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A Dynamical Basis for Action Systems

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Introduction

Students of the neural basis of cognition might well take as their dictum the first phrase in the gospel according to St. John: "In the beginning was the word." In this chapter, we beg to differ and side instead with Goethe's Faust who, not satisfied with the accuracy of the biblical statement, proposed a rather different solution: "Im Anfang war die Tat"—"In the beginning was the act."[1] Certainly, if there is a lesson to be learned from the field of neuroembryology, it is that motility precedes reactivity; there is a chronological primacy of the motor over the sensory.[2] Although one of our main premises is that any distinction between *sensory* and *motor* is an artificial one (cf. Kelso, 1979), this brief sojourn into developmental embryology affords what we take to be a main contrast between the topic of concern in this chapter—the control and coordination of movement—and the subject matter of the rest of this book.

Our goals in this chapter are twofold. First, we want to describe some of the main developments in the field of movement control (as we see them) that have occurred in the last six to seven years. The developments hinge around a central problem that has continued to plague the physiology and psychology of movement almost since its inception, that is, the identification of significant units of coordination and control. In the last *Neurosciences Research Program Bulletin* that dealt specifically with motor control, Szentagothai and Arbib (1974) suggested that

> While the term synergy has not been explicitly defined here, it is evident that the traditional Sherringtonian usage is too restrictive to capture the concepts. . . . One now awaits a re-

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[1] With due deference to the celebrated embryologist V. Hamburger (1977).

[2] It is well established that the basal plate, or the motor part, of the spinal cord proliferates and differentiates long before the altar plate, or dorsal part, which receives sensory input. This observation has led some to speculate on the primacy of motor function, in a way that might provoke the cognitive neuroscientists: "The elemental force that embryos and fetuses can express freely in their spontaneous motility, sheltered as they are in the egg and uterus, has perhaps remained throughout evolution the biological mainspring of creative activity in animals and man and autonomy of action is also the mainspring of freedom" (Hamburger, 1977, p. 32).

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> definition of synergies to revitalize motor systems research along the behavioral lines of investigation successfully used in the visual system. (p. 165)

Much earlier, of course, the Soviet school under Bernstein's dominant influence (cf. Bernstein, 1967) had advocated the synergy as a significant unit, and the idea was taken up seriously in this country by Greene (1972), Boylls (1975), Fowler (1977), Turvey (1977), Kelso (1979), and Saltzman (1979a,b), among others. In fact, Boylls (1975) provided an elegant definition of *synergy* (or *linkage*, in his terms), which contrasts sharply with the traditional Sherringtonian concept: A *linkage* is a group of muscles whose activities covary as a result of shared afferent and/or efferent signals, deployed as a unit in a motor task.

A number of laboratories, including our own, have been working out the details of functional synergies (or, synonomously, muscle linkages or coordinative structures). In the first part of this chapter, we explain briefly *why* the synergy concept is necessary, how synergies can be identified in many different activities, what their chief characteristics are, and how they are modulated by various sources of contextual information. All along, we try to show that there is a subtle and mutually dependent relationship between the small-scale, neural, informational aspects of the system and the large-scale, power-producing machinery—the muscle dynamics. The first part of this chapter is largely review, with a few novel nuances, but some of the organizational features that emerge are worthy of note in that they compare in an interesting way with recent theorizing about neuronal assemblies and brain functions (cf. Edelman & Mountcastle, 1978). At the end of the chapter, we make these comparisons explicit because they suggest a common ground for understanding the coherent behavior of muscle and neuronal ensembles.

Although we can supply a solid justification for the use of the synergy concept, and although we can provide hints—from the motor control literature—about how synergies can be regulated to accomplish particular acts, a principled basis is still required for understanding how the many free variables in the motor system can be harnessed in the first place. How do stable spatiotemporal organizations arise from a neuromuscular basis of many degrees of freedom? And what guarantees their persistence and stability? What principles underlie the cooperative behavior among muscles that is evident during coordinated activity?

In the second part of the chapter, we take up these and related questions seriously. In contrast to "machine theories," which consider the many degrees of freedom to be regulated as a "curse" (cf. Bellman, 1961) and nonlinearities as a source of complication (cf. Stein, 1982), we advocate a set of "natural" principles gleaned from systems that *require* many degrees of freedom and in which nonlinearities are *requisite* conditions for the emergence of ordered phenomena (cf. Kelso, 1981; Kelso, Holt, Kugler, & Turvey, 1980; Kugler, Kelso, & Turvey, 1980, 1982; Turvey, 1980; see also Chapter 12, this volume). This "natural" perspective (Kugler *et al.*, 1982) takes its impetus from (and is parasitic on) contemporary physics,[3] and views the problem of coordination

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[3] Emerging primarily from Iberall and colleagues' Honeokinetic Theory (e.g., Iberall, 1977, 1978; Soodak & Iberall, 1978; Yates, 1980) but drawing also on Prigogine and colleagues' Dissipative Structure Theory

and control as continuous with, and a special case of, the more general problem of cooperative phenomena (cf. Haken, 1977). In this view, autonomy, self-organization, and evolution of function are stressed as system attributes. Our guess is that these attributes will prove difficult, in the long run, for the student of action to ignore, and, to the extent that they pertain to a theory of brain function, the cognitive neuroscientist as well.

A Fundamental Problem: The Selection of Units

The General Problem of Units

It is the time-honored thesis of classical physics that macroscopic states can be explained through microscopic analysis. The basic structure of nature is thought to be understood, first and foremost, through recourse to elementary units.[4] With the addition of a set of derived concepts (the laws of nature), natural phenomena can be explained. Biology has largely followed this paradigm by partitioning living systems into atomistic entities and laws of combination. Witness, for example, the dramatic successes in genetics, molecular biology, and neurophysiology: in some circles, units such as genes, molecules, and neurons, when synthesized appropriately, are thought to provide the basis of biological order.

One problem with this view, pointed out by Goodwin (1970), is that the analytical reductionist program, with its accompanying resynthesis, works only when there is a simple and direct relationship between the units of a system and its higher-level behavior.[5] In biological systems, however, the units themselves are complex, and thus, there are many ways for higher-order phenomena to arise. The scientist is then faced with the mammoth task of exploring all possible interactions among units and discovering those that could produce the observed higher-order behavior. Even if this dubious strategy were possible, the problem of explaining the "macro" from the "micro" is not simply one of specifying *interactions* among elemental units. This is because at each level of complexity, novel properties appear whose behavior cannot be predicted from knowledge of component processes. To paraphrase Anderson (1972), there is a shift from quantitative to qualitative; not only do we have more of something as complexity increases but the *"more" is different*. This is a physical fact (but eminently applicable to biology and psychology) arising from the theory of *broken symmetry:* As the number of microscopic degrees of freedom increases, matter undergoes sharp, discontinuous phase transitions that violate microscopic symmetries (and even macroscopic equations of motion) and leave in their wake only certain characteristic

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(e.g., Prigogine, 1980; Nicolis & Prigogine, 1977), Haken's Synergetics (Haken, 1977, 1978), Morowitz's Bioenergetics (Morowitz, 1978, 1979) and Rosen's Dynamical Systems' Theory (Rosen, 1970, 1978). A synthesis of these theories appears in Kugler, *et al.*. (1982).

[4] Physical science still pursues this strategy with some vigor in certain circles, although not without its skeptics. Thus, some have remarked that "elemental units"—as the least divisible parts—are not necessarily "fundamental units," and that indivisibility is no criterion for fundamentality (cf. Buckley & Peat, 1979).

[5] A good example is that of a gas, whose molecular kinetic energy can be averaged to provide a macrostate observable such as temperature.

behaviors. As we shall see, symmetry breaking is a natural property of systems whose constraints are subject to change. We shall make much of this later on, because it is a central theme that may allow us to envision how coordination might arise in systems with many degrees of freedom—that is, how we can take a multivariable system and control it as if it had just one or a few degrees of freedom.

Units in Action versus Units of Action

A great hindrance to the development of a theory of motor control and coordination has been the confusion between units *in* and units *of*. The unit is analyzed as if it were a piece in a puzzle or an ingredient in a cake, rather than in terms of its relational properties. For example, a pendulum consists of a number of components that can be thought of as the units *in* a pendulum system, but it is the *relations among components* that define the function of the pendulum system (cf. Ghiselin, 1981, for an informed discussion of units). With a few notable exceptions, students of action have classified units in terms of their anatomy rather than their function. Yet, if there is a truism about action, it is that significant units are differentiated according to their function rather than according to the neuromuscular machinery that constitutes them.

Witness, for example, Gallistel's (1980) "new synthesis of the organization of action," in which the reflex arc is chosen as a major building block or unit of behavior because it contains "all the elements necessary to explain the occurrence of muscular contraction or relaxation or glandular secretion." According to Gallistel, "the necessary elements are those Sherrington recognized: an effector, a conductor, and an initiator" (p. 399). Would that this connectionist metaphor provided the necessary criteria for units of action! Gallistel's Cartesian attitude of decomposing the system into its parts (configured in a fixed arrangement) and his offering of some glue (in the form of neural potentiation and depotentiation) to stick them together again must, if our discussion of units is relevant, be off the mark. Admittedly, Sherrington was the main figure in reflex physiology, but even he recognized that the reflex was a "probable fiction" or at best a "purely abstract conception" (Sherrington, 1906). Aside from the recognition that a pure reflex is seldom, if ever, observed as a unique part of an act, few of us would want to build a theory of movement's control with fictions as the substrate (cf. Kelso & Reed, 1981).

Decomposing the system into arbitrarily defined analytical units evokes serious consequences for measurement. In all likelihood, the physical decomposition obscures the system's dynamics so that the unit's observable properties are no longer relevant. A good example is the three-body problem in physics (cf. Rosen, 1978), such as the earth–sun–moon system. Decomposing the system into analytically tractable single and two-body subsystems brings us no closer to an analytic solution for the original three-body problem. To solve the three-body problem, new sets of analytic units must be discovered that are defined by new observables, so that the partitioning respects the original dynamics. These may look nothing like the units that we have chosen for so-called simplicity, or that we refer to as basic "building blocks." The functional units of behavior that we discuss here are not anything like simple reflexes, and only in certain very restrictive cases do they correspond to other proposed units of analysis such as "single muscles or groupings of muscles acting normally around a joint" (cf. Stein, 1982). Moreover, the criteria underlying their selection are not at all like those employed by Gallistel—or Sherrington, for that matter. As Reed (1982) pointed out, the units of action are not triggered responses that can be chained together by central or peripheral processes, but postures (which he called "persistences in an animal-environment relation") and movements (transformations of one posture into another). In fact, one of the claims we try to substantiate here is that a unit of action at any level of analysis must be so designed that persistence of function is guaranteed.

