To appear in: H. Haken (Ed.) <u>Synergetics of Complex Systems in Physics, Chemistry and Biology</u>, Springer-Verlag.

Cooperative Phenomena in Biological Motion*

J. A. S. Kelso and J. P. Scholz
Haskins Laboratories, New Haven, Connecticut, 06511, USA

1 Introduction

The production of a "simple" utterance, such as the syllable /ba/, involves the cooperation of a large number of neuromuscular elements operating on different time scales, e.g., at respiratory, laryngeal, and supralaryngeal levels. Yet somehow, from this huge dimensionality, /ba/ emerges as a coherent and well-formed pattern. Similarly, were one to count the neurons, muscles, and joints that co-operate to produce the "simple" act of walking, literally thousands of degrees of freedom would be involved. Yet again, somehow walking emerges as a fundamentally low-dimensional cyclical pattern--in the language of dynamical systems, a periodic attractor. In physics, an infinite dimensional system, described by a complicated set of partial, nonlinear differential equations can be reduced--when probed experimentally or analyzed theoretically--to a low-dimensional description [1,2]. In all these cases, it seems, information about the system is compressed--from a microscopic basis of huge dimensionality--to a macroscopic basis of low dimensionality.

Our particular interest is how such compression occurs in the multidegree of freedom actions of people and animals. How does an internally complex system "simulate" a simpler, lower dimensional system? As we shall see, an important feature of our efforts to understand the control and coordination of movement is the concept of <u>order</u> <u>parameter</u> [3,4, see also 5]. Order parameters define the col-

lective behavior of the system's many components in terms of its essential variables alone; they are few in number even in very complicated physical and chemical systems. Note how the emphasis on discovering order parameters takes us away from a focus on individual elements (regardless of the level at which these elements are described): Just as the motion of a single molecule is not relevant to the essential description of the behavior of a gas, so too, one suspects, the action of a single reflex is not relevant to the essential description of an organism's behavior.

Our focus here is on the spatiotemporal patterns formed by the <u>ensemble</u> activity of neurons, muscles, and joints during the performance of a coordinated act. As WEISSKOPF [6] emphasizes in a different context, such problems rest with defining relations between different aggregates of atoms or molecules, and of the modes of transition from one structure to another. The abstraction of a system's order parameters is thus of paramount importance, because it allows one to separate the essential from the non-essential, thereby enabling a complex phenomenon to become more transparent. This "macroscopic" strategy is brought to bear here on our efforts to discover the principles underlying the control and coordination of movements. In the following we first summarize briefly evidence for the existence of unitary processes in complex actions and denote some of the characteristic properties of such units. From such analysis, the phase relation among the motions of skeleto-muscular components will emerge as a candidate order parameter. We then contrast various theoretical notions about pattern generation in movement and introduce some recent evidence in favor of a synergetic approach. Synergetics motivates the treatment of complicated biological motion as fundamentally a cooperative phenomenon. In support of this view, certain kinds of activities will be shown to display the features of a nonequilibrium phase transition.

2 <u>A</u> <u>Unitary</u> <u>Process</u> (Coordinative Structure)

For the Soviet physiologist BERNSTEIN [7], the existence of a large number of potential degrees of freedom in the motor system precluded the possibility that each was controlled individually at every point in time. Rather, he hypothesized that the central nervous system (CNS) "collects" multiple degrees of freedom into functional units that then

behave, from the perspective of control, as a single degree of freedom. During a movement, the internal degrees of freedom are not controlled directly, but constrained to relate among themselves in a relatively fixed and autonomous fashion. But is it, in fact, the case that in coordinated actions, the many neuromuscular components actually function as a single degree of freedom?

Support for the hypothesis that a group of relatively independent muscles and joints forms a single functional unit would be obtained if it were shown that a challenge or perturbation to one or more members of the group was, during the course of activity, responded to by other remote (non-mechanically linked) members of the group. We have recently found that speech articulators (lips, tongue, jaw) produce functionally specific, near-immediate compensation to unexpected perturbation, on the first occurrence, at sites remote from the locus of perturbation [8]. The responses observed were specific to the actual speech act being performed: for example, when the jaw was suddenly perturbed while saying the syllable /bæb/, the lips compensated so as to produce the final /b/, but no compensation was seen in the tongue. Conversely, the same perturbation applied during the utterance /bæz/ evoked rapid and increased tongue muscle activity (so that the appropriate tongue-palate configuration for a fricative sound was achieved) but no active lip compensation.

