

Contrasting Perspectives on Order and Regulation in Movement

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ABSTRACT

Current theorizing in movement control explains order and regulation in terms of central programs or the reference levels of closed-loop servomechanisms. Specifically, the order and regulation observed results from a priori prescriptions, and the devices responsible are conceptually separate from that which they regulate. Neither theory adequately addresses how the free variables of the system are regulated (Bernstein's [1967] degrees of freedom problem). In the alternative perspective, promoted here, order and regulation are seen as a posteriori emergent consequences of the dynamical behavior of the system. In this view, solutions to the degrees of freedom problem may lie in the principles of Iberall's (1977) Homeokinetic Physics, which characterizes biological systems as ensembles of nonlinear, limit cycle oscillators, coupled and mutually entrained at all levels. Homeokinetics provides a secure basis for recent developments in neuroscience and offers an alternative rationale for some relevant facts in movement control and coordination.

INTRODUCTION

Actions must be precisely ordered spatially and temporally. But how is such order to be understood? One popular account uses the computer "machine" analogy where order originates from a central program that elicits instructions to

select the correct muscles and contract and relax them at the right time. Much of the data concerning movement control and coordination can be given a reading in this terminology. Evidence on a variety of sequencing skills—laboratory and real life—is to be found in an excellent review by Keele (1980). In the early part of this chapter I consider some of the data on movement sequencing from a program perspective. Despite the appeal of conventional "programming" explanations, I argue later that such accounts are not necessary to represent order and regulation in natural systems. Rather, I promote an alternative view—already elaborated in several recent papers (Kelso, Holt, Kugler, & Turvey, 1980; Kelso, Tuller, & Harris, in press; Kugler, Kelso, & Turvey, 1980; in press)—that natural systems are composed of ensembles of coupled and mutually entrained oscillators and that spatiotemporal order is a *consequence* of this fact. This latter view, grounded jointly in the newly emerging theories of homeokinetics (Iberall, 1977; Iberall & Soodak, 1978; Yates, 1980, in press; Yates & Iberall, 1973) and "dynamic patterns" (Fentress, 1978; Katchalsky, Rowland, & Blumenthal, 1974; Szentagothai, 1978), contrasts deeply with the programming conception in which there exists an a priori prescription independent of and casually antecedent to systemic behavior. Instead, order is seen as an emergent property, as an a posteriori fact, dependent on the dynamical behavior of the system.

This apparently exotic claim is not completely new. Many have considered the need for a rhythmical (oscillatory) organization to account for the multitude of overlapping and closely patterned neuromuscular events when an animal acts (Lashley, 1951; Lenneberg, 1967; Martin, 1972). Indeed the evidence for endogenous neural networks capable of rhythmical patterns in vertebrates and invertebrates is virtually unassailable (Davis, 1976; Miles & Evarts, 1979; Stein, 1978) and maybe the rhythmic structure for biological systems should even be considered a principle (Aschoff, 1979). What is new here is that spatiotemporal order can be seated in the principles of physical biology and in the language of dynamics. If this view is correct, there may be no need to introduce the special mechanisms of modern control theory (algorithms, reference levels, comparators, error correction mechanisms, and so on) to explain order and regulation. Such notions may be obviated by a dynamic scheme in which internal states are a consequence of the interaction of nonlinear, limit cycle oscillators called "thermodynamic engines" (Soodak & Iberall, 1978). Cyclical behavior then does not originate in special biological mechanisms but rather is a general physical property of systems undergoing energy flux.

To anticipate somewhat, we note with Fentress (1978), that the concept of order is fundamental to the description and interpretation of behavior. A central theme in the neurophysiological and behavioral analyses of movement is that levels of order can be ranked hierarchically (Keele & Summers, 1976). A major question for this view is how levels of order relate to and influence each other. Our perspective offers a possible answer by advocating a set of principles consistent with contemporary physical theory that are *level-independent*.

ORDER AND REGULATION IN MOVEMENT: A CONVENTIONAL PERSPECTIVE

Motor Programs: Definitions and Issues

From an early and influential definition as a set of prestructured commands organized prior to movement and run off uninfluenced by peripheral feedback (Keele, 1968), the concept of central program to explain spatiotemporal order has undergone revision. In part, there was confusion regarding the role of peripheral information. The program concept was only thought viable when peripheral inputs were: (1) effectively removed by sensory deafferentation; or (2) not employed (e.g., so-called ballistic movements). These are too stringent criteria for many investigators, who doubt the complete effectiveness of the classical preparation for removing sensory information from limbs (dorsal rhizotomy) and given the discovery of putative feedback circuits with rapid loop times (Kelso & Stelmach, 1976; Smith, 1978).

