the other. Instructions in all the experiments were to move the finger(s) continuously over a 10 sec trial in a way that felt most comfortable and required least effort.

PERTURBATION EXPERIMENTS (1 THROUGH 4)

Specific Methods and Procedures

The subjects were right-handed male and female volunteers who were paid for their services. Two groups of subjects were used—a single-hand group (N=6), that completed the experiments using the index finger of only one hand, and a bimanual group (N=6) that used the index fingers of both the left and right hand simultaneously. In the bimanual group, trials were randomized so that the subject received either no perturbation, a perturbation of the left index finger, or a perturbation of the right index finger. Four trials were given in each of the three conditions, a total of 12 trials for each experiment. In the single-hand group, subjects were told which finger to move and a given trial was either perturbed or not perturbed.⁶

In experiments 1 and 2, clamps were placed on the protractor arm of the apparatus, the purpose of which was to constrain movements to a 50° range (40-90° extension). In experiment 1, the perturbing torque was set at 50% of maximum torque output available (40.8 oz-in) for a duration of 100 msec, and was introduced approximately midway through the 10 sec trial. The perturbation was injected in a flexion direction as the finger moved through the extension phase of the cycle. In ex-

⁶On a very few occasions, due to malfunctions in analog-to-digital conversion, a subject's data could not be registered for future analysis. As the Tables indicate however, we still had a sizeable number of observations on which to base statistical comparisons.

periment 2, the torque load was reduced to 25% of maximum (20.4 oz-in) and was introduced about half way through the trial and maintained until completion of the trial. The constant torque load was applied in the direction of limb flexion. Thus, during extension of the index finger the load opposed movement; during finger flexion the load acted in the same direction.

Experiments 3 and 4 were replications of 1 and 2 with the exception that the constraints were removed allowing subjects to select both amplitude and frequency of movement.

Data Analysis

Measurements of movement amplitude and frequency were obtained from converted digital signals. This procedure relied upon a computer-based determination of displacement maxima and minima per cycle in order to arrive at cycle amplitude. Mean values of amplitude and frequency were obtained only for those cycles before and after the perturbation cycle, and appropriate comparisons made using paired t-tests.

To examine the phasic relationships between the two limbs (in the bimanual group), two analyses were employed. The first involved a computer generated display in which the displacement tracings were superimposed such that any phasic lag or difference between them could be immediately observed. For example, the lower tracing on Figure 2 shows an almost perfect superimposition of the upper individual tracings from each individual hand.

In order to quantify phasic relationships, a second method compared the two traces using cross-correlation techniques. The cross-correlation function for two sets of time-domain data describes the general dependence of the values of one set of data on another. For example, if $u(t)$ corresponds to the signal for the right index finger and $v(t + \tau)$ corresponds to the signal for the left index finger delayed by the interval τ (tau), an estimate of the cross-correlation function for a given tau may be obtained by taking the average product of the two values over the observation time T . The resulting average product will approach an exact cross-correlation as T approaches infinity. In this way the actual phase lag or tau between the waveforms of each hand and the correlation at that lag were calculated for all cycles before and after the perturbation on each trial.

Results

Frequency between and within limbs. The pre- and post-perturbation analysis for the frequency data in the bimanual group across all four experiments is shown in Table 1. Clearly, the results of this analysis point to a very tight periodic relationship between pre- and post-perturbation cycles within each limb. It may be noted that the frequency changes following a brief perturbation range from 0 to .03 cycles per sec. Similarly, the frequency of a limb that subsequently receives a constant load remains virtually unchanged (0 to .05 cycles per sec). None of the pre-post

CONSTRAINED CYCLICAL MOVEMENTS

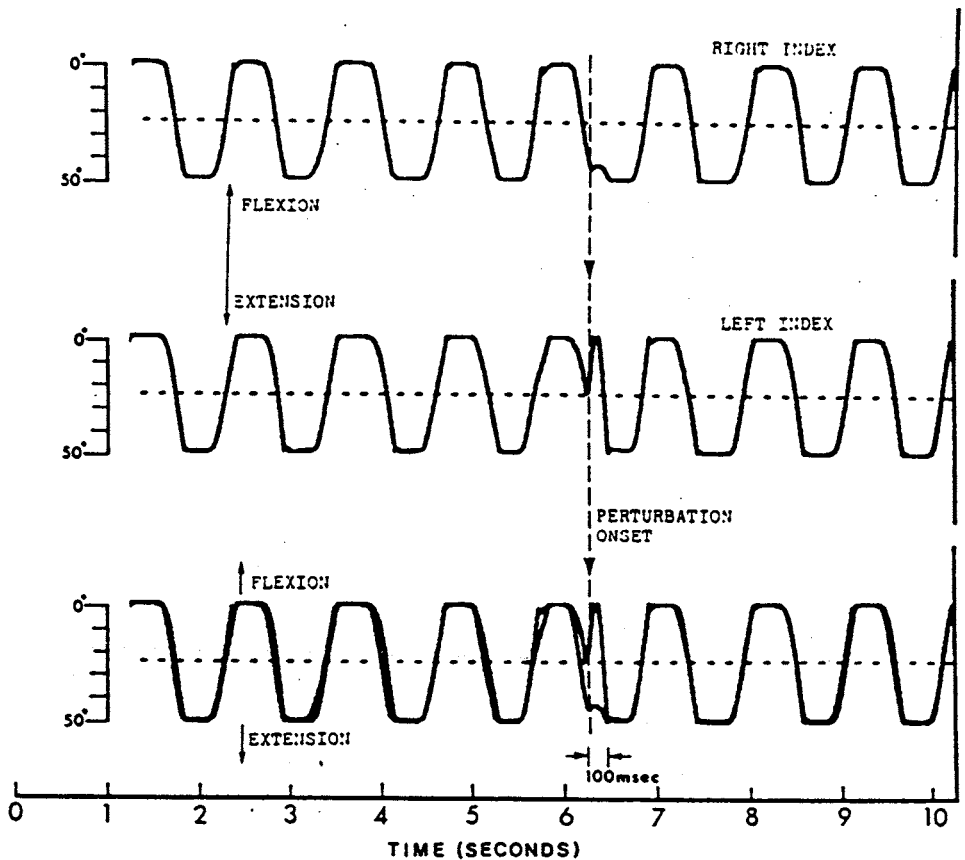


Fig. 2—Two-handed cyclical movements between physical constraints. The right index finger was deflected in the direction of flexion as it was extended. In the lower tracing, the two upper tracings are superimposed. The almost perfect overlap reflects the tight period and phase linkage between the fingers. It is interesting to note that the two fingers regained their phasic relationship within the same trial as the perturbation occurred.

differences in frequency attained statistical significance ($p > .05$).