Units of Action in Multivariable Systems

The Concept of Coordinative Structure

As we have already intimated, the problem of identifying units of action has long been a thorny issue, and it continues to be debated in both the neural and the behavioral literature. The elegant remarks of Greene (1971), made over a decade ago, still seem to apply in many circles:

> The masses of undigested details, the lack of agreement and the inconclusiveness that mark the long history of investigations of motor mechanisms arise from our limited ability to recognize the significant informational units of movement.

There are signs, however, that some consensus is being reached concerning the units of action. This may reflect a growing appreciation of the fundamental problem of control and coordination identified by Bernstein (1967); namely, that of regulating a system with many degrees of freedom. Bernstein's key insight was that the large number of potential degrees of freedom of the skeletomuscular system precludes the possibility that each is controlled individually at every point in time. He then proposed a scheme whereby many degrees of freedom could be regulated through the direct, executive control of very few. In this view, individual variables of the motor system are organized into larger functional groupings called "linkages" or "synergies" (Boylls, 1975; Gurfinkel, Kots, Pal'tsev, & Fel'dman, 1971); "collectives" (Gel'fand, Gurfinkel, Tsetlin, & Shik, 1971); or "coordinative structures" (Easton, 1972a; Fowler, 1977; Kelso, Southard, & Goodman, 1979; Turvey, 1977). During a movement, the internal degrees of freedom of these functional groupings are not controlled directly but are constrained to relate among themselves in a relatively fixed and autonomous manner. The functional group can be controlled as if it had many fewer degrees of freedom than comprise its parts, thus reducing the number of control decisions required.

One example of a functional constraint on movement, a coordinative structure, is exhibited by people performing the task of precision aiming. When a skilled marksperson aims at a target, the wrist and shoulder joints do not change independently but are constrained to change in a related manner. Specifically, any horizontal oscillation in the wrist is matched by an equal and opposite oscillation in the shoulder, thus reducing the variation around the target area (Arutyunyan, Gurfinkel, & Mirsky, 1969). In an unskilled marksperson, movement at the wrist joint is unrelated to movement at the shoulder, allowing the arm to wander.

As the foregoing example reveals, coordinative structures are units of action, emphasizing the functional aspects of movement. Constraints are thought to arise temporarily and expressly for particular behavioral purposes (Boylls, 1975; Fitch & Turvey, 1978). The same degrees of freedom may be constrained in different ways to achieve different purposes, and different degrees of freedom may be constrained to achieve the same goal. Thus, coordinative structures are significant units not by virtue of their shared degrees of freedom, but by their capability of achieving a common goal. In this regard, the way we use the term *coordinative structures* differs from that of Easton (1972a), who views them as reflex-based. Indeed, there is evidence that even reflexes exhibit functional specificity, adjusting to the phase of movement that the animal is in when the reflex is elicited. For example, Forssberg, Grillner, and Rossignol (1975, 1977) examined reflex behavior in the spinal cat. A tap to the paw during the stance phase of stepping was associated with increased activity in the extensor muscles; a tap applied during the transfer phase enhanced activity in the flexor muscles. Such behavior is significant in that it performs an *adaptive* function for the animal, lifting the paw over an obstacle (see also Fukson, Berkenblit, & Fel'dman, 1980). Thus, movements are seldom simply reactive; they are adaptive, functionally specific, and context-sensitive (for many motor examples in the ethological literature, see Bellman, 1979; Reed, 1982).

Note also that the coordinative structure perspective differs from open-loop models of control (which give privileged status to efference), as well as from closed-loop models (in which afference is dominant). The state of the marksperson's wrist joint, for example, is viewed not only as providing information about its own position (afference), but also as specifying the appropriate positions of the linked elements (efference). Thus, afference and efference both provide information relevant to the linkage, and neither one has priority over the other (Kelso, Holt, Kugler, & Turvey, 1980; Kugler *et al.*, 1980).

Coordinative Structures as Dynamic Linkages Defined over Units of Action

Although constraining skeletomuscular variables result in an increase in control, it does so at the expense of range of motion. The number of possible trajectories of the limb is reduced, but the individual trajectory is not uniquely determined by constraints. When free variables are linked to perform a function, a balance exists between the linkage's flexibility, or freedom to undergo change, and limitations on its flexibility (Pattee, 1973; see also Fowler, 1977; Fowler, Rubin, Remez, & Turvey, 1980). Systems that do not perform functions are either too tightly constrained (e.g., rigid objects) or hardly constrained at all (e.g., an aggregate of grains of sand). Systems that perform functions are *selectively limited* in their actions, not uniquely determined.

In our earlier discussion of units, we pointed out that complex systems exhibit discontinuities in structure and behavior (broken symmetry); that is, new modes of organization and behavior appear that are not easily predictable from the preceding modes. These new spatiotemporal structures are sometimes referred to as *emergent properties*. In the domain of movement, there is a tendency to account for the appearance of new phenomena—such as a novel movement pattern to accomplish some goal—by reference to the generativity embodied in a generalized motor program (e.g., Schmidt, 1975); a motor engram (e.g., Heilman, 1979); or a schema (cf. Head, 1926; Pew, 1974; Schmidt, 1975).

Rather than adopt this latter strategy, it may be better to recognize that all that has really happened is that our mode of description has failed at the point at which the novelty appears, requiring us to adopt a new mode of description that may be quite unrelated to the old one[6] (cf. Rosen, 1978). The main difficulty with an analysis of emergent properties lies, as Rosen (1978) cogently remarked, *"in the tacit assumption that it is appropriate to describe a natural system by a single set of states"* (p. 91, italics his). This strategy necessarily restricts the observables that are possible and eliminates the possibility for new ones. However, when dynamical interactions occur, either among the states of a system, or when the system interacts with its environment, new observables are possible that were meaningless or invisible in the absence of coupling. As a consequence, an entirely new set of state descriptions of the system is possible because the observables have changed.

Let us bring these abstractions down to earth and back to the domain of movement. A coordinative structure, as we have defined it, is a functional *linkage* among previously unrelated entities—it is a prototypical example of an emergent phenomenon. By the arguments given above, a coordinative structure offers an *alternative description* of a system because it is defined on observables that bear little or no relationship to those of its components. By being a dynamic coupling among component variables, its state space offers a much richer set of trajectories than is possible in a system having the identical set of components but described by a single set of states.

Coordinative Structures as Nonlinear Vibratory Systems

Dynamical linkages (equations of constraint) selectively reduce the number of independently controlled degrees of freedom, thereby allowing a rich sets of trajectories. But what kind of system is produced when elements of the motor apparatus are linked dynamically? Recent work on motor systems has identified functional units of action with nonlinear mass-spring systems. An attractive feature of such systems (among some others) is that they are intrinsically self-equilibrating: when the spring is stretched or compressed and then released, it will always equilibrate at the same resting length. Thus, the final equilibrium position is not affected by the amount that the mass is displaced—a property called *equifinality* (cf. von Bertalanffy, 1973).

In its more detailed (but, we would add, unevenly interpreted) version, a given joint angle may be specified according to a set of muscle equilibrium lengths (cf.

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[6] In the case of perception, for example, we find it hard to understand how extensive, physical variables (like decibels) give rise to intensive, psychological effects (like roaring jets and rock bands). As Shaw and Cutting (1980) pointed out, this is a "structure-creating" transfer function that maps continuous variation of linear variables onto discontinuous categorical changes that, by definition, are nonlinear. At least two solutions can be offered to this problem: one is to assume that the perceptual apparatus is creative in nature and gives meaning to meaningless sensations (much like a schema for movement rearranges the spatiotemporal orderings of muscles in a creative, generative way); another is to adjust the basis of measurement so that it is common to the perceiver (producer) and the perceived (that which is produced).

Fel'dman, 1966a,b). Once these are specified, the joint will achieve and maintain a desired final angle at which the torques generated by the muscle sum to zero. Such a system exhibits equifinality in that desired positions may be reached from various initial angles and despite unforeseen perturbations encountered during the motion trajectory. Thus, if the length of a muscle at a joint is currently longer than the equilibrium length, active tension develops in the muscle; if the current length is shorter than the equilibrium length, the muscle relaxes. We can see how this concept is akin to a coordinative structure. The control of many variables (e.g., degree of activation in various muscles at a joint) is simplified by establishing a constraint: given a set of muscle equilibrium lengths, the torque generated by tension in each muscle is dependent on its current length.

Recent support for this account comes primarily from work on limb and head movements. For example, Kelso (1977) and Kelso, Holt, and Flatt (1980) have shown that normal and functionally deafferented humans are more accurate in reproducing the final position of a limb from varying initial positions than in reproducing movement amplitude. In addition, Bizzi and his colleagues (Bizzi, Dev, Morasso, & Polit, 1978; Polit & Bizzi, 1978) have shown that normal and rhizotomized monkeys can reproduce learned target positions of the head or arm even when the movement trajectory is perturbed by the application of a load. Similar results have been found in humans (Kelso & Holt, 1980), and predictable effects of changing the effective mass of a limb have also been observed (e.g., Fel'dman, 1966b; Schmidt & McGown, 1980). The findings are not easily accounted for by traditional motor control models. For example, closed-loop models could account for the accurate reproduction of final position in spite of changes in the initial position of the limb, or perturbations of the limb trajectory, but they could not explain why equifinality holds when the limb is deafferented. In theory, open-loop programming models could handle the deafferentation findings but—at least, in conventional form—are unable to explain satisfactorily adjustments to unanticipated perturbations.

A fundamental point, from our perspective, is that considering final limb position as the equilibrium state of a constrained collective of muscles allows for the independence of final position from initial position without requiring processes of measurement and comparison. Although we could describe a dynamical system like a mass spring in terms of externally imposed reference levels, and though we could mathematize it into canonical feedback form, little would be gained by doing so (cf. Yates, 1980, for additional remarks). A muscle collective qua spring system is intrinsically self-equilibrating: conserved values such as the equilibrium point emerge from the system's parameterization, and consequently, there is no need to introduce a "representation" anywhere. Such systems belong to a generic class of dynamical system called *point attractors*, that is, those characterized by an equilibrium position to which all trajectories tend.