Recent work has also varied the phase of the jaw perturbation during bilabial consonant production. Remote reactions in the upper lip were observed only when the jaw was perturbed during the closing phase of the motion, that is, when the reactions were necessary to preserve the identity of the spoken utterance. Thus the form of cooperation observed is not rigid or "hard wired": the unitary process is flexibly assembled to perform specific functions (for additional evidence in other activities, see [8]). Elsewhere we have drawn parallels between these findings and brain function in general [5]. Just as groups of cells, not single cells are the main units of selection in higher brain function [9], so too task-specific ensembles of neuromuscular elements appear to be the significant units of control and coordination of action.

Stunning evidence attesting to this self-organizational style of neural and behavioral function comes from recent microelectrode studies of somatosensory cortex in adult squirrel and owl monkeys by MERZENICH and colleagues (see [10] for review): when the middle finger of the monkey's hand was surgically removed, brain regions representing the other adjacent fingers progressively shifted (over the course of a few weeks) into the missing finger's hitherto exclusive brain region. Also, if a portion of cerebral cortex was injured, the appropriate somatosensory "map" moved to the region surrounding it--a spatial shift of nerve cell activity as it were. These data challenge a view of neural functioning that is determined by "hard-wired" or "fixed" anatomic connections established before or shortly after birth. Just as we have observed rapid "soft" forms of compensation in speech production, so it seems, the brain has a functionally fluid, self-organizing character that allows longer-term compensation for injury.

3 Characteristic Properties Of A Unitary Process

A main way to uncover the intrinsic properties of a functional unit of action is to transform the unit as a whole (e.g., by scaling on movement rate; amplitude etc.) and search for what remains invariant across transformation. The discovery of such "relational invariants" (e.g., [11]) could provide a useful step toward explicating the design logic of the motor system.

Much evidence now exists from a wide variety of movement activities that relative timing among muscles and kinematic components is preserved across scalar changes in force or rate of production. For example, when a cat's speed of locomotion increases, the duration of the "step cycle" decreases [12,13] and an increase in activity is evident in the extensor muscles during the end of the support phase of the individual limb. Notably, this increase in muscle activity (and corresponding development of propulsive force) does not alter the relative timing among functionally linked extensor muscles, although the duration of their activity may change markedly (see [12,13] for reviews).

Interestingly, there is some limited evidence that this style of organization applies also to speech production. What makes a word a word in spite of differences among speakers, dialects, intonation patterns and so on? Our view is that the key to this question lies in understanding how the coordinated movements of the vocal tract articulators structure sound for a listener. According to this view, the invariance which allows us to perceive the sounds of a language in so many different contexts exists in the functionally-defined behavior of the articulatory system. But how is such behavior to be described? It is well-known, for instance, that the same word has markedly different kinematic, electromyographic, and acoustic attributes when produced in different contexts. A solution to this dilemma may lie in the finding by TULLER, KELSO, and HARRIS [15] that the relative timing of activity in various articulatory muscles is preserved across the very substantial metrical changes in duration and amplitude of muscle activity that occur when a speaker varies his/her speaking rate and stress pattern (for evidence in other motor skills see [14]). An important extension of these earlier EMG findings is the discovery that the relative timing of articulator movements is stable across different speaking rate and stress patterns. Presently, these results apply to the cooperative relations among lips, tongue, jaw and larynx (see [16] for review).

How is the relative timing invariant to be rationalized? A popular view is that time is metered out by a central motor program (see below) which instructs the articulators when to move, how far to move and for how long. A reconceptualization and consequent reanalysis of the TULLER and KELSO [16] data, however, strongly suggests that time, per se, is not directly controlled. Using phase plane techniques to represent the motions geometrically, we have shown that critical phase angles--relating one articulator's position-velocity $(x, \dot{x})$ state to another--appear to be most crucial for orchestrating the coordination among articulators [17,18]. The beauty of this gestural phase analysis (which is autonomous and does not require an explicit representation of time) is that it provides a topological description of articulatory behavior that remains unaltered across manifold speaker characteristics. Moreover, critical phase angles are revealed by the flow of the dynamics of the system, not externally defined. Thus, they

can serve as natural sources of information for guaranteeing the stability of coordination in the face of scalar (metrical) change (for more details, see [18]).