In the single hand experiments, it can be seen again that frequency changes following brief perturbation and the addition of a constant load are small, although they tend to be a little higher than in the bimanual case (.01 to .07 cycles per second, see Table 2). Again, none of the differences attained statistical significance ($p > .05$), nor is there any systematic directional bias in the small frequency changes that are observed.

Phase relationships between limbs. The tight periodic relationship in the pre- and post-perturbation cycles within a limb is matched by a tight periodic and phase relationship between the hands. In Figures 2, 3 and 4, examples of the superimposed displacement curves for each experiment are shown. It is clear that despite the imposition of different perturbations, a tight phasic link between the two fingers is preserved.

Table 1

Means and standard deviations of frequency for cyclical movements of two hands

Condition		N ^a	PRE-PERT		POST-PERT		t
			Mean ^b	SD	Mean	SD	
Experiment 1: Amplitude constrained, brief perturbation							
Right perturbed:	right hand	23	1.39	0.46	1.40	0.44	-0.63
	left hand	23	1.49	0.56	1.46	0.49	0.84
Left perturbed:	right hand	25	1.45	0.50	1.43	0.47	1.98
	left hand	25	1.45	0.47	1.47	0.47	-1.26
Experiment 2: Amplitude constrained, constant perturbation							
Right perturbed:	right hand	22	1.37	0.29	1.34	0.27	1.12
	left hand	22	1.33	0.30	1.28	0.27	1.72
Left perturbed:	right hand	25	1.25	0.31	1.24	0.29	0.58
	left hand	25	1.25	0.29	1.22	0.26	1.73
Experiment 3: Free, brief perturbation							
Right perturbed:	right hand	19	1.68	0.18	1.69	0.16	-0.78
	left hand	19	1.69	0.20	1.71	0.16	-0.53
Left perturbed:	right hand	19	1.72	0.19	1.74	0.18	-1.27
	left hand	19	1.72	0.17	1.73	0.14	-0.29
Experiment 4: Free, constant load							
Right perturbed:	right hand	19	1.79	0.19	1.78	0.13	0.27
	left hand	19	1.79	0.18	1.79	0.13	0.25
Left perturbed:	right hand	19	1.82	0.16	1.84	0.19	-0.68
	left hand	19	1.81	0.16	1.82	0.21	-0.19

^aNumber of data pairs^bFrequency in Hertz (cycles per second)

Quantification of these data using cross-correlation techniques verified the extremely close period and phase of the two fingers. The mean tau values and the correlations at those values averaged across trials for each subject are shown in Tables 3 and 4. Absolute values of phase lag τ both pre- and post-perturbation are small, and correlations (with only a few exceptions) are extremely high.

Amplitudes between and within limbs. Analysis of the amplitude data for the bimanual and single-handed groups is provided in Tables 5 and

Table 2

Means and standard deviations of frequency for cyclical movements of one hand

FREQUENCY ^a	CONDITION	N ^b	PRE-PERT		POST-PERT		t
			Mean	SD	Mean	SD	
Expt. 1:	Left hand alone	18	1.56	0.43	1.53	0.39	1.52
	Right hand alone	17	1.48	0.38	1.49	0.47	0.35
Expt. 2:	Left hand alone	18	1.57	0.48	1.56	0.48	0.67
	Right hand alone	17	1.58	0.43	1.49	0.31	1.83
Expt. 3:	Left hand alone	19	1.82	0.52	1.77	0.54	2.05
	Right hand alone	18	1.90	0.80	1.88	0.51	0.66
Expt. 4:	Left hand alone	19	1.88	0.57	1.95	0.63	-2.93
	Right hand alone	19	2.01	0.50	1.99	0.55	0.44

^ain Hertz

^bNumber of data pairs

FREE CYCLICAL MOVEMENTS

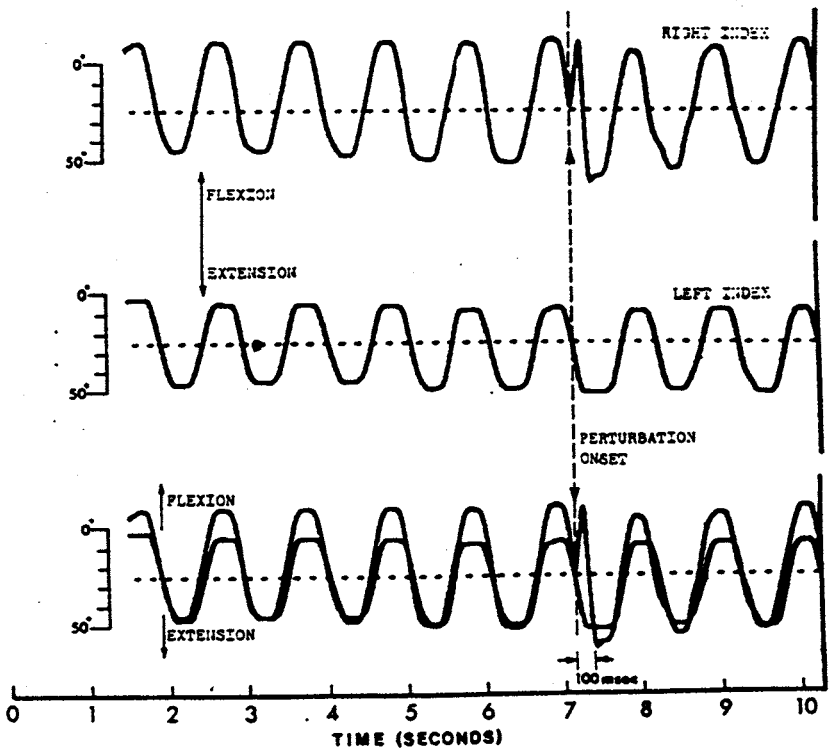


Fig. 3—Two-handed cyclical movements without constraints on movement amplitude. Note that the right hand showed a greater range of flexion/extension than the left, with a greater velocity. Phase and period of the two hands are again tightly limited and reentrained within the same cycle after brief perturbation of the right index.