However, the notion of a central representation of a skill that can lead to patterned movement is still retained, and the issue—at least concerning the role of peripheral information—is when and how such information is used. Thus, there is no necessary dichotomy between so-called "program" and "feedback-based" control notions even though some may wish to retain it (Adams, 1977). Programming theorists no longer address the question of whether motor programs exist or not; rather they assume some type of planning occurs before movement execution. It is to problems concerning the structure and composition of such motor programs that much of current research is directed.

The Abstract Nature of "Programs"

The early definition of program as a series of prestructured motor commands specifying spatiotemporal messages to the muscles received heavy criticism not only because of its default basis [How else can a skilled pianist perform so quickly? (Lashley, 1951) or how else can an animal move without feedback? (Taub, 1976)], but also because it implied a separate program for every different movement an individual could produce. Concern has been voiced about the so-called "storage" problem that such a view creates—although no limits to CNS storage have ever been demonstrated. Nevertheless programming theorists have pursued parsimony and attempted to avoid the putative storage problem by revising the notion of a program. They have, as it were, pushed the program further back in the head. In one view, the program is considered a *generalized* entity (Schmidt, 1980). In another, the program is considered an abstract representation of a muscle sequence elaborated into its more specific components as information descends the hierarchy (Keele, 1980). Both views agree that parameters can be specified at lower levels without changing the abstract structure of the program. For example, the same program executes throws of different distances.

Or one can use the same program with different sets of muscles. Thus, one's handwriting does not lose its individuality when one writes on a blackboard (Merton, 1972). Also, Raibert (1977) has demonstrated that the handwriting pattern is preserved even when the particular muscular system employed (e.g., the foot) has never previously performed such an activity.

Similarly, there is much evidence that talkers can spontaneously adjust the movement patterns of their articulators in spite of various types of disruption and still produce highly intelligible acoustic output (Kelso, Holt, Kugler, & Turvey, 1980; MacNeilage, 1970). The talking pipe smoker is a good example, but there are formal demonstrations showing that subjects can produce—in their first attempt—steady state vowels with the jaw fixed by a bite block without the need for acoustic feedback (as evidenced by "normal" formant patterns in the first glottal pitch pulse, Lindblom & Sundberg, 1971) and even when proprioceptive information is drastically reduced (Kelso & Tuller, in preparation; Lindblom, Lubker, & Gay, 1979).

Should we attribute this creative or generative ability under novel contextual conditions in speech as different in kind from the ability to write intelligibly with the big toe? Perhaps not. A dominant feature in both activities is the preservation of certain relationships that maintain the essential character of the activity in spite of changes in values of particular dimensions. This suggests similarities in principle (see pp. 444-448).

The Parameters in the Program

The notion that the motor program undergoes progressive elaboration from some abstract, nonmotoric level (specifying the actor's goals) to a level specifying the parameters defining the spatiotemporal course of the movement has led to consideration of the contents and construction of such programs.

To answer such questions, reaction time has been used to index the amount of central preparation required for particular features of the upcoming movement. Thus, if a motor program is prepared in advance, preparation time should be a reflection of the upcoming movement's complexity. However, if no prior preparation takes place, that is, if the movement essentially unfolded with feedback triggering each response component, complex movements should take no more time to prepare than simple ones. Considerable evidence appears to favor the former proposition in both simple and choice reaction-time paradigms (Klapp, this volume).

Unfortunately, much of the data linking reaction time to features of upcoming movements is equivocal. Excluding one or two robust results, for example, that reaction time increases as a function of the number of segments in a sequence (Henry, 1980), agreement across experiments is unimpressive. Often experiments examining effects of the same parameter on RT produce opposite results. It seems that one could choose any aspect of an upcoming movement and relate it to RT if one constrained the experiment appropriately.

Models relating movement parameters to reaction time often fail to recognize that task-defined parameters (such as arm, direction, and extent) may be quite different from those used by the motor control system (Goodman & Kelso, 1980; Rosenbaum, 1980). For instance, distance or extent of movement is not, as Keele (1980) points out, in the language of muscles but instead is a consequence of the muscular forces that accelerate and decelerate the limb. For reasons given shortly, the evaluation of programming effects on kinematic variables may be quite inappropriate: Kinematic measures are, after all, only the result of the system's dynamic parameters. Let us pursue the dynamic theme in more detail and attempt to show why, in the long run, it may offer significant insights into the coordination and control of movement.

CONTRASTING ORIENTATIONS ON ORDER

A Priori Versus A Posteriori

A major problem for the program conception of spatiotemporal order, already highlighted, is that the putative transfer function between higher, mental entities (algorithms, perceptual traces, templates, etc.) and the language of the skeletomotor apparatus is simply ignored (for exceptions, see Raibert, 1977, & Saltzman, 1979). The brain as the source of signals for coordination and control is held conceptually separate from the putative recipient of such messages, the high-power energy-converting muscular system. Such notions, as emphasized by Yates, Marsh, and Iberall (1972), attempt to account for the small signal, information aspects of the system but undervalue the equally important energy-converting machinery (the power fluxes). Yet a viable analysis of motor activity (and living systems) must embrace—and understand—the mutuality between informational and power processes. Since Lashley's (1951) paper on serial order, it has been assumed that this coupling involves some type of translation step: "The translation from the spatial distribution of memory traces to temporal sequence seems to be a fundamental problem of serial order [p. 128]."