Finally, there is a strong hint that phase constancy reflects an evolutionary design principle. From the invertebrates, in which many groups employ large numbers of propulsive structures (limbs, tube feet, or cilia) for swimming and locomotion, to the vertebrates which walk, run or jump using one, two, three or four pairs of legs, the same design property is apparent, viz. all of these creatures possess processes that communicate information about the phase of activity among component structures [19,20]. Below we will develop in more detail the notion that phase is an essential parameter of complex, coordinated action. Suffice to emphasize at this point that a phase constancy indicates a functional constraint on movement, what we call a coordinative structure or unit of action (cf. [21,22,23,24]). Thus, during an activity the spatiotemporal behavior of individual components is constrained within a particular relationship. Flexibility can then be attained by adjusting control parameters over the entire unit.

4 Theories of Pattern Generation

The core idea expressed in Sections 2 and 3 above--that a system possessing a large number of potential degrees of freedom is compressed into a single functional unit of action (or coordinative structure) that requires few control decisions is unorthodox. It differs in significant ways from more conventional treatments of movement which are based on either the information processing notion of a motor program or the neurally-based notion of a central pattern generator. The motor program, by definition, is an internal representation of a movement pattern that is prestructured in advance of the movement itself. Analogous with a computer program, it constitutes a prescribed set of instructions to the skeletomuscular system. In MACKAY's [25] analysis of a dynamic activity, the locomotory step cycle, the many kinematic details are ordered a priori by a sequence of commands/instructions to the skeletomuscular apparatus whose role is to implement these instructions. The format of the program is that of a formal machine; sym-

bol strings are employed to achieve (or explain) the order and regularity of the step cycle. As in most programming accounts, the control prescription is highly detailed and the role dynamics play in fashioning the pattern is ignored. So also is the interface between the small-scale "informational" contents of the program and the large-scale, energetic requirements of the muscle- joint system. Finally, the contents of the program are not rationalized: a principled basis for selecting desired quantities (e.g., apply flexion torque for 100 ms) is omitted.

The neural counterpart of the motor program is the central pattern generator (CPG). Here too, the order and regularity observed in the world is attributed to a device inside the CNS (a neural circuit) that when activated coordinates the different muscles to produce movement [26]. Though subject to feedback influences, the circuit is "hard-wired" and the goal is to locate the neurons that constitute the network and to define their properties and interrelations. Though an admirable enterprise, there are questions about its propriety. For example, the parameter space of a CPG, e.g., the membrane properties of its elements, synaptic connections, etc. has been variously estimated to be 46 or 55 (compare [27] to [28]; also [29]). Presumably not all of these are necessary to understand a CPG, but principles beyond those of neurophysiology are surely needed to guide the selection of relevant parameters in such a high-dimensional space. As LOEB and MARKS [30] emphasize, principles of operation constitute the knowledge for understanding a CPG and these are disembodied from the actual device (or its model). In addition, even if all the details of a putative CPG were known, the problem of relating the known microproperties to characteristic macroproperties such as the amplitude, phase and frequency of a wing beat or a step cycle would still remain.

The question then is this: where do the necessary principles come from? For some years now, we have advocated an approach in which problems of biological motion are treated in a manner continuous with cooperative phenomena in other physical, chemical, and biological systems, i.e., as synergetic or dissipative structures [5,31,32]. Common features of the latter are that--like movement--they consist of very many subsystems. Unlike the theoretical approaches discussed above, however, where the emphasis is on

detailed prescriptions for control, in synergetics, when certain conditions (so-called "controls") are scaled up even in very non-specific ways, the system can develop new kinds of spatiotemporal patterns. The latter are maintained in a dynamic way by a continuous flux of energy (or matter) through the system [4]. Although there is pattern formation in the nonequilibrium phenomena treated by synergetics, e.g., the hexagonal forms produced in the Bénard convection instability, the transition from incoherent to coherent light waves in the laser, the oscillating waves of the Belousov-Zhabotinsky chemical reaction, etc., there are strictly speaking no pattern <u>generators</u>. That is, the emphasis is on the lawful basis, <u>including</u> the necessary and sufficient conditions, for pattern <u>formation</u> to occur. The explanation is derived from first <u>principles</u>: it <u>never</u> takes the form of introducing a special mechanism--like a motor program--that contains or represents the pattern before it appears.