FREE CYCLICAL MOVEMENTS

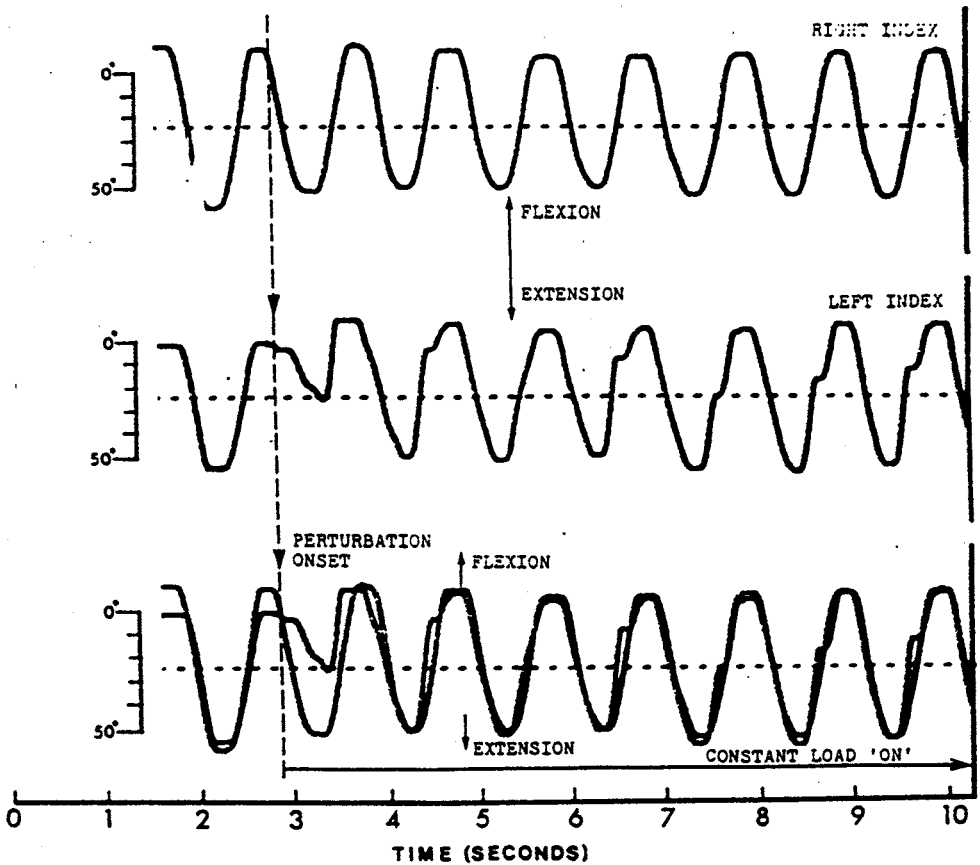


Fig. 4—Two-handed cyclical movements without constraints on movement amplitude. A constant load was added to the left index finger in the direction of flexion, while the subject moved in extension. The result on the first cycle was a dramatic decrease in velocity and amplitude. In the remaining cycles, compensation occurred such that not only were phase and period relationships maintained, but also the kinematics—velocity and amplitude.

6, respectively. In general, amplitudes tended to remain constant with a couple of anomalous findings (see, for example, Experiment 4, Table 5, and Experiments 1 and 2, Table 6).

However, in several of the analyses of free bimanual movements (unconstrained), it is clear that the amplitude differences almost reached significance and given greater power may have done so. Of course the foregoing analysis is quite global in the sense that it clouds potential amplitude adjustments that may have occurred on individual cycles before or after perturbations. With this in mind, we compared amplitudes of individual cycles in Experiments 3 and 4 (single and bimanual groups) on those trials in which at least five cycles preceded and followed the perturbed cycle (P). Table 7 provides a summary of those cycles reaching significance ($p < .05$). Out of a possible number of 28 significant differences within each cell, it can be seen that the maximum number to reach significance is only eight. Furthermore, there

Table 3

Cross-correlation analysis of pre-perturbation cycles (two hands)

Subject	EXPERIMENT 1				EXPERIMENT 2			
	Correlation		TAU(msec) ^a		Correlation		TAU(msec)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	.94	.17	5.71	3.20	.95	.02	4.29	3.19
2	.97	.02	11.43	4.40	.98	.01	0.00	0.00
3	.99	.01	10.00	9.58	.98	.01	10.63	8.08
4	.98	.01	14.00	4.90	.97	.01	13.75	6.00
5	.97	.01	12.50	8.54	.97	.01	12.50	6.12
6	.97	.04	5.00	5.35	.94	.05	13.75	8.93

Subject	EXPERIMENT 3				EXPERIMENT 4			
	Correlation		TAU(msec)		Correlation		TAU(msec)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	.98	.01	6.25	4.84	.95	.04	15.00	11.02
2	.99	.01	5.80	3.21	.95	.02	17.05	2.50
3	.98	.01	5.63	6.34	.91	.07	15.63	10.74
4	.97	.01	12.50	2.50	.96	.02	13.13	4.29
5	.96	.01	11.43	6.93	.96	.03	11.50	9.27
6	.94	.04	14.38	17.40	.94	.04	16.43	13.02

^aphase lag with resolution to 5 msec

does not appear to be any systematic pattern among those cycles that are statistically different from each other. Thus if subjects were adjusting amplitude over several cycles following the perturbation, we might have expected a larger number of differences between those cycles immediately preceding perturbation onset (P-1, P-2) and those cycles immediately following the perturbation (P+1, P+2). Although there was a greater number of pre- post differences in amplitude overall, there was nothing to suggest—even in the individual amplitude data—any progressive recalibration on the first or second post-perturbation cycle back to pre-perturbation values.