In short, the contents of the so-called program are discrete, timeless, and context-free; yet the characteristics of activity are continuous, dynamic, and context-sensitive. In modern theories of movement control, Lashley's problem is circumvented by simply assuming the existence of a "between thing" (Dewey & Bentley, 1948), for example, a translation mechanism, that will map a static, timeless representation into a four-dimensional dynamic action that emerges in real time (see Fowler, Rubín, Remez, & Turvey, 1980 for further discussion).

We have argued elsewhere that the need for "between things" may be obviated once the causal and logical support for behavioral phenomena is better understood (Kugler, Kelso, & Turvey, 1980, in press; Shaw & Turvey, in press). For present purposes, some examples illustrating the "emergent" perspective may be more appropriate. Consider an artifact well-known to researchers of

movement, namely, the cybernetic closed-loop system (Adams, 1977; Powers, 1978). In such a system, a template or reference level compares the input it receives to its own value. Based on this comparison, orders go to an effector system to eliminate possible error, thus assuring the stability of the system. Reference levels or "set points" feature heavily in explanations of biological systems, but how does a given reference level attain its constancy? An infinite regress results from the claim that a referent signal at one level is simply the output of another, higher-order servomechanism. A better claim, we would argue (see following) is that constancy in biological systems is an emergent and distributed property (a steady state operating condition) of physical processes. To buttress this view, consider an activity whose regulation has long been thought to rely on a system of set points.

The Message from Temperature Regulation

Temperature regulation shares many of the problems of order and regulation common to other systems. A dominant view is that the reference level for temperature regulation resides in the thermosensitive cells of the preoptic area of hypothalamus (Satinoff, 1978, for review). Given this, to understand thermoregulation is: (1) to determine what extra hypothalamic factors input to the reference signal (i.e., inform the animal of the state of the body temperature); and (2) to work out the controller equations for the effectors and how they react to the direction and magnitude of the error signal. But the situation is not quite that simple. Findings showing different thermoregulatory responses when different parts of the nervous system are lesioned or heated with thermal probes have led to the conclusion that the orderly sequence of thermoregulatory behaviors in response to thermal stress results from a system with not one but *multiple* set points arranged in hierarchical fashion (Satinoff, 1978).

There are, however, empirical grounds for suspecting the validity of the set-point concept. According to Snellen (1972; Mitchell, Snellen, & Adkins, 1970), there is no such thing as an anatomical structure providing a reference signal to the integrating centers of the thermoregulatory system. When other (physical) factors are considered such as the regional distribution of blood flow, what is called "set point" is the input-output relationship between the heat lost and heat produced by the system. When the net balance between these factors is altered (e.g., by exercise), the so-called set point undergoes a shift. Here, set point is an emergent and distributed property (a steady state operating condition) of physical processes involved in local heat balance.

Similarly Werner (1977) has shown that heat-flow equations for all local body coordinates result in two kinds of characteristic function. The first, a "controller" characteristic of negative slope, is the dependence of metabolism, U , on core temperature, T_c , all other variables held constant. This relationship may be altered ("tuned") by the onset of exercise or the intake of pyrogenic agents. The

second, a steady state positive slope function of the "passive" system, is the effect of metabolic rates on core temperature via heat-transport processes. This function is tunable by ambient air conditions such as humidity or air temperature. The common point between the functions *for any given body part* defines the steady state temperature of the system. Thus, as Werner (1977) emphasizes, "neither a reference signal nor a comparison of neuronal signals with different temperature coefficients is necessary, as the reached steady state is the only one which is possible under the assumed conditions [p. 95]."

The message from Snellen and Werner is clear: Core temperature is an a posteriori fact of the system, not an a priori reference signal imposed on or prescribed for the system. More generally, when the complementary components of the system are fully explored and understood, there may be no need to posit a special regulator or even a set hierarchically arranged to account for a system's conservation of a certain value.

Once Again the Mass-Spring (Oscillatory System) Story

Just as the concept of set point in thermoregulation is best viewed as an emergent and distributed physical property of the system, so it is, if recent evidence be a guide, that the plan for an act is an effective organization of the muscles that is concomitant with, not a precursor to, the activity (Fowler, 1977). Kinematic details and discrete movement segments that repeat in a particular order are a posteriori facts of a systemic organization; there is no reason to believe that they are symbolically represented anywhere (Fitch & Turvey, 1978; Fowler et al., 1980; Kugler et al., 1980).