The Importance of Dynamical Analogy

We should make our position clear on the identification of functional units of action with nonlinear vibratory systems such as mass springs. It is obvious that a muscle has springlike properties (the length–tension properties of isolated muscle, for example, are well known; e.g., Rack & Westbury, 1969), and hence it is tempting to treat each individual muscle participating in an activity as a separate mass-spring system. The resulting system would likely require large look-up tables for the purpose of specifying parameters such as stiffness and equilibrium length for each muscle (cf. Sakitt, 1980). Moreover, such a strategy emphasizes the model's material embodiment—the structural characteristics of muscle—which, though quantifiable and relatively easy to measure, tell us nothing about the nature of the organization among muscles when people perform tasks. In the spirit of Rashevsky's (1938) *relational biology*, and its enlightening extensions by Rosen (1978), we view the importance of the mass-spring analogy not in terms of the system's material structure but as indicative of a particular *functional organization*. The key insight for us is recognizing the dynamical analogy between a mass-spring system and a constrained collective of muscles and joints in terms of their functionally similar behavior (Kelso, Holt, Kugler, & Turvey, 1980; Kugler *et al.*, 1980; Saltzman & Kelso, 1983). In this respect, as Fel'dman (1966b) remarked:

> The motor apparatus . . . is similar to many physical systems, for example, a spring with a load; although its movement as a whole is determined by the initial conditions, the equilibrium position does not depend on them and is determined only by the parameters of the spring and the size of the load. (p. 771)

Thus, if one ignores the question of *what* oscillates (the material structure) and instead asks what the functional organization is, it becomes clear that many physical and biological systems (including muscles and mass springs) admit common dynamical descriptions even though they consist of utterly diverse structures. Their dynamical equivalence—to belabor the point—lies not in their physicochemical likeness but in their sharing an abstract organization. Note that this dynamical description of the cooperative behavior among muscles has little to do with the individual behavior of a muscle or its sarcomeres and fibrils. The power of the approach, however, is that it allows one to see how a wide variety of different systemic behaviors can obey the same dynamical laws. In fact, dynamical analogy may be a basic strategy open to any natural science whose "ultimate aim," in Planck's (1926) words, is "the correlating of various physical observations into a unified system" (cited in Saunders, 1980).

Nonlinear systems of masses and springs have been traditional characterizations of many different phenomena, ranging from the vibrational modes of atoms to the behavior of vocal tracts and hearts. The deep relationship among the behavior of all such structures is that they are realized by the same abstract functional organization. In a later section we shall explore this regularity in greater detail, for it can be argued that the principles governing the cooperation of many subsystems are identical regardless of the structure of the subsystems themselves (cf. Haken, 1977).

Modulation of Coordinative Structures

Some Remarks on Functional Nonunivocality

A second fundamental insight of Bernstein's (1967) was the realization that actors are mechanical systems, subject to gravitational and inertial forces as well as to reactive forces created by movements of links in the biokinematic chain. A consequence of this fact is that the relationship between motor impulses and their outcome in movement must be indeterminate (nonunivocal). This problem may be considered as the mirror image of a problem that perceptual theorists have long recognized, that is, the lack of a simple one-to-one relationship between a physical stimulus and a psychological percept. In speech perception, for example, many different acoustic patterns may, in different contexts, be perceived as the same phoneme, and the same acoustic pattern may be perceived as different phonemes (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Rakerd, Verbrugge, & Shankweiler, 1980; among many others). In motor control, different contextual conditions may require very different patterns of innervation in order to bring about the same kinematic movement, whereas the same pattern of innervation may produce very different movement outcomes. The different "contextual conditions" of a movement depend not only on environmental changes, but also on the dynamic state of component segments. This problem is magnified in biokinematic chains (such as humans): the body segments have mass and, once impelled, gather momentum and develop kinetic energy, which may, in turn, provide forces on other segments in the chain.

Consider this anatomical/mechanical source of indeterminacy in a bit more detail. The fact that a link in a biokinematic chain is accelerating does not necessarily imply that the movement is under direct muscular control. Acceleration of a link may also be a function of reactive forces contingent on movements of adjacent links. Further, the force that one link exerts on another is dependent not only on muscle forces exerted on the first link, but also on the manner in which the first link is moving relative to the second. For example, during locomotion, the transition from hip flexion through hip and knee extension is largely due to passive forces. The inertial torque generated by flexing the hip is sufficient to continue the forward movement of the leg from the hip and to extend the knee and ankle (Arshavskii, Kots, Orlovskii, Rodionov, & Shik, 1965; Grillner, 1975). Such is the case even when the hip musculature is slightly active, a condition that, in the absence of other forces, would bring the leg backward (Bernstein, 1967).

Another (very different) source of indeterminacy between central commands and movement consequences is of physiological origin. Most fibers of the pyramidal motor system of primates, once thought to synapse directly on the motoneurons, actually synapse on spinal or brain-stem interneurons (cf. Evarts, Bizzi, Burke, DeLong, & Thach, 1971; Dubner, Sessle, & Storey, 1978). The "state" of the interneurons is dependent on the combined influence of supraspinal descending pathways, spinal interactions, and afferent nerve impulses. Thus, the interneuronal system may provide an excitatory or inhibitory *bias* of the motoneurons. If the bias is such that the membrane potential of the motoneuron is close to threshold, a very small additional depolarization results in its firing. As Granit (1977) remarked, "the internuncial apparatus does what the gamma motor fibers do for the muscle spindle by contracting their intrafusal fibers; it determines the motoneuron's bias from moment to moment as required by the task at hand" (p. 162). Thus, the same descending activity might encounter very different "states" in the spinal interneurons, with considerable variation in the motor effect. Central influences, then, are thought to serve an organizing function by biasing lower-level systems toward producing a class of actions, but the lower-level systems can adjust autonomously to varying contextual conditions. We consider in more detail below some forms that modulation or tuning of coordinative structures might take.

"Tuning" Coordinative Structures

Constraints—analogous to the grammar of a language—do not uniquely determine a movement's trajectory; rather, they allow a rich set of controlled trajectories. How, then, can actions be modulated according to changing environmental circumstances, yet still maintain their fundamental form? A clue may be gleaned from Gel'fand and Tsetlin's (1971) argument that *well-organized* functions allow a mutable partitioning of variables into those that preserve qualitative aspects of a movement's structure (termed *essential*) and those that produce quantitative, scalar changes (termed *non-essential*). Bernstein (1967) argued along similar lines, noting that for living things, qualitative characteristics of space configurations and of the form of movement predominate over quantitative ones. For example, a birch leaf differs from a maple leaf by qualitative properties of the first order, whereas all maple leaves belong to the same class in spite of the large amount of biometric variation among members of the class.

Boylls (1975) has formalized a set of constraints on the electromyographic (EMG) activity of linked muscles that could preserve relational aspects of an action over scalar change. First, the timing of activity in components of a functional unit is relatively independent of the amplitude of activity. Second, the ratios of EMG activity among muscles remain roughly fixed relative to the time frame and the absolute levels of individual activity. Thus, according to Boylls, most actions can be partitioned into three relatively independent descriptions: (1) a temporal description that refers to the relative timing of activity in components of the linkage; (2) a structural description that defines the ratio of activity among linked variables and changes slowly with respect to real time; and (3) a metrical specification that operates as a scalar multiplier of activity in the linkage. As we shall see, it is the relationships among muscles that persist (hence, "essential") over metrical variation.

The foregoing characterization of constraints immediately suggests three important questions. First, can we see constancies in the timing relations among components of diverse activities across metrical changes? Second, do these constraints hold only at the level of muscle activity, or do they also describe the kinematics of movement? Third, what are the sources of metrical modulation? With regard to the first question, because the timing of an act is hypothesized to be independent of the force requirements, one should be able to uncover timing constancies by altering the metrics (e.g., to change the speed or force of production). Those variables that are unaltered across scalar change may prove crucial if a given motor pattern is to be characterized as an instance of a certain class of actions.

This strategy has proved successful in uncovering coordinative structure styles of organization in many different types of activities. The most well-known and abundant data come from studies of locomotion. For example, when a cat's speed of locomotion increases, the duration of the "step cycle" decreases (cf. Grillner, 1975; Shik & Orlovskii, 1976) and an increase in activity is evident in the extensor muscles during the end of the support phase of the individual limb (when the limb is in contact with the ground). Notably, the increase in muscle activity (and the resulting increase in propulsive force) does not alter the relative timing of activity among functionally linked extensor muscles, although the duration of their activity may change markedly (Engberg & Lundberg, 1969; Madeiros, 1978; MacMillan, 1975; see also Schmidt, 1980, and Shapiro & Schmidt, 1982, for further reviews).

Constancy of timing relationships in muscle activity has been reported for other obviously cyclical activities, such as mastication and respiration (see Grillner, 1977, for review). More recently, however, the stability of the timing prescription over metrical change has been shown to characterize muscle activity associated with less obviously cyclical or stereotyped activities, such as postural control (Nashner, 1977) and voluntary arm movements (Lestienne, 1979). There exists as well limited electromyographic evidence that this style of organization is characteristic of speech production. Tuller, Kelso, and Harris (1982a) found that the relative timing of activity in various articulatory muscles was preserved across the large changes in duration and amplitude of activity that accompany suprasegmental variations in syllable stress or speaking rate.

With regard to the question of generalizability to kinematics, there is a growing empirical base in which kinematic descriptions of motor actions are qualitatively similar to the electromyographic descriptions we have been discussing. For example, in handwriting, a highly developed motor skill, the relative timing of major features within a word does not change with variations in writing speed (Viviani & Terzuolo, 1980). In speech production, the relative timing of articulatory movements in a given utterance is stable across different speaking rates and stress patterns (Tuller, Kelso, & Harris, 1982b, 1983). A similar situation occurs in bimanual movements: relative timing between the limbs is preserved even when they are performing different spatial tasks with different force requirements (Kelso, Southard, & Goodman, 1979a,b). This organizational style may also apply to the kinematics of coordinated systems with very different physical structures. For example, when subjects are asked to produce a string of monosyllables while tapping their finger, they have no trouble with the task. But when subjects are asked to perform the tasks at different rates, they do so by using small integer sub- or superharmonics. A true dissociation in the timing of speech and manual gestures does not appear to be possible when both tasks are involved (see Kelso, Tuller, & Harris, 1983, for details).