Discussion

The finding that frequency (period) within a finger remains constant despite the addition of brief and constant loads strongly supports the

Table 4
Cross-correlation analysis of post-perturbation cycles (two hands)

Subject	EXPERIMENT 1				EXPERIMENT 2			
	Correlation		TAU(msec) ^a		Correlation		TAU(msec)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	.93	.04	8.57	5.80	.87	.06	4.29	6.39
2	.97	.01	6.43	3.50	*			
3	.99	.01	10.71	4.95	.89	.06	11.25	7.40
4	.98	.00	23.00	9.80	.87	.04	43.50	10.31
5	.98	.02	7.50	5.59	.84	.05	15.63	9.50

Subject	EXPERIMENT 3				EXPERIMENT 4			
	Correlation		TAU(msec)		Correlation		TAU(msec)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	.97	.02	13.75	8.93	.84	.06	10.71	6.78
2	.99	.00	7.36	2.61	*			
3	.98	.01	4.38	4.64	.72	.07	22.50	13.46
4	.96	.17	14.38	7.26	.76	.26	10.00	8.66
5	.96	.02	14.29	11.16	.89	.06	21.88	13.21
6	.90	.09	21.88	20.76	.89	.05	10.29	10.83

*insufficient data

^aphase lag with resolution to 5 msec

view that the limbs behave like limit cycle oscillators. The first criterion for limit cycle processes—that frequency (period) and amplitude tend to be maintained despite perturbations—receives good support in our data. Further support for the limit cycle account is evident in the tight phase and period relationships between the fingers of the two hands.

Perhaps the crucial test of the entrainment property of non-linear oscillators is the perturbation experiment. It is clear in all four experiments reported here, that quickly after the perturbation of one finger, both fingers become re-entrained within one or two cycles; there is neither a phase lag nor a difference in periodicity between the two fingers. This result is reminiscent of work in animal locomotion. Thus Shik and Orlovskii (1965) temporarily prevented one of the limbs of a locomoting cat from initiating the transfer phase of its step cycle—a procedure that necessarily disrupted the phase relations among all four limbs. Within a few full cycles however, the limbs returned to their

Table 5

Means and standard deviations of Amplitude for cyclical movements of two hands

Condition	N ^a	PRE-PERT ^b		POST-PERT		t	
		Mean	SD	Mean	SD		
Experiment 1: Amplitude constrained, brief perturbation							
Right perturbed:	right hand	23	50.92	2.24	51.50	4.81	-0.78
	left hand	23	50.80	2.16	48.84	5.89	1.78
Left perturbed:	right hand	25	51.16	2.34	50.27	5.47	0.86
	left hand	25	51.93	1.80	51.31	3.02	1.16
Experiment 2: Amplitude constrained, constant perturbation							
Right perturbed:	right hand	22	52.27	3.34	51.27	4.13	1.62
	left hand	22	52.64	6.21	51.24	3.39	1.03
Left perturbed:	right hand	25	51.31	1.77	48.54	8.08	1.69
	left hand	25	51.29	1.81	49.92	4.35	1.52
Experiment 3: Free, brief perturbation							
Right perturbed:	right hand	19	69.76	16.38	67.38	18.27	1.28
	left hand	19	66.29	15.19	64.58	14.35	1.34
Left perturbed:	right hand	19	65.25	14.82	66.35	16.42	-0.98
	left hand	19	70.52	20.70	70.27	21.86	0.20
Experiment 4: Free, constant load							
Right perturbed:	right hand	19	71.77	25.43	75.91	30.49	-2.26*
	left hand	19	67.15	16.50	68.00	13.79	-0.80
Left perturbed:	right hand	19	65.40	18.01	74.05	20.38	-4.44**
	left hand	19	64.50	18.50	60.72	21.28	-1.98

^aNumber of data pairs

^bAmplitude in degrees

* $p < .05$

** $p < .01$

previously established phase relationships, as in the present experiments.

The general finding that amplitude tends to be preserved in both limbs in spite of load perturbations applied to one, provides additional support for the limit cycle oscillator view and extends previous work on single trajectory movements (e.g., Fel'dman, 1966a,b; Kelso & Holt,

Table 6

Means and standard deviations of amplitude for cyclical movements of one hand

AMPLITUDE ^a	CONDITION	N	Mean	SD	Mean	SD	t
Expt. 1:	Left hand alone	18	50.56	2.73	50.71	2.86	-1.53
	Right hand alone	17	55.05	3.70	56.77	5.85	-2.88*
Expt. 2:	Left hand alone	18	51.68	2.71	52.25	2.35	-3.35*
	Right hand alone	17	57.96	4.71	58.80	5.70	-1.15
Expt. 3:	Left hand alone	19	60.13	24.33	61.15	23.63	-0.81
	Right hand alone	18	63.10	25.29	60.49	21.94	1.59
Expt. 4:	Left hand alone	19	58.43	22.75	60.35	13.53	-0.60
	Right hand alone	19	53.88	12.95	51.46	13.66	1.51

^ain degrees* $p < .05$

1980; Polit & Bizzi, 1978) to voluntary cyclical movements (see also Fel'dman, 1980). A noteworthy feature of the data is the kinematic differences within and between limbs when the system is perturbed. For example, in Figure 4, even though frequency is maintained in the constant load condition, velocity (as reflected in slope differences) and amplitude differ for the two limbs. This finding draws our attention to a fundamental point that we have made in earlier papers; observed kinematic details are consequences of the system's dynamics (e.g., mass, stiffness, damping) and are determined by those dynamics (cf. Fowler et al., 1980; Kelso & Holt, 1980).

FURTHER DEMONSTRATIONS OF ENTRAINMENT

There are two additional properties of non-linear, limit cycle oscillators that we shall consider under the heading of entrainment. The first is that when coupled, oscillators of slightly different frequencies will tend to entrain at some intermediate frequency. As von Holst (1937) remarked, the striking feature of coordinated movements is their "accordance in tempo." He called this frequency detuning or mutual entrainment property "the magnet effect"; simply a tendency of one rhythm to impose its tempo on another. A second form of mutual interaction among oscillators occurs if the frequency of one is an integer multiple of another to which it is coupled, a property termed subharmonic entrainment or frequency demultiplication. In the following experimental demonstrations, both types of oscillatory interaction, mutual and subharmonic entrainment, are clearly evident.

Mutual Entrainment

The basic tack on this issue was to first determine the preferred frequency of each limb in isolation and then examine possible interactions

Table 7

T-test matrix of total number of significant differences between individual cycles. All subjects on Expts. 3, 4 one and two hands.