The strongest evidence for this position comes from work on limb localization in monkeys and humans (Bizzi, 1980; Kelso, Holt, Kugler & Turvey, 1980) showing that a steady state equilibrium position of the limb can be attained despite: (1) changes in initial conditions (Fel'dman, 1966; Kelso, 1977); (2) unexpected and abrupt load disturbances applied during the movement trajectory (Kelso & Holt, 1980; Polit & Bizzi, 1978); and (3) both (1) and (2) when monkeys undergo dorsal rhizotomy (Polit & Bizzi, 1978) and humans are reversibly anesthetized (Kelso, 1977; Kelso & Holt, 1980) or the joint capsule is surgically removed (Kelso, Holt, & Flatt, 1980).

The most (neuro)economical explanation of these data is that the limb behaves qualitatively similar to a nonlinear oscillatory system, in which the steady state position of the limb (its equifinality characteristic) is determined by the dynamic parameters (mass, stiffness, damping) of the system. Hollerbach (1980) has extended the mass-spring model by showing that cursive handwriting may be produced by coupled oscillations of horizontal and vertical joints of the wrist-hand linkage. Modulating the oscillation at particular times in the cycle and with specific phase and amplitude changes permits the transformation of one basic pattern of shapes into another. For example, amplitude modulation of the vertical

spring-mass oscillator can yield different letter heights. Also, some of the stylistic constraints imposed by slant constancy and letter shaping can be satisfied by assuming a variable stiffness setting of agonist-antagonist muscle pairs (Hollerbach, 1980).

The important points to emphasize from recent work on limb localization and handwriting skill are twofold: First, the many kinematic details that we observe in movement do not require individual specification. Second, and relatedly, it cannot be said that an oscillatory system such as a mass-spring embodies a (symbolic) representation of kinematic events. To the contrary, kinematic details are consequences of underlying oscillatory processes and are determined by them.

Summary

Here we have contrasted two views of order and regulation in movement. In the more popular, conventional view, order and regulation result from central programs (following the computer metaphor) or reference levels (following the cybernetical, closed-loop device). More precisely, the orderliness of movement results from explicit a priori prescriptions. Moreover, the devices responsible for the orderliness are separate from that which they regulate and hence require a mediary or translation mechanism. In the alternative perspective, insights gained from thermoregulation and posturing of limbs suggest that order and regulation are a posteriori consequences of the dynamical behavior of the system. This latter view envisions coordination and control as an emergent characteristic of the system. Priority is not given to the *order* grain of analysis (as in the programming account); rather the emphasis is on the mutuality of components and an explication of the systematic *relations* holding among variables, when humans and animals perform activity. We now turn to the identification of systematicities in movement behavior and to a rationalization of those systematicities.

THE RELATIONAL INVARIANTS APPROACH OR WHAT IS THE DESIGN LOGIC OF THE MOTOR SYSTEM?

In rationalizing relations observed in systematic behavior we observe invariances which give us important clues about the design logic of the system (Yates, in press).

It was Bernstein (1967) perhaps who first presented logical argument against conventional assumptions that the many free variables of the skeletomuscular system are individually controlled. He argued that variables are organized into larger units called "synergies" (Gurfinkel, Kots, Paltsev, & Feldman, 1971),

"collectives" (Gelfand, Gurfinkel, Tsetlin, & Shik, 1971), or "coordinative structures" (Easton, 1972; Turvey, 1977). Within a muscle collective, the values of component variables are mutually dependent or constraining and hence can be regulated in a unitary way.

Coordinative structures are units of action that are not restricted to a set of muscles having fixed actions at a joint, nor are they limited to inborn reflexes (Easton, 1972). Rather coordinative structures connote the use of muscles in a behavioral situation: They are marshalled temporarily and expressly for the purpose of accomplishing particular acts (Boylls, 1975; Fitch & Turvey, 1978).

A major way of uncovering these "significant units" (Greene, 1972) is to alter the metrics of the activity (speed it up, do it more forcefully). In this way, it is possible to observe which variables are modified and which variables, or relations among variables, remain unchanged. Note that changing the metrical properties of an act could obscure its basic form by altering properties of individual components that might otherwise remain stable. Alternatively, these changes may index the major ways that invariance can be observed: Some variables must change but others must remain the same if the structure of the act is to be preserved and if a given pattern is to be categorized as an instance of the same act.

Note that the previous criteria are exactly those applied to the identification of motor programs. In contrast to some of the programming approaches discussed on pp. 440-441, which consider the preparatory period before an act is initiated, this approach seeks out invariant properties of the space-time pattern during the act itself. However, the systematic features (kinematic, electromyographic) of acts observed in such experiments may be rationalized on quite different grounds than those of motor programming.

A dominant idea about so-called programs is that they should be "playable" at different speeds without disrupting their internal structure; that is, certain preferred stable relationships among muscles will be preserved in spite of instabilities that are created by scaling up on rate. Consider the hypothetical motor activity shown in Fig. 25.1. Although muscle activities are illustrated, the basic idea can also be applied to kinematic and discrete events such as typing and piano playing. The crucial feature in Fig. 25.1 is that the relationships among muscles are preserved over changes in rate. The absolute duration of the activity changes and the amplitudes and durations (within limits) of individual muscle events can change without disrupting the overall pattern.