5 <u>Phase</u> <u>Transitions</u> <u>in</u> <u>Biological</u> <u>Motion</u>

There are already strong hints in the motor system's literature that a highly detailed prescription from higher neural centers is not necessary to produce either a stable spatiotemporal pattern (say among the legs of a locomoting animal) or an abrupt change in ordering among the legs, as in locomotory gait changes. An early indication comes from remarkable experiments by VON HOLST [19] on the centipede <u>Lithobius</u>. By amputating leg pairs until only three such pairs were left, von Holst transformed the centipede's gait (a pattern in which adjacent legs are about one-seventh out of phase) into that of a six-legged insect. Further, when all but two pairs of legs were left, the asymmetric gaits of the quadruped were exhibited. It is hard to imagine that the nervous system of the centipede possessed stored programs or pattern generators for these gaits in anticipation of its legs being amputated by an innovative experimenter. Rather, given a novel configuration, the system appears to adopt spontaneously those modes of locomotion that are dynamically stable. Synergetics attempts to predict exactly which new (or different) modes will evolve in complex systems particularly when the system undergoes qualitative macroscopic changes [4].

More direct evidence that rather diffuse inputs ("controls") can lead to highly ordered behavior comes from Russian studies on (decerebrate) locomoting cats [33]. A steady increase in midbrain electrical stimulation was sufficient not only to induce changes in walking velocity, but also—at a critical stimulation level—abrupt gait changes as well. Interestingly, unstable regions were also noted in which the cat vacillated between trotting and galloping.

A final clue suggesting that gait transitions belong to the class of nonequilibrium phase transitions comes from work on the energetics of horse locomotion. It is well-known that animals use a restricted range of speeds (within a given gait) which corresponds to minimum energy expenditure. HOYT and TAYLOR [34], however, forced ponies to locomote away from these "equilibrium states" (see Fig. 1) by increasing the speed of a treadmill on which the ponies walked. As shown in Fig. 1, it becomes metabolically costly for the animal to maintain a given locomotory mode as velocity is scaled: For example, the walking mode becomes unstable, as it were, and "breaks" into a trotting mode (the next local minimum). Likewise, it is energetically expensive to maintain a trotting mode at slow velocities, a fact that appears to require switching into the walking mode (although no data on hysteresis are giv-
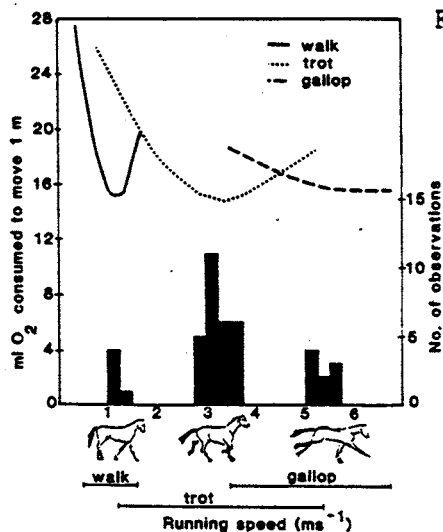

Fig. 1. Oxygen consumption and preferred speed of walk, trot and gallop of locomoting horses (See text for details). From HOYT and TAYLOR [34.]

en). As in many other systems treated by synergetics, when a critical value is reached, the system bifurcates and a new (or different) spatiotemporal ordering emerges. Note that in Fig. 1 these locomotory mode changes are not necessarily hard-wired or deterministic. Horses can trot at speeds at which they normally gallop, but it is metabolically costly to do so.

The notion that gait shifts correspond to instabilities that arise as the system is pushed away from equilibrium would be greatly enhanced if qualitatively similar phenomena were observed in other types of activities--perhaps even of a less stereotypical "innate" kind than locomotion. The remainder of this paper will be devoted to the elaboration of a phase transition that occurs in voluntary cyclical movements of the hands [11,35]. Below we will describe the phenomenon and illustrate briefly how it has been modeled using concepts of synergetics and the mathematical tools of nonlinear oscillator theory [36]. Finally, we will show that the phenomenon contains some of the principal features of other nonequilibrium phase transitions in nature. Interestingly, this synergetic account not only handles a variety of phenomena typically described by motor programs/CPG accounts, but generates new predictions that have not come to light from either of these theories.