Comparison pre-pert cycles					Comparison post-pert cycles					Comparison pre-post					
P-5	P-4	P-3	P-2	P-1 ^a	P+5	P+4	P+3	P+2	P+1 ^b	P+1	P+2	P+3	P+4	P+5	
P-5	3	2	1	0	P+5	0	3	2	2	P-5	3	8	5	5	3
P-4		1	0	2	P+4		2	3	3	P-4	5	4	4	3	2
P-3			1	1	P+3			4	3	P-3	3	5	5	3	2
P-2				0	P+2				4	P-2	2	5	6	4	1
										P-1	4	6	4	5	4

^a P-N = Nth cycle preceding perturbation

^b P-N = Nth cycle following perturbation

^c Total possible significant differences in each cell = 28

between the limbs when they perform together. The basic procedure was similar to that employed in the previous experiments. Each of six, right-handed subjects (none of whom participated in any of the previous studies) completed four trials with the left hand only, the right hand only and both hands combined. The twelve trials, each lasting 10 sec were randomized for all subjects. The subject was instructed to move the finger(s) cyclically at a frequency and amplitude that felt most comfortable. No constraints or perturbations were imposed at any time during the trial.

Mean amplitude and frequency data for each trial were again obtained from the converted digital signals. The means for all subjects are shown in Table 8. The frequency data meet the predictions of limit cycle oscillators in that the left hand is "attracted" to the right hand which in turn shows only a very small and statistically insignificant frequency

Table 8

Means and standard deviations of preferred frequency and amplitudes in one-handed and two-handed cases (N = 6)

		One hand		Two hands		Combined
		Left	Right	Left	Right	
FREQUENCY ^a	Mean	1.973	2.001	1.996	1.995	1.996
	SD	0.03	0.05	0.03	0.03	0.03
AMPLITUDE ^b	Mean	62.93	66.91	57.57	65.84	61.71
	SD	4.31	3.59	9.17	3.84	4.01

^ain Hertz

^bin degrees

modulation. Clearly the overall effect is modest, as one would expect in an experiment using simple cyclical movements of the two hands. There are obvious ways to amplify the extent to which one limb imposes its rhythm on another by changing, for example, limb dynamics (e.g., mass, lever arm) or by fatiguing one limb or the other. Our intent here, however, has been simply to demonstrate the mutual entrainment effect. That the right hand does exert an "attracting force" on the left in right-handed subjects illustrates another mode of cooperation among oscillators. This finding is also a testimony to the difficulty subjects have in performing two different rhythms at the same time. Entrainment, we suspect, represents a major limitation on what activities can actually be performed. As von Holst (1937, 1939) remarked, it appears to be an important principle of central order. Yet entrainment has received little or no attention in theories of how skills are acquired, or how movements are controlled.

Subharmonic Entrainment

There is at least one situation in which individuals do *not* experience difficulty in performing separate rhythms with the hands, and that is when they both share a common time base. Recently Klapp (1979) has shown "interference" between the two hands in a repetitive key pressing task when the periodicity of each is different, as measured by the subject's ability to match a pacing tone. When the periodicities share common timing, even though shifted in phase, no such interference occurs. These results may be accounted for by another property of oscillator interaction, namely, low integer subharmonic entrainment. This form of entrainment is such an overwhelming phenomenon in human motor activity that we simply illustrate it here (see Figure 5). Subjects were asked to move one finger at their preferred frequency and to move the other finger at a different frequency. We show two examples of one subject's performance. As illustrated in Figure 5, the oscillation of the limb moving at slower frequency exactly coincides with the appropriate oscillation at the faster frequency—one is a simple (2:1, 3:2) subharmonic of the other.⁷ The example also illustrates the interesting property of amplitude modulation (von Holst's *superimposition* effect). Thus, on some coinciding cycles, a "beat" phenomenon can be observ-

⁷Two things should be emphasized in this section. The first is that all we offer here is a demonstration of a phenomenon which is coherent with the theoretical picture. A more formal analysis of sub-harmonic entrainment is being undertaken and some preliminary results have been presented (Kelso, Note 5). Second, as pointed out by R. A. Schmidt (Note 6) the pattern classified as 3:2 in Figure 5 is not 3:2 in the musical sense. In fact, the "3" part is really a blank-move-move which is the same as the "2" part. Again, this analysis attests to the difficulty subjects have in performing independent rhythms with the hands.