This is exactly what is observed, of course, in locomotion. For example, Grillner and Zangger (1975) compared the relative phase position of seven hind-limb muscles in normal and deafferented cats. The same timing of muscles in relation to each other was generally observed in both preparations. Similarly, when lobsters (MacMillan, 1975) and humans (Madeiros, 1978) walk at different speeds, there is considerable variability in the onsets and durations of EMG bursts but the overall phase relationships among different muscles are preserved.

HYPOTHETICAL MOTOR ACTIVITY PERFORMED AT DIFFERENT RATES
A 'RELATIONAL INVARIANTS' APPROACH

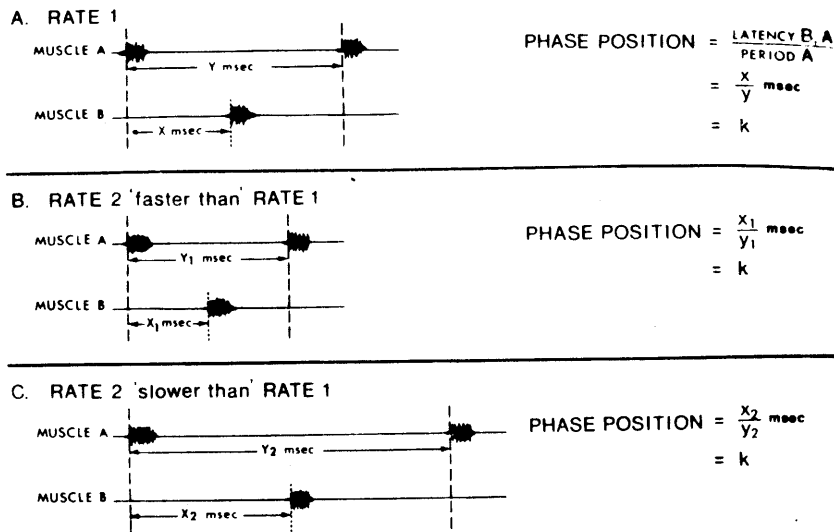


FIG. 25.1. A diagram illustrating the preservation of relative timing among muscles across various rates of movement.

In addition, pulling or carrying a weight leads to a reduction in variability but does not alter noticeably the timing relationships among muscles.

Changes in the speed of locomotion are known to be accomplished by distributing more force into the support or stance phase of the cycle. The duration of this phase decreases as an animal speeds up but the duration of the transfer phase changes very little in comparison (in this way, more distance is covered per unit time). What is significant is that increases in propulsive force during the stance phase do not disrupt the *relative timing* among linked extensor muscles, even though the absolute duration changes considerably. Force and relative timing, within limits, appear to be independent properties of coordination.

Can the feature of relative timing as an invariant characteristic of locomotion be extended to other motor activities? Increasing evidence suggests the affirmative on both micro and macro scales of motor behavior. At a micro level, consider the phenomenon of physiological tremor, a low-amplitude oscillation (around 10 Hz) that occurs in an extremity when muscles are tonically activated to maintain a fixed posture. Imagine that, as one is measuring the tremor of the finger (specifically the first dorsal interosseus muscle), subjects are instructed to produce a variety of force outputs to correspond to a voltmeter display. Significantly, tremor rate or frequency remains stable with variations in force, but

tremor amplitude systematically increases with rising force (up to 7 kg; Freund & Dietz, 1978, Fig. 3).

At a more macro level, that of discrete ballistic movements, Freund and Büdingen (1978) had subjects produce isometric or isotonic movements as fast as possible under self-defined conditions and conditions in which a target force or angle was specified visually to the subject. Under all conditions, the rise time of voluntary contraction was constant no matter how strong the contraction was or how far the limb had to move. According to Freund and Büdingen (1978) "the independence of the time of contraction of skeletal muscles from the final force level or angle of movement is regarded as a necessary condition for the synchrony of synergistic action [p. 2]."

We might suppose that the preservation of constant timing relationships in these simple activities maintains the unity of the act and metrical changes allow for flexibility. This seems to be the case in more complicated and less "stereotyped" skills like typing, handwriting, and piano playing. Terzuolo and Viviani (1979) had experienced typists (speeds over 80 words per minute) type the same words in a variety of contexts. Even though the overall durations for the word are different (up to 60% in some cases), *the ratio between times of occurrence of each letter pair is constant*. When the individual word data are in turn expanded or contracted to approximate the average duration, the resulting pattern is highly invariant. [Also, if loads are added to the fingers during typing (up to 3 times the mass of the fingers), absolute but not relative timing is affected (Terzuolo & Viviani, 1979)].