6 Nonequilibrium Phase Transitions In Bimanual Action

6.1 The Basic Phenomenon [5,11,35]

Consider an experiment in which a human subject is asked to cycle his/her fingers or hands at a preferred frequency using an out-of-phase, antisymmetrical motion. Under instructions to increase cycling rate, it was observed that at a critical frequency the movements shifted abruptly to an in-phase, symmetrical mode involving simultaneous activation of homologous muscle groups. When the transition frequency was expressed in units of preferred frequency, the resulting dimensionless ratio or critical value was constant for all subjects, but one (who was not naive and who purposely resisted the transition--although with certain energetic consequences, see [35]). A frictional resistance to movement lowered both preferred and transition frequencies, but did not change the critical ratio (~1.33).

As an interesting aside, the ratio of transition speed to preferred speed for walk-trot and trot-gallop gait shifts, shown in Fig. 1, also gives a value ~1.32. This dimensionless number (analogous, perhaps to a Reynolds' number in hydrodynamics) may provide a rough estimate of "distance from equilibrium."

In summary, the main features of the bimanual experiments are: a) the presence of only two stable phase (or "attractor") states between the hands (see also [23,37], for further evidence); b) an abrupt transition from one attractor state to the other at a critical, intrinsically defined frequency; c) beyond the transition, only one mode (the symmetrical one) is observed; and d) when the driving frequency is reduced, the system does not return to its initially prepared state, i.e., it remains in the basin of attraction for the symmetrical mode.

6.2 Modeling [36]

In complex systems it is clearly hopeless to try to investigate the motion of each microscopic degree of freedom. Rather the challenge is to identify and then lawfully relate singular macroscopic quantities to the interactions among very many sub-components. Close to instability points, it can be shown that the the behavior of the whole system is determined by one or a few order parameters [3]. Such order parameters are not only created by the cooperation among the individual components of a complex system (e.g., by the interactions among atomic spins in a magnet), but in turn govern the behavior of those components (e.g., the magnetic field is an order parameter for a ferromagnet).

Identifying order parameters, even for physical and chemical systems, is not a trivial manner. Certain guidelines exist, however, which can be used for the selection of viable candidates. Two such selection criteria are: 1) the order parameter, by definition, changes much more slowly than the subsystems, i.e., its time constants are much longer than the time constants of the components; and 2) the order parameter's long term behavior changes qualitatively at the critical point.

In the case of our bimanual experiments and, we suspect, many other kinds of biological motion also, relative phase, ϕ, meets these criteria quite well (cf. Section 3.0). Using relative phase as an order parameter, HAKEN, KELSO, and BUNZ [36] modeled the bimanual data by specifying a potential function, V (corresponding to the layout of attractor states defined above) and showed how that function was deformed as a control parameter (corresponding to driving frequency) was changed. The choice of V--a superposition of two cosine functions--represented the simplest form that could describe the pattern of results. The series of potential fields generated for varying values of b/a (the ratio of the cosine coefficients) is shown in Fig. 2.
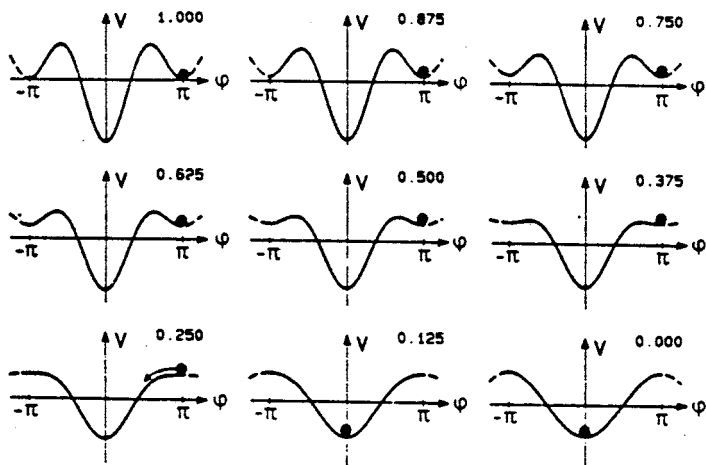

Fig. 2. The potential V/a for the varying values of b/a.
The numbers refer to the ratio b/a (from [36]).