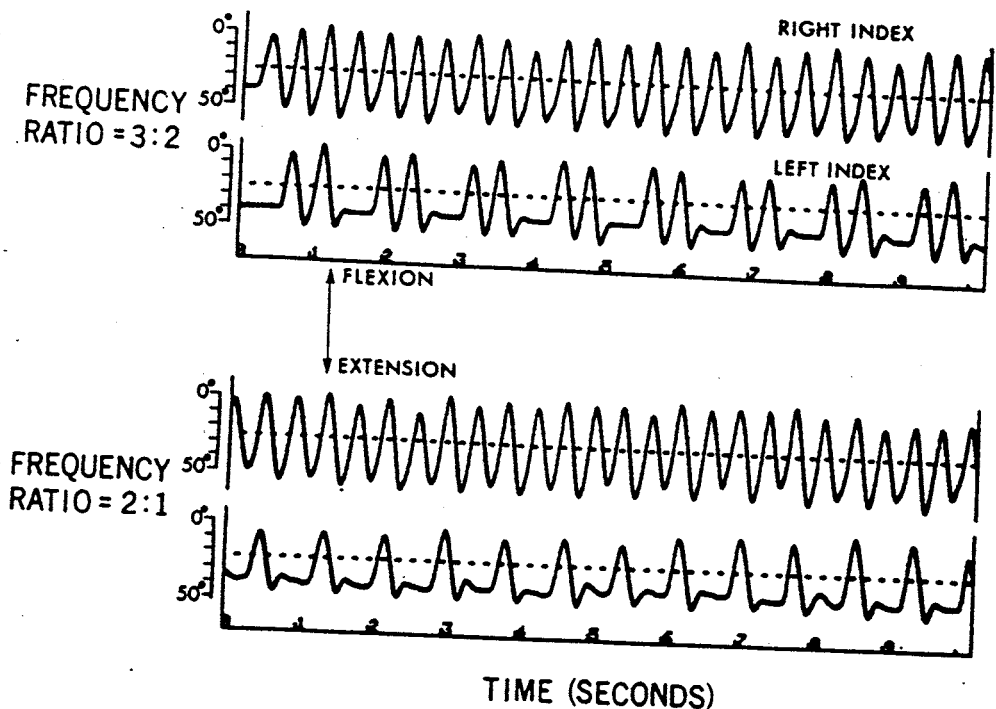


Fig. 5—An example of a subject's response to instructions to move the fingers at different frequencies. Beats in the lower frequency hand tended to coincide with the beats of the higher frequency hand. On some coinciding cycles, a "beat" phenomenon can be observed in which the amplitude of the higher frequency hand increases in relation to non-coincident cycles (see especially the 2:1 ratio). In addition, slight movement during the "quiet" phase of the low frequency rhythm is indicative of the highly constrained nature of the two-hand linkage.

ed (particularly in the 2:1 ratio) in which the amplitude of the higher frequency hand increases on the occasion that the lower frequency oscillation takes place. Note also that in the lower frequency oscillation the finger is never completely still. Although its amplitude is much smaller, it is clear that there is a small oscillation, especially in the 2:1 ratio condition. In effect, both fingers are cycling at the same frequency—only the amplitude or force distribution to each finger varies. The foregoing result fits nicely with recent work by Shaffer (1980) on highly skilled pianists. Shaffer showed that the pianist's right hand carrying the melody plays with more "weight" than the left, and that gradual and sudden changes in both hands can be made without disrupting timing. It is tempting to suppose that Shaffer's pianist is displaying (admittedly in a more refined way) the basic superimposition principle for combining the outputs of coupled oscillators (see also Gallistel, 1980, and Kelso, 1981, for additional examples).

It is worth noting that the entrainment properties demonstrated above are not restricted to movements of the fingers, but are also apparent in systems that share little or no anatomical similarity. In an analysis of the interrelationships between speaking and manual activity (Kelso, Tuller, & Harris, in press), we have shown that subjects, when asked to repeat a

simple syllable (the word "stock") at a different rate than their preferred finger rate, do so by employing low integer subharmonics. The situation is reversed (though not necessarily symmetrically) when subjects are instructed to move their hands at a rate different from their preferred speaking rate. Again the ratios chosen are always simple ones (e.g., 2:1). We interpret these preferred relationships as emergent characteristics of a non-linear oscillator ensemble; the collection of entrained oscillators functions in a single unitary way. Entrainment therefore ensures a stable resolution of simultaneous temporal processes throughout the whole system. Moreover, the form of entrainment is limited to a relatively restricted range of preferred relationships—a feature captured in Iberall and McCulloch's (1969) phrase as an "orbital constellation."

NON-RESONANCE PROPERTIES

A characteristic of linear oscillators but not of the non-linear limit cycle oscillator under examination here, is that when driven at its fundamental frequency it will display resonance—a behavior that results in an increase in amplitude of oscillation. A final experiment examined whether amplitude changes would be observed when the limb was driven by an external rhythmic source at its preferred frequency, and at other frequencies higher and lower than the preferred frequency.

Four paid volunteers, none of whom had participated in the earlier work, took part in this study. The procedures were very similar to those already discussed, with the following exceptions. Before the experiment proper, the preferred frequency for each individual subject was obtained by finding the mean and standard deviation of five trials (10 sec each) in which the subject chose his/her rate and amplitude. Our previous work indicated that this was more than enough time to achieve stable measures. These data were then used as the basis for driving frequency manipulations effected via a visual metronome. Seven frequency conditions were used (F_0 , the subject's preferred frequency $F_0 \pm 2 SD$, $F_0 \pm 4 SD$, $F_0 \pm 6 SD$). For example, if a subject had a measured preferred frequency of 1.5 Hz with a standard deviation of 0.075 Hz, he/she would be asked to produce one flexion-extension cycle to each metronome beat under the following conditions: 1.5 Hz, $1.5 \pm .15$ Hz., $1.5 \pm .30$ Hz., $1.5 \pm .45$ Hz. Five trials were given in each of the seven conditions which were randomized for each subject, and movements were two-handed in all cases.

The mean amplitude and frequency are displayed in Table 9 for all seven driving frequency conditions. These data were analyzed in a $2 \times 7 \times 5$ (hands [left/right] \times driving frequency \times trials) within subjects analysis of variance. None of the amplitude comparisons was statistically significant, but there were definite effects on frequency in response to the driving stimulus conditions, $F(6, 18) = 19.28, p < .01$. None of the subjects had any difficulty performing the task in any of the driving conditions, as confirmed by scanning the graphical output of

Table 9

Means and standard deviations of frequency and amplitude of two hands when driven by light pulses at different frequencies (N = 6)

FREQUENCY ^a		FO ^c	FO+2 SD	FO-2 SD	FO+4 SD	FO-4 SD	FO+6 SD	FO-6 SD
Left	Mean	1.82	1.92	1.74	2.11	1.61	2.34	1.53
	SD	0.02	0.02	0.03	0.02	0.03	0.03	0.06
Right	Mean	1.82	1.92	1.74	2.11	1.61	2.33	1.55
	SD	0.03	0.02	0.04	0.03	0.04	0.03	0.04

AMPLITUDE ^b		FO ^c	FO+2 SD	FO-2 SD	FO+4 SD	FO-4 SD	FO+6 SD	FO-6 SD
Left	Mean	44.69	48.40	47.06	40.29	40.85	37.28	44.17
	SD	3.65	5.03	3.64	1.75	3.35	2.54	4.43
Right	Mean	52.38	49.98	50.84	45.55	46.25	40.10	49.71
	SD	3.01	5.86	3.18	2.41	3.04	1.66	4.44

^ain Hertz

^bin degrees

^creflects mean preferred frequency

metronome and displacement waveforms. One such example illustrating a fixed maintenance of amplitude across the most extreme driving conditions is shown in Figure 6.

Nevertheless it is apparent from the mean data that there are tendencies for amplitude and frequency to be linearly related particularly at faster driving frequencies. Paradoxically, and if we were dealing with linear oscillators, amplitude should increase with slower driving frequencies—a prediction not borne out by the present data.