A similar situation occurs in handwriting when individuals vary writing speed without altering movement amplitude (Viviani & Terzuolo, 1980). When the tangential velocity records are ranked and scaled (as in typing), velocity changes so as to leave invariant the time of occurrence of major features. Relative timing can even be preserved over changes in forces applied to the limbs when they are performing different spatial tasks (Kelso, Southard, & Goodman, 1979). Moreover in piano playing (Shaffer, 1980) the right hand carrying the melody plays with more "weight" than the left, and gradual and sudden changes in both limbs can be made independently without disrupting timing (although in piano playing timing is built-in to accommodate the structure of the music).

The similarities across a wide number of laboratory and real-life activities suggest strongly that certain variables (called nonessential by Gelfand and Tsetlin, 1962) can produce scalar changes in muscles and kinematic patterns without destroying the structure or topological properties of the act. Significantly this design applies to systems whose structural features are vastly different.¹ Consider the systems for speaking and manual activity. Subjects can easily coordinate

¹Note that nothing has been said about mechanism here: an enterprise that is probably premature and maybe even misguided. The physicist Bohm () points out, for example, how strange it is that biology and psychology are moving closer to mechanism while physics (especially quantum theory) focuses on systems of interlocking dimensions not unitary mechanisms.

speaking and moving when asked to produce cyclical movements of the right index finger while simultaneously uttering a string of identical syllables. Now imagine that the subject is instructed to vary the stress of alternate syllables in a strong-weak manner (phonetically, /'stak, stak, 'stak, stak . . . /) while maintaining amplitude and frequency of finger movement constant. Finger movements are modulated, in spite of instructions not to do so, so as to conform to the stress of speaking: that is, longer finger movements accompany stressed syllables, and shorter finger movements accompany unstressed syllables. This is not a consequence of the speech system "driving" the motor system. A parallel experiment required subjects to keep stress of speaking constant but to vary the extent of finger movement (i.e., alternating long and short excursions). In many cases, the change in amplitude of finger movement was accompanied by a change in the pattern of syllable production. Longer movements were associated with syllables of higher amplitude and shorter movements with syllables of lower amplitude (Kelso, Tuller, & Harris, in press).

In concluding this section, we should first emphasize that the speech-limb coordination experiments demonstrate mutuality rather than competition between speaking and manual performance. Second, and perhaps more important for this discussion, activities that require coupling among very dissimilar anatomical systems seem to operate on the same principles as activities such as walking, handwriting, and coordinating the limbs in typing and piano playing. In short, when an individual speaks and moves at the same time, the degrees of freedom are constrained such that the parameterization is over the total unit. The ubiquitous feature characterizing all the motor behaviors discussed, from physiological tremor to coordinating the limbs with speaking, is the independence of the force or power expressed by the muscle collective and the relative timing of activities (electromyographic and kinematic) within that collective. The available data suggest that the motor system has a preferred mode of operation: where possible, scale up on power but keep timing constant. The invariance in timing relations and the flexibility attained by adjusting control parameters hints strongly of a design logic. A first pass at rationalizing the logic on principled grounds follows.

ORDER AND REGULATION IN MOVEMENT: A DYNAMICAL PERSPECTIVE

Programming theorists have found it difficult to rationalize the presence of timing constraints as a major characteristic of coordinated activity without proposing a muscle selector and a clock whose "ticks" define when muscles will actuate or not (Rosenbaum & Patashnik, 1980). But dynamics—the physics of motion and change—offers an alternative in terms of physical principles. To anticipate, the physics of systems undergoing energy flux defines living things as rhythmic and time-locked. More important, no new mechanisms need to be introduced to account for this fact (Morowitz, 1979).

Homeokinetics

In the past, dynamics has not been considered particularly appropriate for an analysis of biological systems because it has dealt almost exclusively with linear conservative systems. Consider, for example, simple mechanical systems such as a mass-spring, where the equation of motion describes a trajectory toward an equilibrium state. Such a linear system is represented by a second-order differential equation:

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

In Equation 1, oscillatory motion will decay in proportion to the magnitude of the viscous (frictional) term (c). All this is predicated on the second law of thermodynamics—time flows in the direction of entropy. Yet living systems are characterized by sustained motion and persistence; as Schrödinger (1945) first remarked, living systems "accumulate negentropy." Living systems are not statically stable; they maintain their form and function by virtue of their dynamic stability.

But how can sustained motion be assured without violating thermodynamic law? Consider again the familiar mass-spring equation, but this time with a forcing function (e):

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

Obviously it is not enough that a forcing function, e , be supplied to the system described in Equation 2; it must also be supplied at the right place and time in the oscillation. To guarantee persistence (and to satisfy thermodynamic strictures) the forcing function must exactly offset the energy lost in each cycle. Real systems meet this requirement by including a function, called an escapement, to overcome dissipative losses. The escapement constitutes a nonlinear element that taps the source of potential energy (as long as it lasts) to overcome local thermodynamic losses. Thus a pulse or "squirt" of energy is released via the escapement such that, averaged over cycles, the left-hand side of Equation 2 equals the right-hand side and sustained motion is thereby assured.