It seems obvious that our first two questions can be answered in the affirmative: timing relations among electromyographic and kinematic events appear stable over metrical change. But what are the *sources* of metrical change? Can coordinative structures be "tuned" by other than direct CNS command? Put another way, what can we get "for free" or with minimal computational cost before we burden the nervous system with the sole responsibility for control? For example, turning the head seems to bias the system for extension of limbs on the side to which the head is turned, and for flexion of limbs on the opposite side. Similarly, Easton's (1972b) experiments show that when cats look up, stretching their eye muscles, there is spinal biasing that facilitates extension of the forelimbs. When the cat looks down, there is a bias toward forelimb flexion. Such tuning relationships may be exploited by athletes (Fukuda,

1961) or under conditions of fatigue (Hellebrandt, Houtz, Partridge, & Walters, 1956). The exploitation of systemic relations may also help account for certain details of ipsilateral eye–hand coordination in split-brain monkeys. Gazzaniga (1966, 1969) reported that split-brain monkeys had to orient the eyes, head, and neck toward the target food in order to reach accurately, although the reach itself did not appear to be under moment-to-moment visual control. Although this interpretation is ours and not Gazzaniga's, it may be that the monkeys were exploiting systemic biasing relations to facilitate arm extension.

Another source of physiological tuning that is currently receiving much attention is the biasing of spinal organization that occurs before and during voluntary movements (cf. Gottlieb, Agarwal, & Stark, 1970; Kots, 1977). Such experiments examine changes in the excitability of motoneuronal pools by eliciting a monosynaptic Hoffman reflex and recording its amplitude over time. Gottlieb *et al.* required their subjects to track a visual target by controlling the amount of force on a foot plate. Approximately 60 msec prior to any evidence of voluntary EMG activity in the agonist muscle for the upcoming movement, there is a progressive increase in the agonist muscle's reflex excitability. In other words, the increase in reflex excitability acts to facilitate the upcoming movement. Simultaneous with increased excitability in the agonist muscle, the level of excitability in the antagonist muscle is depressed (Kots & Zhukov, 1971). Thus, prior to any actual movement, boundary conditions arise that predispose the nervous system to produce one of a restricted class of movements (see also Fowler, 1977; Kelso, 1979; Lee, 1980; Saltzman, 1979a, for a more expansive review of preparatory tuning).

The relationships among muscle systems are not the only sources of tuning for movement. The different perceptual systems can be extremely rich sources of modulation. Dietz and Noth (1978), for example, provided convincing evidence that optical information is a source of control in motor actions. In their experiment, the subjects were asked to fall forward, hands first, onto a platform that could be tilted so that different falling distances were required. Electromyographic activity was monitored in the triceps brachii, which were used to extend the arms for bracing against the fall. When the subjects were able to see the platform, the onset of EMG activity began a constant amount of time before impact (and thus a variable amount of time after starting the fall), regardless of how far away the platform was. When the subjects were blindfolded, the muscle response began at the beginning of the fall (see also Lee, 1976, 1978; Lee & Lishman, 1974).

Orientation-specific optical change can also bias an actor toward performing a class of movements, although no movement actually occurs. For example, when a large disk of colored dots is placed in a cat's line of sight and rotated to the left (optically indicating a tilt of the cat to the right), the extensor reflexes on the cat's right side and the flexor reflexes on the left side are enhanced (Thoden, Dichgans, & Savadis, 1977). Had the cat actually been tilted in the direction specified by the optical flow, the reflex changes would have facilitated the cat's regaining an upright position.

The perceptual tuning of the action system is not tied to a particular sense modality. For example, one vision-substitution device for the blind transmits a pattern of intensity differences from a camera to a bank of mechanical vibrators on the "viewer's" back. In this situation, rapid expansion of the tactile array specifies a large, rapidly approaching surface, which the viewer moves to avoid (White, Saunders, Scadden, Bach-Y-Rita, & Collins, 1970; for details concerning how global expansion of the optical array might specify movements of the observer, or of large objects in the environment, see Gibson, 1950, 1966). Other sources of tuning of the action system may be vestibular (e.g., Melville-Jones & Watt, 1971a,b) or auditory (Davis & Beaton, 1968; Pal'tsev & El'ner, 1967; Rossignol, 1975; Rossignol & Melville-Jones, 1976).

In summary, we have seen how constraints defining coordinative structures preserve relationships among components but still enable flexibility by allowing variables to take on different values. The chief characteristic of coordinated activities, we have argued, is that they exhibit relational invariance over metrical change. Metrical specification, as we have noted, amounts to a tuning of the coordinative structure. As emphasized by Greene (1972) and later by others (e.g., Fitch, Tuller, & Turvey, 1982), tuning an otherwise invariant structure is an efficient way of producing flexibility with a minimal amount of reorganization.

Units of Action as Rationalized by Nonlinear Systems Analysis

We have noted that a chief feature of units of action rests in a mutable (functionally specific) partitioning of component variables into those that preserve the structural or "topological" (in the Bernstein sense) organization of movement and those capable of effecting scalar transformations on the structure. Here we address briefly—because it is laid out in more detail elsewhere (cf. Kelso, 1981; Kelso, Holt, Kugler, & Turvey, 1980; Kugler *et al.*, 1980, 1982)—the theoretical framework that may best rationalize units of action. Moreover, the framework that we shall elaborate allows us to identify other criterial properties of action units that are crucial from a biological perspective, though seldom if ever recognized. Fundamentally, a functional unit at any level can be defined as *a cluster of elements of various kinds that is just sufficiently organized to produce a persistent function* (cf. Iberall, 1978a,b). Unlike currently popular theories that view control as effected through a preestablished arrangement among component parts (a cybernetic machine) or as being due to a set of prescribed orders (an algorithmic machine), this definition recognizes that first and foremost, biological systems belong to a class of physical systems that are *open* to fluxes of energy and matter with their surround. In contrast, cybernetic and algorithmic machines are closed to exchanges of energy and matter with their environment and hence are likely to apply to a very limited set of circumstances. The order and regularity observed in living organisms are brought about, in Bertalanffy's (1973) words, "by a dynamic interplay of processes," based on the fact that living things obey the laws of open, irreversible thermodynamics. Unlike machines, open systems can actively evolve toward a state of higher organization.

The recognition that the flow of energy through the system plays an active organizing role and that stability can be maintained only at the price of energy dissipation (e.g., Haken, 1977; Iberall, 1977, 1978a,b; Iberall & Soodak, 1978; Katchalsky *et al.*, 1974; Morowitz, 1978, 1979; Prigogine & Nicolis, 1971; Yates, 1980) provides a key to understanding the temporal stability that we have highlighted as a main feature of units of action. Energy dissipated, of course, must be replaced if persistent function is to be possible; it is this requirement that allows us to see that the stability is not a static one in the equilibrium sense, but a *dynamic* stability consisting of stable periodicities and cycles. Morowitz's (1978, 1979) theorems offer a needed insight: Work is accomplished anytime there is a flow of energy from a source of high potential energy to a lower potential sink; this source–sink flow leads to at least one cycle in the system (for numerous biological examples, see Yates, 1980, and for a detailing of neural periodicities, see Iberall & Cardon, 1966). A clarification of the *type* of cycle that characterizes biological systems affords a unique opportunity to identify fundamental properties of action units. Specifically, we shall see that action units are *persistent, temporally stable, and autonomous* entities (cf. Iberall, 1975; Yates & Iberall, 1973; Yates, 1980; Kugler *et al.*, 1980, for applications to movement).

Consider the ideal, linear harmonic oscillator as a class of device that exhibits repetitive motion. Once started, such a system can continue indefinitely without dissipative losses. But for that reason, it is not a realistic physical entity, because all real systems dissipate energy. We can introduce a dissipative term (such as damping due to friction) into the following equation of motion:

$$m\ddot{x} + b\dot{x} + kx = 0 \tag{1}$$

where x = displacement, m = mass, k = stiffness, b = damping. However, the motion that results will run down, because no means are provided to overcome the energy losses. To obtain persistence of motion in a dissipative system—that is, to compensate for energy losses due to friction—a nonlinear coupling term must be introduced. The latter constitutes an "escapement" forcing function that permits a pulse of energy, ε, to be drawn from a continuously available source of potential, and to be injected into the system at appropriate phase, θ:

$$m\ddot{x} + b\dot{x} + kx = \varepsilon(\theta) \tag{2}$$

It is important to emphasize that the "escapement" forcing function (like the escapement in a grandfather clock) is not strictly time-dependent; hence, it is autonomous in the conventional mathematical sense: it is an intrinsic timing mechanism in the sense that $\varepsilon(\theta)$ is drawn from a potential energy source that is part of the system itself. There is no ghost driving the machine from the outside or providing instructions to the oscillatory component (cf. Minorsky, 1962; Yates, 1980).

Equation (2) can be rewritten to reveal that the escapement pulse exactly offsets the energy loss averaged over each cycle, so that periodic motion is assured:

$$m\ddot{x} + kx = \overline{\varepsilon(\theta) - b\dot{x}} = 0 \tag{3}$$

where the bar expresses an average. Systems described by nonlinear equations such as (2) and (3) are called *limit cycles* because they settle into steady, near-isochronous motion of fixed amplitude independent of sporadic disturbances and initial conditions (see also the Section on coordinative structures as nonlinear vibratory systems). Thus, if an oscillatory component is displaced with a push of large amplitude, its loss of energy will be greater than the escapement pulse can provide to offset it. The system will lose amplitude until energy balance (orbital stability) is achieved. Similarly, a small change in initial displacement is associated with smaller frictional losses than the energy pulse injected. Amplitude will therefore grow until the system reaches a balanced state, characterized by limit cycle behavior, that is, a closed cycle of events on the phase plane (cf. Jordan & Smith, 1977; Minorsky, 1962). The limit cycle, then, constitutes a *periodic attractor,* in current terminology (see Gurel & Rössler, 1979, for many examples), to which all deviated states tend. Limit cycles have been used to model many different neural phenomena, from EEG (Basar, Demir, Gönder, & Ungan, 1979; Freeman, 1975; Kaiser, 1977) to excitatory and inhibitory interactions in neurons (cf. Wilson & Cowan, 1972). More fundamentally, however, the persistent, self-sustaining, autonomous, and orbitally stable trajectories of nonlinear, limit cycle systems are manifestations of thermodynamic engines. Such engines sustain cyclic motion by absorbing over the course of each cycle an amount of free energy that just balances the energy dissipated per cycle. Without this energy balance, the system would simply decay toward a static equilibrium state (Iberall, 1977, 1978a, 1978b; Yates, 1980; Yates & Iberall, 1973).