In short, the responses of the limbs to different driving frequencies seem to display both linear and non-linear characteristics. This is not particularly surprising for non-linear systems are capable of exhibiting linear behavior over a range of parameter values. The distinguishing feature of non-linear oscillators is that their behavior can be dramatically altered in terms of phase and amplitude when driven at certain frequencies. Much more needs to be done to determine if, and under what conditions, amplitude (and/or phase) changes occur as "saltatory jumps" at certain frequencies; that is, when one stable orbit is forsaken for another.⁸

⁸In fact, more recent work (reported in Kelso, Note 5) indicates that if the two limbs operating out-of-phase (flexion in one and extension in the other) are driven at a certain critical frequency, they will change phase abruptly (in less than a cycle period) to an "in-phase" pattern. The 180°

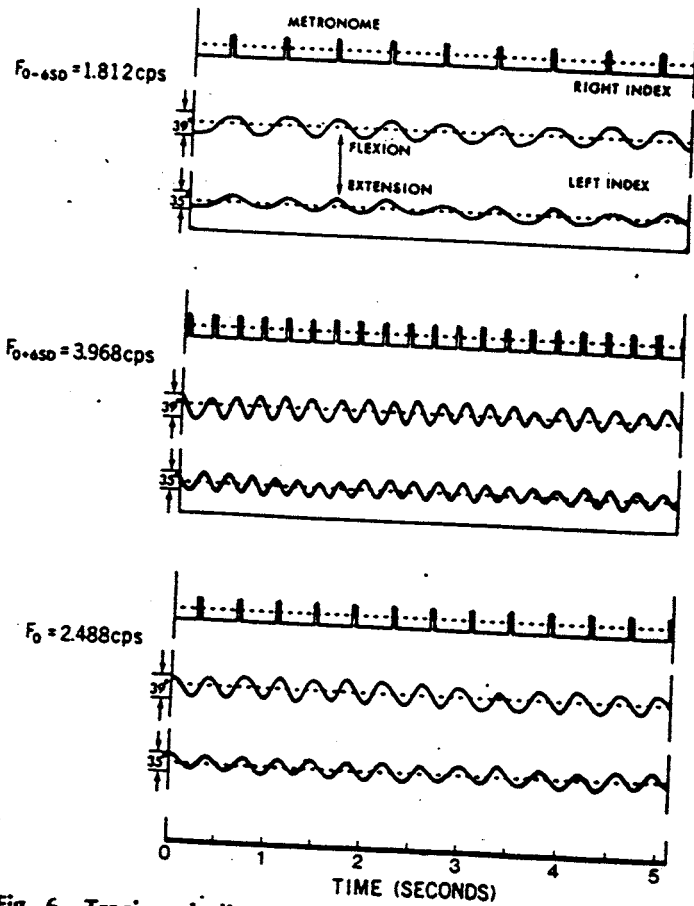


Fig. 6—Tracings indicate a constant amplitude in the two hands when driven at different frequencies by a visual metronome (a pulsing LED). The onset of a light pulse in most cases was synchronized with the point of maximum extension or flexion. Slight deviations of the finger oscillations from the metronome period can be observed in some cycles.

The point that should not be lost here is that oscillatory systems can behave in a linear manner yet still be non-linear in nature. Consider the intuitive example of dolphin locomotion. At low speeds, dolphins cruise with little energy cost because of their streamlined shape; water flow

Footnote Continued

transition in phase brought about by a scalar increase in driving frequency is perhaps the principal feature of one of the simplest non-linear systems modelled by the Duffing equation. Thus, through a continuous change in one variable (e.g., frequency) a discontinuous change in another (e.g., phase) can be observed. That is, an elementary cusp catastrophe or bifurcation occurs (Saunders, 1980; Thom, 1972). Importantly, there is no a priori prescription for the changed mode of organization anywhere.

over their body surface is laminar. At higher swimming speeds however, the creation of turbulence can increase energy costs by an order of magnitude (see Brookhart & Stein, 1980). As the relationship between velocity and energy costs becomes non-linear, the dolphin divorces the swimming mode for its novel and more economical "running" mode. In short, scale changes reveal the non-linearities in the system and are capable of effecting qualitative changes in behavior. A major enterprise then for a science of movement becomes one of identifying the necessary conditions under which such bifurcations or "phase transitions" occur (for clues, see Yates, in press; Yates, Marsh, & Iberall, 1972).

GENERAL DISCUSSION

In previous papers and in the introduction to this one, we have considered ways in which the motor system might solve the degrees of freedom problem, first identified by Bernstein (1967). Our approach is double-edged: first we have sought to identify and analyze rigorously functional groupings of muscles—synergies or coordinative structures—constrained to act in a unitary way; and second, we have attempted to establish the language of dynamics as the appropriate vocabulary upon which to rationalize the properties of coordinative structures. More specifically, we have provided theoretical grounds suggesting that a group of muscles organized as a single functional unit possesses behavioral properties qualitatively similar to a non-linear oscillator. That constrained collectives of muscles exhibit a likeness to oscillatory mechanisms was intuited many years ago by Bernstein (1947; see Greene, 1978) and advanced on empirical grounds by Fel'dman's mechanographic analysis of arm movements (Asatryan & Fel'dman, 1965; Fel'dman, 1966a,b). More recent data (see Section 4) have borne out Fel'dman's work in detail, and led to an elaboration of the potential advantages that such a view offers in terms of economy of neural control (cf. Greene, 1978; Kelso & Holt, 1980).

The present research is continuous with the above cited work which suggests that muscles acting at a joint—to a first approximation—exhibit behavior qualitatively similar to a mass-spring system. But it also recognizes the universal fact that biological devices must necessarily incorporate non-linear features if local thermodynamic losses are to be compensated for and behavior sustained. The mathematical description for persistent cyclical operation is known as the limit cycle, and the present experiments have shown that patterns of coordination between the limbs (and within a single limb) can be accurately predicted from limit cycle properties. To summarize briefly, we have shown a clearcut tendency for cycling limbs to maintain fixed amplitude and frequency under a variety of experimental conditions (brief and constantly applied load perturbations, the presence and absence of fixed mechanical constraints, different external driving frequencies). In addition, the tight phasic and timing relationships observed before and after imposed perturbations, as well as the demonstration that limbs cycling at different

frequencies reveal non-arbitrary subharmonic relationships, attests strongly to the entrainment property of non-linear, limit cycle oscillatory processes.