This brief analysis (for more details, see Andronov & Chaiken, 1949; Iberall, 1975; Kelso, Holt, Rubin, & Kugler, 1980; Kugler, Kelso, & Turvey, 1980, in press; Yates & Iberall, 1973) draws our attention to some fundamentally important concepts: First, stability in the system can only be established and maintained if work is performed; second, work is accomplished by the flow of energy from a high source of potential energy to a lower potential energy "sink." This continuous flow of energy through a system and the ability to do work distinguishes open, irreversible systems (which exchange energy with their surrounds) from the isolated closed systems of classical reversible thermodynamics that tend to run down toward a disordered state. Energy flow then can give rise to order in a system and, for a system to maintain order, energy flow must be continuous (Morowitz, 1979). Third, and perhaps most significant, for an account of the

timing constraints we observe in movement is Morowitz's (1979) main theorem: The flow of energy from a source to a sink will lead to at least one cycle in the system.

It has long been recognized that cyclicity lies at the very heart of biological functioning. A quote by Goodwin (1970) captures the message perfectly: "Oscillatory behavior is the fundamental dynamic mode of living, self-producing systems as we know them at and above the cellular level. The oscillation is not imposed by the environment; nor is it incidental to the living process. It is central to the organization [p. 8]." But, as emphasized here, cyclicity is not some epiphenomenal property of biological systems. It is central because the only known stability for systems that degrade free energy (as do all natural systems) is a dynamic stability necessarily consisting of periodicities or repeated motions (Yates, Marsh, & Iberall, 1972).

Cyclicity, as we have noted, is a nonlinear phenomenon. In effect the escapement is a nonlinear element that can make up for local thermodynamic losses and sustain oscillatory behavior. Such cycles are called limit cycles because they are capable of returning to a stable mode regardless of disturbances that speed up or slow down the cycle. Self-organizing, autonomous systems become viable, it is thought, when many cyclical processes become entrained. The latter homeokinetic scheme denotes systemic behavior as established by an ensemble of nonlinear oscillators that are entrained into a coherent harmonic configuration (Iberall, 1978; Soodak & Iberall, 1978). For homeokinetics, limit cycle entrainment ensures a solution to the degrees of freedom problem of movement control.

The features of coordinated movement identified in the previous section can now be rationalized on grounds other than motor programs. Coordinative structures, we suspect, are nonlinear oscillators of the limit cycle type, whose design necessarily guarantees that the timing and duration of "squirts" of energy will be independent of their magnitude within a fixed time frame (a period of oscillation, see Kugler, et al., 1980). Referring back to Equation 2, the magnitude of the forcing function will be some proportion of the potential energy available, but the forcing function itself is not dependent on time (Iberall, 1975; Yates & Iberall, 1973). Nonconservative, nonlinear oscillators are truly autonomous devices in a formal mathematical sense: time is nowhere represented in such systems (Andronov & Chaiken, 1949) and energy is provided in a "timeless" manner.

Perhaps the example that best captures the autonomous self-organizing nature of coordinative structures comes from Orlovskii's (1972) study of mesencephalic locomotion. Stimulation of the hind-limb areas of Red and Dieters nuclei in a stationary cat energizes the flexor and extensor synergies that correspond to the locomotory swing and stance phases, respectively. During induced locomotion, however, continuous stimulation of one site or the other has an effect only when the respective synergies are actually involved in the step cycle. Supraspinal influences (the energy supply) are only tapped in accordance with the basic oscillator design of the spinal circuitry. It is the latter that determines when the

system receives its pulse of energy as well as the *duration* of the pulse (see Boylls', 1975, discussion of spinal "slots").

Elsewhere we have shown that several important aspects of movement control result from a nonlinear limit cycle design. All the studies showing equifinality following limb perturbations can be given a reading in these terms (see pp. 443-444; also Fowler et al., 1980; Kelso & Holt, 1980; Kelso, Holt & Flatt, 1980; Schmidt, 1980). In addition, limit cycle oscillators have the entrainment property—already mentioned—that simple oscillatory systems such as a mass-spring do not possess. Entrainment is the chief mode of cooperation among self-sustaining oscillators and can take several forms. Mutual entrainment occurs when oscillators with similar but nonidentical frequencies interact such that both adopt an intermediate frequency (for examples, see Kelso et al., 1980; also von Holst's, 1973, "magnet effect"). Harmonic entrainment is that form of interaction that results when one oscillator adopts a frequency that is an integer multiple of another to which it is coupled (for examples of moving two limbs at different rhythms, see von Holst, 1973, and Kelso et al., 1980). These effects are omnipresent even in tasks that require the use of different structural systems. Individuals who are instructed to speak at a different rate than hand movement (and vice versa) either perform both activities synchronously or make one a subharmonic of the other (see Kelso et al., in press). In sum, entrainment is an emergent property of the interaction of nonlinear oscillatory systems; it is a self-organizing process in the sense that a collection of mutually entrained oscillators functions in a unitary way. The existence of timing constraints in many actions, we suspect, is not pernicious and accountable for by increasingly elaborate motor programs. In contrast, cyclicity is a necessary consequence of the physics of living systems (homeokinetics). Without timing constraints like entrainment, I suspect there could be no temporal resolution of the many simultaneous processes that occur when animals move.