As far as the control and coordination of movement are concerned, the implication of this discussion is that a unit of action at any scale of analysis must fulfill thermodynamic criteria (cf. Kugler *et al.*, 1980). Moreover, the chief distinguishing features of a coordinative structure—the dissociation of power and timing and the fixed proportioning of activity among elements (see the previous section)—are neither arbitrary nor exotic. On the contrary, the phase-dependent energy input pattern guarantees that the timing and duration of energy inputs will be independent of the magnitude within a fixed time frame (a period of oscillation). Also, the magnitude of the input, or "squirt," will be a fixed proportion of the power supply. The stability regime realized by a nonlinear system such as a coordinative structure is asymptotic and orbital; the limit cycle "quantizes" action (formally, the product of energy and time; cf. Iberall, 1978a,b), and the system's conserved values or equilibrium operating conditions are specified in the loose coupling among limit cycle processes (see, for example, Goldbeter, 1980; Kawahara, 1980; Smith, 1980).

Extending the foregoing identification of coordinative structures with limit cycles may allow us to intuit how the dynamic organization of the action system for a particular activity may constrain where and when perceptual information can be most effectively "picked up" (Gibson, 1950, 1966, 1979). We have seen that the design of the system—with its source of potential energy, nonlinear escapement, and oscillatory component—determines when in the cycle the energy source will be tapped. The mathematical description of this is an autonomous one in which time itself is not formally represented; no "extrinsic" timing mechanism is required (see Fowler, 1980, for a comparison of models of "extrinsic" and "intrinsic" timing). Such a description fits the work we have already mentioned on so-called reflex reversal (Forssberg *et al.*, 1977), in which the same input can have very different behavioral effects when it occurs in different phases of the step cycle. Similarly, in Orlovskii's (1972) work on cat locomotion, neural stimulation of Deiter's nucleus in the mesencephalon of a stationary cat results in limb extension. Continuous stimulation of the same nucleii in a walking cat enhances extension only during the extensor phase of the step cycle. Neural stimulation (perceptual information?) is gated according to the nature of the systemic organization and is limited to that phase of the cycle where its effect is adaptive.

The identification of functional units of action (coordinative structures) with limit cycle mechanisms offers a number of attractive features for a programmatic approach to problems of coordination and control. Chief among those undergoing empirical exploration (see Kelso, Holt, Kugler, & Turvey, 1980; Kelso, Holt, Rubin, & Kugler, 1981; Kelso, Tuller, & Harris, 1983) are stability (in the face of unforeseen perturbations), persistence (as a rhythmical pattern), mutual entrainment (between like and different anatomical structures), and capability of exhibiting new modal forms (see the following section). Our perspective interfaces nicely with earlier (e.g., von Holst, 1937/1973) and newly emerging oscillator theoretic views of neural control (cf. Delcomyn, 1980; Gallistel, 1980; Grillner, 1977; Stein, 1977), although it differs in important and nontrivial ways. The attributes we have articulated here arise not necessarily because of special biological mechanisms (like central programs), but because living systems belong to a particular class of open, physical system.

Currently, dominant model constructs for movement control stress the reflex arc and the servomechanism as basic building blocks. The reflex arc is composed of effector, conductor, and initiator elements (Gallistel, 1980). Modern servocontrol theory keeps the effector (output) and the initiator (input as referent level) and adds additional processes such as feedback, comparison, and error correction. But in the present view, machine concepts having to do with adaptive controllers, feedback, and programs are not likely to be useful to our accounts of the order and regularity displayed by biological systems (cf. Kelso, 1981; Kugler *et al.*, 1982, for more detailed arguments). Living things, as Yates (1982) cogently remarked, "are not hard-wired, hard-programmed, hard-geared, or hard-molded. They persist, as ill-defined systems, marginally stable in a nonlinear sense (while being linearly unstable)." As dynamical systems with active, interacting components and large numbers of degrees of freedom, they are capable of spontaneous organization and evolution of function.

Up to now, we have been concerned with those principles that guarantee structurally stable modes of coordination in the face of quantitative variation in control parameters. Now we address the other side of the coin: How do new forms of spatiotemporal organization come about? How do old "kinetic forms" give way to new ones?[7] We first consider some examples in nature that may allow us to intuit an answer (cf. Haken, 1977; Katchalsky *et al.*, 1974; Kugler *et al.*, 1982, for more details); then, we consider some specific examples that are continuous with our earlier discussion

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[7] The sentiment here follows that of the great Canadian ice-skating champion Toller Cranston, who in a television interview (NBC, January 31, 1982) remarked that he has always considered his work to be artistic "fundamentally as kinetic form." Of course the science of form continues to be a hotly pursued area of study (e.g., Gould, 1971; Rosen, 1978; Thompson, 1917/1942).

of oscillatory systems, and that are based on our own and others' movement research. A fundamental feature of all these examples is that qualitatively new modes of organization emerge when certain parameters are scaled past critical bounds. Importantly, these new modal behaviors may reduce the requirement for *a priori* programs in the sense of a prescription for a phenomenon existing before the phenomenon appears.

Dynamics of Natural Systems

We are concerned here—as we have been all along—with systems of many degrees of freedom that somehow cooperate with each other to produce regular and orderly behavior (at a macroscopic level). Cooperative phenomena are well known in physical systems and have provided a basis for many technical applications. Common to all of these (e.g., the laser, tunnel diodes, and ferromagnetism) is a transition from a disordered state to a more highly ordered one. Unlike, say, semiconductors, which achieve ordered states when temperature is lowered toward equilibrium, systems such as the laser undergo phase transitions only when they are driven far from equilibrium; they are dissipative or synergetic structures by virtue of degrading a good deal of free energy (cf. Haken, 1977; Katchalsky *et al.*, 1974; Prigogine, 1980; see Kelso, Holt, Kugler, & Turvey, 1980, and Kugler *et al.*, 1980, 1982, for empirical and theoretical treatment of a dissipative structure perspective on action). Although it is a minor point, elsewhere (after Katchalsky *et al.*, 1974), we have preferred the term *dynamic pattern* to *dissipative structure* because it removes any ambiguity between classical notions of the term structure and Prigogine and colleagues' dissipative structure (Kelso *et al.*, 1983). Both terms, however, are synonymous and refer to a functional or dynamic organization.

Physical Examples of Emergent Modes

Several examples will allow us to demarcate the main features of dynamic patterns and the conditions under which they arise. Some of these attributes have been considered already in the previous section. These examples are necessarily sketchy from a mathematical point of view, but they allow us to convey a flavor of the approach.

Consider the simple example of turning on a faucet. At low levels of water pressure (flow through the nozzle), the flow of water is nonturbulent, or laminar. Although laminar flow seems well ordered, in fact the movement of water molecules follows a random statistical law. As the tap is opened more and water pressure is increased, the flow may no longer be laminar in appearance. In fact, at a *critical point* of pressure, water takes on a turbulent or "muscular" appearance (in accord with the theme of this chapter) in which molecules now display coherence in the form of powerful streams. If the tap is opened still more, other abrupt changes—vortices and the like—are possible. The theme that emerges here is that the continuum of atomisms (laminar flow) becomes unstable and, at a point at which inertial forces greatly predominate over viscous ones (characterized by a dimensionless ratio called a *Reynolds number*), gives rise to a new stability (observed as turbulence).

The *convection instability* of Bénard allows us to secure these ideas more firmly. When a fluid layer (such as spermaceti oil) is placed in a large pan, heated uniformly from below, and kept at a fixed temperature from above, initially—if the temperature gradient is small—the fluid remains quiescent. In this case, heat spreads through the fluid by heat conduction, a process in which molecules undergo thermal vibrations and transfer a part of their thermal energy in collisions without, on the average, changing their positions. As the temperature gradient is increased, a state of thermal nonequilibrium is reached and convection occurs. At the beginning, small convection streams (macroscopic motions) are suppressed, but as the temperature gradient is increased to a critical value, fluctuations are amplified and macroscopic motions occur. These take the form of rolls or hexagons, depending on boundary conditions (cf. Kochsmeider, 1977). The new ordered states are themselves open to increased structuralization because at higher values of the temperature gradient, further patterns (such as oscillatory "spokes") are possible. Fluctuations play a vital role because without them, higher-order states cannot evolve. Moreover, the nature of the fluctuations themselves significantly affects the new order that is established (e.g., polygons or hexagons; cf. Kochsmeider, 1977 for many more details of a much more complicated story than that relayed here). One interesting aside about the Bénard effect that is relevant to our earlier discussions of equifinality in the motor system and to dynamic patterns in general is that given patterns need not relate to a unique mechanism; conversely, different mechanisms may generate a common pattern (cf. Katchalsky *et al.*, 1974). Thus, biological systems are not unique in displaying convergence (many-to-one mappings) and divergence (one-to-many mappings) (see the concluding section).

Summary 1

There are several lessons to be learned from the foregoing examples in physical systems before we consider matters of biology. First is the notion mentioned earlier, that systems at many scales of magnitude exhibit transitions from one state to another that are discontinuous even though the factors controlling the process change continuously. Second, and relatedly, transitions from one mode to another are discontinuous, not because there are no possible intervening states but because none of them is *stable*. Thus, the transition from one state to another is likely to be brief compared with the time spent in stable states. Third, and in the Poincaré–Thom tradition, for new modes to appear, all that need change mathematically is the qualitative shape of the potential curve that occurs only when an equilibrium condition is created or destroyed. A consequent implication is that there may be a relatively large number of ways for a system to exhibit *continuous* change, but only a relatively smaller number of ways for it to change *discontinuously*. We associate the discontinuities with nonlinear properties that are revealed when the system is scaled (putatively a continuous process) to some critical value.

Biological Examples of Emergent Modes

Let us see how the foregoing style of inquiry is relevant to matters of greater interest to the motor physiologist and the cognitive psychologist. Consider first the forms of gait that an animal might display and the causal basis for transitions among gaits. Relatively little is known about locomotory patterns or the transitions among them. It is tempting, however, to assume that a given gait is governed by a central program (or in noncomputer jargon, a central pattern generator) that prescribes the kinematic details for cyclical flexion and extension of limbs. Switching among gaits could be accounted for by assigning a "gait selection process" to the animal (cf. Gallistel, 1980). There are good reasons to be skeptical of such a view, which ranks in the "just so" category. A primary one stems from a remarkable experiment by von Holst (1937/1973), in which he amputated the legs of a centipede *(Lithobius)*, leaving only three pairs of legs intact (see also von Buddenbrock, 1921, for a similar but less drastic manipulation). Regardless of how large an anatomical gap was left between the remaining legs (up to five segments), the centipede (which normally walks with adjacent legs about one-seventh out of phase) assumed the gait of a six-legged insect. Furthermore, the asymmetric gaits of the quadruped were displayed when all but two pairs of legs were amputated. Von Holst (1937/1973) used these experiments to argue against "any fixed reflex locomotor relationship between the legs"—but the message surely applies equally to central pattern generators. It is facetious to suggest that the animal stored all possible representations of locomotory patterns in anticipation that some innovative experimenter (or small boy) might perform an amputation! It seems more likely—and a route for the scientist to explore—that the design of the animal places considerable constraints on which locomotory states are dynamically stable in the equilibrium sense and which are not.