Though motivated by quite different concerns, the present experimental results fit rather well with Fel'dman's most recent work (cf. Fel'dman, 1980), in which subjects performed rhythmic movements of the right elbow joint at different frequencies and under various loading conditions. Like us, Fel'dman found that after unloading, rhythmic movement was preserved without visible change of either phase or frequency (see Fel'dman, 1980, Figure 5). According to Fel'dman, this result indicates that the "central generator" is independent of afferent influences created by the unloading. The latter conclusion is compatible with new data on phasic movements of the ankle joint (cf. Gottlieb & Agarwal, in press). When torques were applied at various points during movement initiation and execution, both early, myotatic (40-100 msec) and later, post-myotatic (100-300 msec) reflex responses to load changes were suppressed. Such was the case regardless of whether the phasic movements were of a slow, ramp nature or a fast, ballistic nature. Gottlieb and Agarwal (in press) suggest that there is substantial "preprogramming" of both types of movement, and that phasic movements in general are not assisted by effective load-compensating reflex mechanisms.

While the neurophysiological findings of Fel'dman and Gottlieb and Agarwal provide encouraging support for the present work, their focus is on the details of the neuromuscular response to externally imposed loads on a single joint. In contrast, the present experiments used load perturbations (among other manipulations) as a tool to discover patterns of coupling between the limbs, predictable from the properties of non-linear oscillators (see also Yamanishi, Kawato & Suzuki, 1979, 1980, who use discrete visual, verbal, or manual events to perturb cyclic finger tapping). Of the latter, we have argued that the property of entrainment may be most significant for a viable theory of coordination.⁹

As an example, entrainment (often under a different name, see Section 6), may well account for the stable phase and timing relationships that characterize the various gaits of animal locomotion (for an excellent review, see Gallistel, 1980). It now appears that interneurons—at least in the central nervous systems of crayfish and cockroach—carry coupling or entraining signals that enable one limb to coordinate with another (cf. Delcomyn, 1980; Stein, 1976). The role of such "coordinating

⁹Norbert Wiener (1964) in a lecture prepared posthumously discusses the benefits of entrainment as a non-linear, self-organizing phenomenon in biology and engineering. There are indications in this paper that Wiener was seeking solutions to nervous system organization in the dynamics of non-linear oscillators—with entrainment as a major feature. This view, as we have argued here, is rather different from the closed-loop, cybernetic theory that Wiener popularized.

neurons" is currently being explored within a conceptual framework provided by the mathematical theory of coupled oscillators (Stein, 1976, 1977).

While we are sympathetic to the foregoing enterprise, we are also reminded of Davis' (1976) warning that properties of command, oscillation, coordination, and so on are not invested in any *specific* neuron. Coordination and oscillation are functions that reflect the interaction of cells, and are most correctly thought of as emergent properties. Davis (1976) provides several examples in which a particular function arises from a neuronal network even though no single neuron within the network possesses that function.

The theme that functions like coordination are emergent, a *posteriori* consequences of systemic interactions among cells (or muscles), as opposed to a *priori* prescriptions invested in a single cell (or program), is consonant with the dynamical perspective offered here (see also Fentress, 1976, for a similar "relational dynamics" perspective). For the physical theory of living systems (homeokinetics), entrainment is the chief mode of cooperation among self-sustaining oscillators; it is an emergent, self-organizing process in the sense that a collection of mutually entrained oscillators functions as a single unit. Therein lies its appeal, of course, for a principled solution to the degrees of freedom problem.

A further, and by now self-evident consequence of the homeokinetic view concerns the role of oscillation. It has long been recognized that cyclicity lies at the heart of biological functioning (cf. Goodwin, 1970, p. 8). Yet in the domain of movement, it has been commonplace (with certain notable exceptions) to consider fluctuating events as mere nuisances—as unwanted sources of variability. It has been easier to model control in terms of quasilinear servosystems, than to search for ways in which oscillation may be *exploited*. In closed-loop servomechanisms, oscillation is undesirable because it means that there is a discrepancy between the input and the reference level or set point, and hence the system is unstable. However, a more important role for oscillatory processes is in non-linear systems which do not possess reference levels but which attain stability by virtue of entrainment.

The present studies and our preliminary work on the interaction of speech and gesture (Kelso, Tuller, & Harris, in press) are motivated by the latter theme. Relatedly, the approach to understanding motor control pursued in these experiments follows precisely the line of research proposed recently by Delcomyn (1980) following an extensive review of the neural basis for rhythmic behavior in lower phyla. Delcomyn (1980) identifies three problem areas, answers to which ". . . will bring neuroscientists much closer to the ultimate goal of understanding how nervous systems function" (p. 497). These are: "(i) the nature of an oscillator, (ii) the interaction of oscillators, (iii) the way in which sensory inputs interact with oscillators and their output to shape the final motor output." (p. 497). The arguments proposed herein suggest that principled solutions to the foregoing problems may lie in physical biology,

particularly in Homeokinetics and Dissipative Structure theory (see Kugler et al., 1982; Yates, in press; Prigogine, Note 4, for comparisons and contrasts).

In our concluding remarks, we wish to make explicit one further contrast (that may already be apparent) between the present view and current concepts in the motor behavior area. As we noted at the beginning of this article, the conventional view attributes the regularities we observe in movement to an explicit, *a priori* prescription. But in an oscillator ensemble, there are no fixed dominance relationships in the sense that a program or reference level stands in a fixed, autocratic relation to the muscles responsible for implementation. There are different modes of interaction (e.g., frequency and amplitude modulation) and there may be "preferred" phase relationships under conditions of maximum coupling. A wide variety of behavioral patterns emerge from these interactions; there is structure and presumably a complex network of neuronal interconnections to support such cooperative phenomena, but strictly speaking, there is no dominance relation. If this view is correct, coordination is not prescribed by anything; it is more properly viewed as an emergent consequence of the dynamical behavior of a system whose design is fundamentally periodic.

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Submitted November 15, 1980

Revision submitted April 8, 1981