CONCLUDING REMARKS

Homeokinetics characterizes biological systems as ensembles of nonlinear, limit cycle oscillators coupled and mutually entrained at all levels of organization. The appropriate (physical) image, as Yates (in press) points out, is one of multiple oscillators, not keeping time particularly well but weakly coupled in such a way that the ensemble is characterized by multiple rhythms, some timed quite precisely (as in some of the experiments mentioned earlier). The regulated state of the system in the homeokinetic view is defined by the operating conditions of interacting limit cycles, not by the reference levels, comparators, or error-detecting mechanisms of cybernetical devices.

This latter perspective—though largely unacknowledged by neuroscience—nevertheless interfaces perfectly with recent developments in that discipline.

Delcomyn (1980), for instance, in an exhaustive review of the neural basis for rhythmic behavior, identifies as new and "fundamentally important problems in neuroscience" precisely what we have considered here, namely the significance of oscillation and how oscillators interact to effect coordination between different parts of an animal (see Delcomyn, 1980, p. 497). According to the present perspective, oscillatory processes are pervasive in biology because living systems are members of a class of physical systems that are open to flux of energy and matter. Cyclicity or oscillation is an inevitable consequence of this fact (Turvey, Kelso, & Kugler, 1980).

Although many motor behaviors exhibit limit cycle properties (and may even be predictable by them), limit cycles per se do not have first-order status in explaining those behaviors. As pointed out at the beginning of this chapter, in order to observe spectrally distributed limit cycle regimes, certain necessary conditions must be present.

For new spatial and temporal organizations to emerge from previously existing steady states, the following constitute essential conditions (Iberall, 1977, 1978; Katchalsky et al., 1974; Kugler et al., 1980; Prigogine & Nicolis, 1971; Yates, 1980):

1. The presence of a large number of stochastically fluctuating elements—a many degree of freedom system.
2. Interactions between elements of a nonlinear kind.
3. A scale change such that nonlinear interactions are amplified.
4. Free energy should be dissipated by the system.

One of the best examples illustrating the application of these conditions to biological phenomena comes from work on termite architecture (Prigogine & Nicolis, 1971; see also Kugler, Shaw, & Turvey, in press). A careful analysis reveals that the elaborate walls, pillars, and arches constructed by a congregation of termites can be explained in terms of physical conditions that generate "dissipative structures"—spatially structured steady states or time-dependent limit cycle regimes that require a continuous flow of matter and energy for their formation and maintenance. Termites, it seems, do not possess a program for arch building that is isomorphic with the product of this behavior. Similarly, with respect to movement, many of the changes that occur when animals change gait may be explained without requiring the selection of a new program for each. Scale changes and nonlinearities in the system generate "phase transitions" and are capable of driving the system to qualitatively new spatiotemporal patterns that are formed and maintained by degrading free energy.

In this chapter I have tried to show by reason and by example that certain biological phenomena such as the preservation of a stable temperature or the acquiring of desired limit postures (pp. 442-444) may be explainable in terms other than programs or servomechanisms. This "other" explanation has its

foundations in the contemporary physical theories of homeokinetics and dissipative structures (or dynamic patterns). The orderliness of systemic behavior in the physical view is not due to an isomorphic prescription for the system but is an a posteriori fact of the system—a necessary consequence of selective constraints and physical law. It is worth noting that certain eminent neurophysiologists have become sensitive to the fact that the neural networks of the brain and related structures offer all the requisite architectural conditions for the emergence of dynamic patterns (Katchalsky et al., 1974; Llinas & Iberall, 1977; Szentagothai, 1978).

Of course, the goal of the present chapter has been to show in a very preliminary way what Yates (in press) suggests life itself shows, that is, how much action can emerge from some relatively primitive arrangements given the presence of a nonlinearity or two. Contemporary physical theory offers a dynamic vocabulary and gives due credit to the intrinsic relationship between plant processes and the small signal, communication aspects of the system. It promises to provide an accurate description of the mechanisms of emergence, of qualitative change in behaviors that cannot be understood with reference to quantitatively known component processes. Above all, it offers a principled account of how a system's internal degrees of freedom are regulated: Bernstein's (1967) problem. Perhaps it is not too early, then, to consider contemporary physics as a serious alternative to the vocabulary of formal machines that invests in the program the very phenomena that a theory of movement has to explain.

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