What, then, of gait transitions? In the case of the quadruped, it is well established that there are only a few modes of locomotion. At low speeds, the common mode is one of asymmetry between limbs of the same girdle characterized by a half-period (180-deg) difference in phase. At higher speeds, the limbs of the front and rear girdle shift—in a fairly abrupt way—to an in-phase symmetrical mode. How might the gait transition be interpreted? A first clue comes from observations that horses (Hoyt & Taylor, 1981) and migrating African gnus (Pennycuick, 1975) use a restricted range of speeds within each gait that corresponds to minimum energy expenditure. In fact, for the horse, the minimum oxygen cost per unit distance is almost the same for walking, trotting, and galloping (cf. Hoyt & Taylor, 1981). As speed is increased, however, the locomotory mode (say, walking) becomes unstable; it becomes extremely costly to maintain that mode at a given rate. The walking mode becomes unstable, as it were, and "breaks" into a trotting mode. Similarly, it is energetically expensive to maintain a trotting mode at slow locomotory speeds, a fact that appears to dictate a switch into the walking mode. The discontinuous nature of these transitions suggests—like some of the physical examples earlier—that when a critical value is reached, the system bifurcates, revealing a qualitative change in its topological structure. More generally, the different gaits may be interpreted as those few stable modes that can arise as a consequence of scaling up on muscle power (see also Kugler, Kelso, &

Turvey, 1980, for more on topological approaches). *The stable range of speed for each modal gait corresponds to regions of minimum energy dissipation*. It should be emphasized that there is a good deal of overlap between the locomotory modes (see Hoyt & Taylor, 1981, Figure 2) and that the account given here is not that locomotory modes are hard-wired and deterministic. Horses can trot at speeds at which they normally gallop, but it is metabolically expensive to do so.

The account of gait shifts in terms of nonequilibrium dynamics would be enhanced if qualitatively similar types of phenomena were observed in other types of activities—activities perhaps of a less stereotypical kind.[8] In our final examples, we discuss voluntary manual activities and speech. Consider an experiment (reported briefly in Kelso, 1981) in which a subject is asked to cycle the hands at the wrist using asymmetrical muscle groups. Thus, direction of movement is the same for each hand; flexion (extension) of one is accompanied by extension (flexion) of the other. The only instruction to the subject is to increase rate of cycling—provided either verbally (at approximately 15-sec intervals) or by a pulsing metronome. An example of the data is given in Figure 1, which plots the displacement-time profile of the hands singly (top half) and against each other (bottom half). It can be seen that the hands shift from an out-of-phase pattern (asymmetrical muscles) to an in-phase pattern between points H and T. The shift is evident in the Lissajous figure below, where it can be seen that within a cycle, the hands "kick" into a different mode. The same data are shown in Figure 2, except that it is easier to see what is going on as one steps through the data file shown on the upper left of the figure. It can be seen that the phase relations between the hands are very stable in Figures 2A and 2B. Were the two motions perfectly sinusoidal with phase π, a straight line would be observed. In Figure 2C, the phase difference between the two hands has undergone a modest increase and has also become more variable, as evident in the widening of the Lissajous trajectories. However, it is also clear that a fairly abrupt change of phase occurs; descriptively, the left hand "slips in" an extra half-cycle while the right hand waits, and then both perform synchronously (symmetrical muscle groups). Figure 3 represents the same data on the phase plane in which position is plotted against the velocity for each hand. It can be seen in the center portion of the figure that the two hands start out in different quadrants of the phase plane but end up in the same quadrant (with approximately the same position–velocity coordinates for each hand; see figure caption for full description).

Although this example warrants more detailed analysis than that given here, it is nevertheless quite clear that a similar qualitative picture emerges for voluntary hand movements as for the gait transitions discussed earlier. That is, a qualitatively new modal pattern emerges as a function of continuously scaling on a single parameter (in this case, rate). The change in phase occurs relatively quickly compared with the time spent in the modes themselves—often within a single cycle. Importantly, these data suggest rather strongly that the new mode is *revealed* by scaling on a system-sensitive

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[8] We balk, of course, at the fairly common description (at least among some psychologists) of locomotion as stereotypical and low-level. Many of the examples we have given in this paper attest to the generativity and context sensitivity of actions, and locomotion is a prime example. We are still at the tip of the iceberg as far as understanding these attributes is concerned—in locomotion or any other "less stereotyped" activity.

parameter. It appears also that only two modes are stable; other phase relations—at least, in unpracticed subjects—appear highly unstable.

We turn now to a final example, one that offers a potentially rich but little-explored domain for the style of inquiry being advanced here. We refer to speech production and perception, and in doing so, we draw principally from the observations and discussions by Catford (1977) and Stevens (1972, 1977).

Speech, of course, is a complex process arising from the interactions among articulators at several levels—respiratory, laryngeal, and supralaryngeal. A good deal of effort has been directed toward the identification of distinctive acoustic attributes

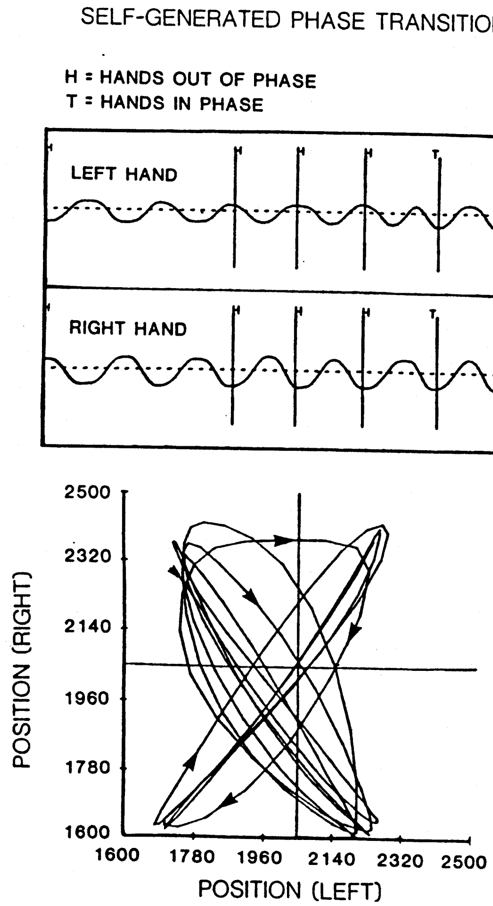

Figure 1. *Displacement-time profiles of left and right hands (top) and position of each plotted against each other (bottom) as a Lissajous figure. "Hands out-of-phase" means that flexion of one hand is accompanied by extension of the other, and vice versa. That is, direction of movement is the same for each hand (ignore plotting convention). "Hands in phase" means that both hands flex and extend at about the same time. The figure shows a shift from out-of-phase to in-phase as rate increases (that is, as one examines the data file from left to right).*

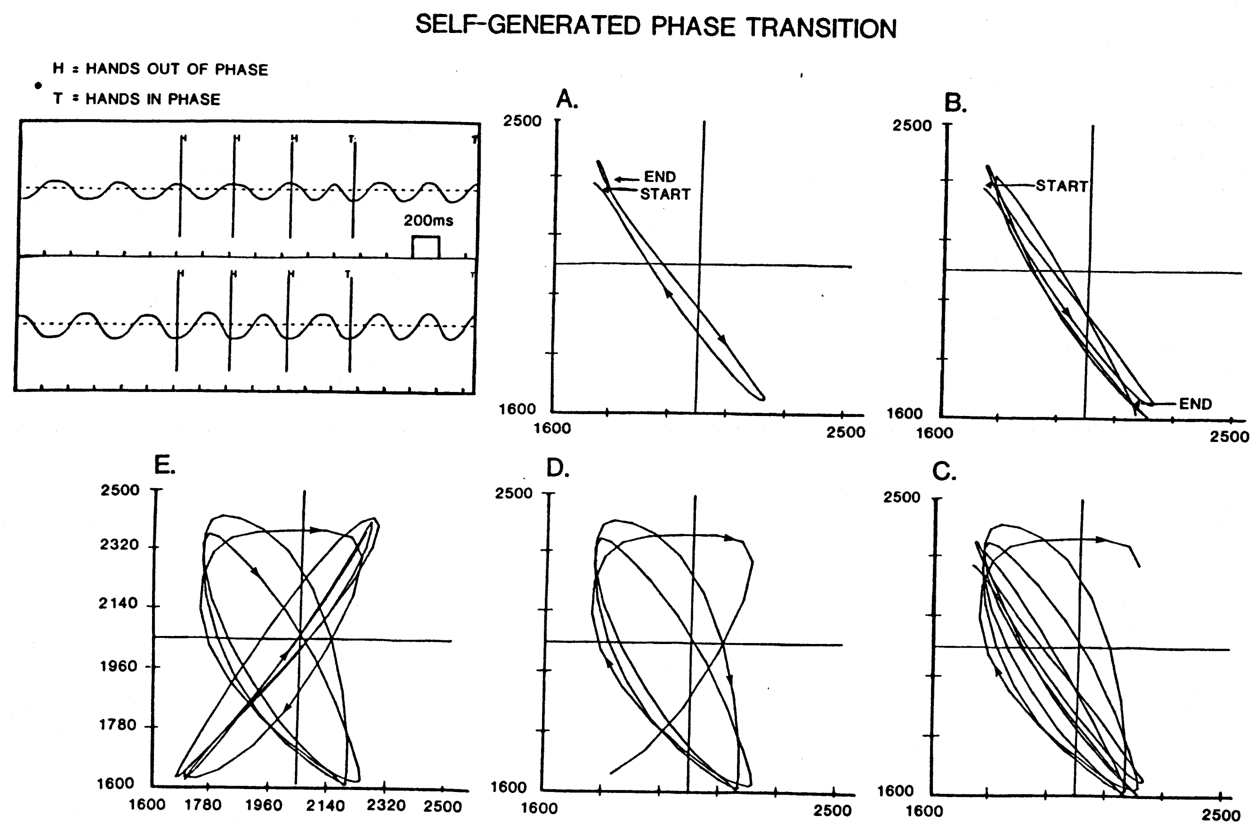

Figure 2. *Same data as displayed in Figure 1, but Lissajous figure of left versus right hand is plotted as one steps through the data file (A–E). For description see text.*

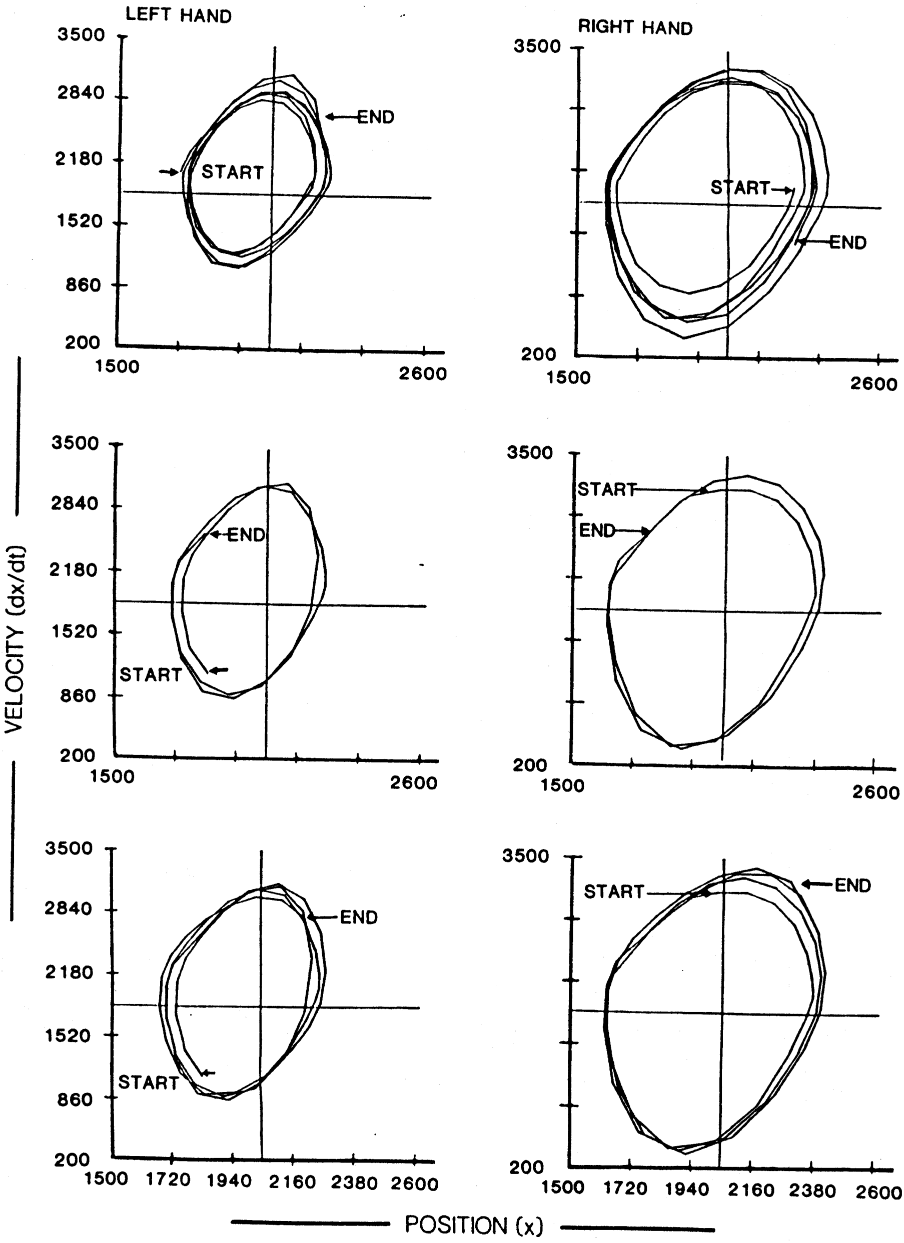

Figure 3. *Same data as displayed in Figures 1 and 2, but plotted as phase plane trajectories for left and right hands. Position and velocity are expressed as arbitrary units. The top third shows the phase plane trajectories of the two hands prior to a phase transition. The hands start and end in different quadrants of the plane. The middle third shows the transition itself with the trajectories sampled over the same time window. It is clear that the left hand produces an extra half cycle so that the hands end up in phase. The bottom third of the figure overlaps with the middle third and proceeds to the end of the file.*

as they may underlie the phonetic categories described by linguists (e.g., Chomsky & Halle, 1968; Halle & Stevens, 1971; Stevens, 1972; Stevens & Blumstein, 1978). For us, however, the acoustic attributes are of interest only to the extent that they shed light on the articulatory dynamics that produce them. It is important to recognize immediately, however, that the postures and movements of the articulators structure the sound but do not themselves generate sounds. To return to a recurring theme, articulatory configurations create the *necessary aerodynamic conditions,* as a consequence of which sound generation is possible. In this regard, our earlier discussion of turbulence as a highly ordered space–time phenomenon is appropriate: the presence or absence of turbulence in the vocal tract plays a significant role in the production of speech sounds such as fricatives. Below a certain critical velocity, airflow through an articulatory channel, such as an open glottis, is laminar and noiseless (so-called nil phonation, cf. Catford, 1977), as in the phonation of [f, s, ʃ]. Above a critical value, turbulent, noisy flow occurs, as in the phonation of stressed initial voiceless sounds [p^h, t^h, k^h].

The Reynolds number, it will be recalled, depends on the diameter of the channel (more generally, the various forms of constriction in the vocal tract), the velocity of flow, and the viscosity of air: it is the ratio of inertial to viscous forces. Beyond a certain value of the ratio, two types of turbulence arise: one, a more general type of *channel* turbulence (discussed above) and the other a vortex-producing *wake* turbulence. Wake turbulence occurs when a high-velocity jet of air is produced against the edges of the upper and lower teeth, for example, in production of /s/ or /ʃ/ as in *sip* or *ship*, respectively. Wake turbulence also plays a role in various laryngeal modes, such as voiceless falsetto (or so-called glottal whistle), which appears to be due in part to periodic vortex formation that develops past the thinned edges of the vocal folds (cf. Catford, 1977).

The nonlinear distinctive effects of turbulence are only one aspect of what may be a larger design principle, one in which gradual, linear changes in certain variables can lead to discontinuous, distinctive outcomes. Continuous adjustments of the vocal folds (e.g., in terms of their positioning in relation to each other, effective mass, and stiffness) also give rise to distinct modes that occur as discontinuous jumps. Like the gaits of the quadruped, there seem to be relatively few stable modes. *Whisper,* for example, occurs at a much smaller critical flow velocity than the production of voiceless fricatives, as a consequence of much smaller glottal constriction. The *voicing* mode occurs when the vocal folds, in a suitably tensile state, form a narrow glottal chink, while the pressure drop across the glottis creates a Bernoulli effect. As a result, the vocal folds are set into vibration: they snap together and are forced open again by subglottal pressure, only to close once more because of their elastic properties and the Bernoulli effect (at least according to myoelastic-aerodynamic theory; see Titze, 1980, for a good review). If the vocal folds are further constricted, so-called creaky voice is evident (though not well understood), and then, when the folds are constricted to a point at which subglottal pressure can no longer drive them apart, the conditions for the production of glottal stops are created. Thus, we see in these examples of laryngeal function that from an apparent continuum of vocal fold maneuvers, a variety of modes arise. These dramatically different modes (and the story is actually much longer than we can tell here) are indicative of "preferred stabilities" (see the section on structural stability, as well as the earlier gait and hand movement examples), and the transitions among the modes can be characterized as unstable.

To bring this discussion into the realm of the speaker/hearer, if we know anything about speech it is that "the diverse, continuous and tangled sounds are . . . perceived as a scant handful of discrete and variously ordered segments" (Liberman, this volume). What befuddles the scientist is that there is no apparently direct relationship—in a linear sense—between the parameters responsible for structuring the sound (the articulatory system) and the acoustic output arising from the source. In certain cases, large changes in articulatory parameters have minimal acoustic consequences, as in Kakita and Fujimura's demonstrations that for the production of the vowel /i/ a wide variety of contractile values on the tongue muscles yield relatively invariant formant structure (Fujimura & Kakita, 1979; Kakita & Fujimura, 1977; see Kelso & Tuller, 1982, for a fuller discussion). In other cases, small changes in relevant observables, such as voice onset time (Lisker & Abramson, 1964), can result in one phonemic class being replaced by another. The former constitute *structurally stable* articulatory parameterizations; the latter refer to *unstable* regions (in the topologist Thom's terms, they belong to the catastrophe set; Thom, 1975).

The existence of these complex relations (apparently at every level of the speech system and probably the ear as well) may be a problem only for the scientist who seeks out one-to-one correspondences between particular acoustic "cues" and that which is perceived. It seems to us—if the parallels we have drawn among the various examples here are appropriate—that the issue is not really one of specifying acoustic attributes that map onto a linguistic featural description (e.g., Halle & Stevens, 1971; Stevens & Blumstein, 1978). As some phoneticians and motor control researchers have remarked, this is a particularly *Procrustean* strategy in that it forces the data into some preestablished linguistic categorization scheme. Rather, it seems to us that the perspective offered here dictates the fairly unexplored strategy of determining which articulatory parameterizations are structurally stable and which are not (and why). More generally, it is to understand those dynamical transformations among articulators that reveal, and ultimately "freeze out," as it were, the modes and phonetic segments of a language.

Summary 2 (with Due Homage to Haken, 1975, 1977)

In this section we have tried to provide a flavor for what we believe to be deep analogies among may different subsystems when they cooperate to produce coherent functions. Characteristic of all the examples is that new "modes" or spatiotemporal regularities emerge when the system is scaled on certain parameters to which it is sensitive. (As an aside, if this view is viable, we suspect a good deal of work will have to be devoted to identifying what these parameters are—an enterprise that is closely affiliated with the ecological approach to perception and action advocated by Gibson, 1966, 1979, and his school: Shaw & Turvey, 1981; Turvey & Shaw, 1979; Turvey, Shaw, & Mace, 1978.) In the various cases we have described, the initial modal pattern becomes unstable, and it is this instability that is a prerequisite for the emergence of new modes. The "mode" is a concept for the collective behavior of many degrees of freedom; it is characterized by a macroscopic description that is not known at a more microscopic level (see also the section on coordinative structures as dynamic linkages). Thus, an oscillating string made up of 10^{22} atoms is described by "macro" quantities like wavelength and amplitude that are entirely different from the description at an atomistic level (Haken, 1977). Similarly, the relevant observables for coordinative structures (and, we would argue, for the control and coordination of movement) are *relational* in time and space; they have little to do with descriptions of the firing properties of motor units.

Unlike machines that are designed by people to exhibit special structures and functions, the functions and structures discussed here develop, as it were, spontaneously: they are self-organizing. Importantly, during the scaling-up process there is no *a priori* specification or representation of the new structure (Kelso, 1981; Kugler *et al.*, 1980). In fact, a new mode often emerges when a random event occurs in an unstable region, when a fluctuation becomes amplified. Such is the case, one suspects, in the gait of a horse (and perhaps the singer at a particular point in the voice range—close to the *passagio;* see Teaney, 1982). Near the unstable region—where it is energetically costly to maintain a given mode—a small change in, say, walking speed, has dramatic effects, and a new mode will arise. Literally, a phase transition occurs.

When we see new forms of organization occur, we are addressing systems possessing many degrees of freedom that are intrinsically nonlinear and dissipative; systems that operate in "preferred" regions of their state space; systems that are structurally stable on the one hand, and capable of a fair degree of flexibility on the other. In short, they are systems in which variance plays on invariance. The bottom line for systems that display so-called critical behavior is that the same fundamental principles pertain regardless of the dimensionality of the system or its material structure, and that these principles are the ones that a theory of action might embrace to account for the emergence of new forms of space–time patterns displayed by the cooperative behavior of muscles and joints. The alternative—when push comes to shove—is a hermeneutic device that prescribes new orderings. If nothing else, the approach offered here promises to try to reduce Hermes' role to a minimum.

Conclusions: Integrating Principles of Higher Brain Function and Principles of Motor System Function

Our discussion of units of action as displaying limit cycle behavior with all their attractive features, as well as our focus on spontaneously organizing systems with their inherent nonlinear, multimodal properties, offers potentially exciting possibilities for a deeper understanding of movement coordination and control. These discussions represent a new and perhaps speculative development of action system's theory, and they lead to new research directions (What are the modes of the action system and their stabilities? How limited are they? What conditions give rise to stability and instability? Can transitional behavior be classified? etc.). In seating action systems in physical biology, there is the promise of adequate theory. What constitutes a "new direction" or an "interesting research problem" is obviously a matter of choice. All we have done here is to make our biases apparent.

In our concluding remarks, we want to end on a "tamer" note by bringing some of the ideas expressed here (mostly in the first section) into the more standard nomenclature and conventions of neuroscience. Our vehicle is a comparison of some of the principles we have elaborated in this chapter (which, as we have intimated, have a long-standing heritage) with some recently developed views of higher brain function (Edelman & Mountcastle, 1978). Although we cannot go into any great detail at this point, we will try to show by way of summary (see Table 1) that many of the kernel ideas in Edelman's "group theory" of higher brain function have been in the motor system's literature for some time (cf. Edelman, 1978). Our view all along has been that nature operates with ancient themes, and in Edelman's compendium, combined with certain notions expressed here, we see some consensus emerging on what these themes might be. We are encouraged to elaborate these themes in part because of an awareness that several noted neuroscientists have become disenchanted with the reductionist paradigm (e.g., Bullock, 1980; Schmitt, 1978; Selverston, 1980). In the past, it has been commonplace for the neuroscientist to talk of neural circuits controlling behavior, but even in the simplest networks (and we use the term *simple* guardedly here; see below), it has proved difficult to relate specific patterns of neural activity to behavioral action. Surely there is a message here: if the strategy is deemed questionable for small circuits in terms of the number of ganglia involved—and there is informed consensus that this is the case (see commentary on Selverston, 1980)—then what hope is there for understanding a brain complex of 15 billion elements?[9] Even if we knew all the parts and their properties, we would still not know how the system operated. As Schmitt (1978) remarked,

> Many theories of higher brain function have been proposed. . . . These theories usually rely heavily upon processes subserved by spike action potential waves travelling in hard-

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[9] Sometimes *number* is sufficient to indicate the degree of complexity, and we take the modularity idea of brain design to be—in part—an effort to come to grips with the problem of dealing with individual neuronal elements. But to put it mildly, number is only a small aspect of complexity. Lest we think otherwise, consider the following list of factors, all of which are part of the domain of neuroscience:

1. Aside from elementary particle physics, neuroscience deals with the molecular and ionic events in cells, aspects of which are the mechanisms of molecular excitability and ion selectivity. The latter involves understanding—among other things—mechanisms of ionic pumps, release and binding of neurotransmitters, growth of neurons, structure of membranes, and conductance properties of membrane channels.
2. Neuroscience attempts to analyze membrane circuitry and the geometry of cell membranes (little is known about the detailed anatomy of the cell being recorded from in physiological studies or the distribution and type of conductance channels in cell membranes; cf. Pinsker & Willis, 1980).
3. The response properties of cells have been the staple diet of neuroscience. These vary on many different dimensions, including threshold, latency, firing rate, tonic versus phasic, brisk versus sluggish, receptive field, refractory period, filter properties, transfer functions,etc.

The list we have provided here refers only to events at the cellular level, but it is enough to illustrate our point, namely, that the number of elements is only one—and perhaps not the major—dimension of complexity.

Table 1. *Some Predictions of Motor Control Metatheory Compared with Some Predictions of Edelman's Group-Degenerate*[a] *Theory of Higher Brain Function*[b]

1. "Groups of cells, not single cells are the main units of selection in higher brain function." (p. 92)	Ensembles of muscles and joints—called *coordinative structures* or *functional synergies*—not single muscles or joints are the significant units of control and coordination of action.
2. "Such cell groups will be found to be multiply represented, degenerate[a] and isofunctionally overlapping. Many-one interactions . . . will be found, with extensive divergence as a sign of degeneracy. At the same time, multiple inputs . . . will be found to converge on the same cell group leading to abstract cell-group codes."[b] (p. 93)	Motor equivalence/equifinality is a property of action systems. The same output can be achieved using different muscle ensembles, and different outputs can be accomplished using the same muscle ensembles. One to many (divergence, degeneracy) and many to one (convergence, abstraction) are common features of multidegree of freedom systems (see 4 below).
3. "No pontifical neuron, or single-neuron 'decision unit' will ever be found at the highest levels of a system of any large degree of plasticity." (p. 93)	Action systems work most efficiently under assumptions of executive ignorance and addressless, distributed control—a minimally intelligent executive intervening minimally.
4. "Selection will be found to play a large, but not inclusive role in forming a first repertoire during embryogenesis . . . no sizeable, precommitted molecular repertoire will be found to explain cell-cell interaction in the developing nervous system." (p. 93)	Certain so-called fundamental patterns of movement may constitute a first repertoire for action systems. But fixed actions at a joint, preassembled reflexes, or central pattern generators (programs) are not the principal bases of action systems. The latter are differentiated by their *functional* significance, not by their anatomical specificity.
5. "Correlations will be found that suggest phased reentrant signaling on degenerate neuronal groups with periods of 50–200 msec." (p. 93)	The behavior of muscle–joint ensembles or coordinative structures expresses a design that is fundamentally cyclical in nature, as a consequence of which persistence of function, stability, autonomy, entrainment, and emergence of function (e.g., modal changes) are possible.

Note: According to Edelman (1978), "the selective theory of higher brain function requires no special thermodynamic assumptions and is free of mentalistic notions" (p. 94). We welcome this assertion but stress that the units of action must be motivated on the grounds of (irreversible) thermodynamics (see prediction 5). Indeed, any unit of brain function (like any unit of action) must be defined not only in terms of its neural structures but also the metabolic machinery that supplies energy and removes by-products. Many of the attractive attributes of action systems elaborated here follow from a dynamic, homeokinetic scheme in which the many degrees of freedom are regulated by means of coupled ensembles of limit cycle, thermodynamic engines (Iberall, 1978a,b). It is this basic characterization, with appropriate extensions, that may allow us, in Edelman's terms, to "avoid an infinite regression of hierarchical states . . . to provide for planning and motor output without a programmer . . . [to] mitigate the need for programming" (p. 94). That has been—and continues to be—the goal of so-called action theory (e.g., Fowler *et al.*, 1980; Kugler *et al.*, 1980; Kelso *et al.*, 1980; Reed, 1982). Although there are obvious differences between group theory and action theory, this shared aim is not one of them.

[a] Roughly, *degeneracy* refers to the capability of different structures or elements to perform similar functions.

[b] Page numbers refer to Edelman, 1978. We have made no attempt to provide all the details of Edelman's theory. We represent here only "the main predictions" (Edelman, 1978, pp. 92–93) because of their striking parallels, evolved independently, with principles synthesized from the movement literature and complex, multivariable systems in general. We should also stress that the list of movement principles presented in the table is far from complete and that we view cooperative phenomena—of neurons, muscles, or whatever—in a much larger context.

> wired circuits. . . . Such circuits usually consist of neurons that are large enough to permit easy impalement by microelectrodes and that possess long axons forming tracts connecting processing centers in general regions of the brain that have been characterized as sensory, motor, associational, frontal, temporal, parietal, and occipital.
>
> Theories based on partial systems are subject to the component-systems dilemma that bedevils all attempts at biological generalization. Such theories fail to articulate and effectively deal with the essence of the problem, which is the distributive aspect that emerges from the complex interaction of functional units . . . in the brain. (p. 1)

Although it is clear that much still remains to be known about the parts—and we may have to wait for technology for much of this—it is equally clear that the behavior of large and complex aggregates cannot be understood in terms of extrapolations from so-called simple circuits. As we remarked earlier in this paper, constructionism breaks down in the face of scale and complexity. At each level of complexity, novel properties appear whose behavior cannot be predicted from knowledge of component processes alone. This is why the form of reductionism that we have taken here—advocated in contemporary physics and an emerging physical biology—is a reductionism to a minimum, but universal set of principles, rather than to elemental properties. This is why we see an interesting link between Edelman's theory and those ideas that have over the years emerged in the area of motor systems. In this chapter, we have tried to reveal the rich heritage involved in the movement domain—stemming from the Bernstein tradition—as well as the important syntheses by people like Greene, Boylls, Turvey, and others. Only in the search for common principles can we see a true integration of very disparate disciplines—a true science of natural systems.

Throughout this paper, we have remarked on the qualitative likeness—in terms of dynamical behavior—exhibited by complex, dissipative systems in spite of dramatic variations in material composition and the scale at which they are observed. Given this state of affairs, the overlap between some of the main postulates of Edelman's theory (but not all of them) and those expressed here is hardly surprising—at least to us. Thus, the principles relate to the behavior of complex systems and cooperative phenomena rather than to any particular structural embodiment. It is understanding coherent behavior that takes precedence here, not whether that coherent behavior is of ensembles of neurons, or muscles, or anything else.

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