It can be seen that at a critical value, ω_c, the system jumps into a local minimum, i.e., there is a transition from the anti-phase mode ($\phi = -\pi$) into the symmetric, in-phase mode, $\phi = 0$. Moreover, the system stays in that minimum even where the driving frequency is reduced below ω_c, thus exhibiting hysteresis.

In a following analysis, HAKEN et al. [36] used nonlinear oscillator theory to show how the model equations for the potential function could be derived from equations of

motion for the two hands and a nonlinear coupling between them. Since the details are published we simply illustrate briefly some recent results of a consequent computer simulation (see also [36], Figs. 6 and 7).

In Fig. 3, Lissajous portraits of the coupled oscillators are shown. The equations describing the motion are

$$\ddot{x}_1 + (\dot{x}_1^2 - 1)\dot{x}_1 + kx_1 = \alpha(\dot{x}_1 - \dot{x}_2) + \beta(\dot{x}_1 - \dot{x}_2)(x_1-x_2)^2 + F_{noise} \tag{1}$$

$$\ddot{x}_2 + (\dot{x}_2^2 - 1)\dot{x}_2 + kx_2 = \alpha(\dot{x}_2 - \dot{x}_1) + \beta(\dot{x}_2 - \dot{x}_1)(x_2-x_1)^2 + F_{noise} \tag{2}$$

In (1) and (2) above, the LHS corresponds to a Rayleigh-type, nonlinear oscillator (Equation 3.6 of [36]); the RHS is a Van der Pol coupling term plus some noise to simulate fluctuating forces (Equation 3.25 of [36]). The only difference between the two simulations lies in the magnitude of fluctuations. Indeed, the transition shown in
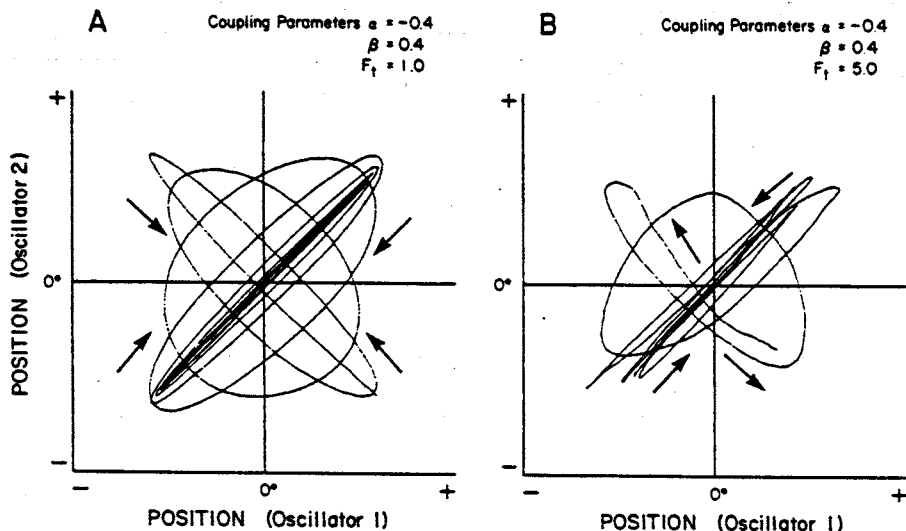

Fig. 3. Lissajous portrait of behavior of two coupled Rayleigh oscillators (see text for details). Intrinsic frequency continuously scaled. Initial conditions of simulations: $x_1 = 25°$, $x_2 = -25°$, $\dot{x}_1 = \dot{x}_2 = 0$. A and B differ only in level of noise component (Bruce Kay performed the simulations).

Fig. 3(b) is remarkably like the behavior we observe typically (see e.g., [5]). Though we have not made a full study of the effects of initial conditions, coupling parameters and fluctuations, our impression is that--given sufficient coupling strength--fluctuations play a major role. Suffice to note at this point that the model captures not only observed decreases in hand movement amplitudes as ω is increased, but also the abrupt change in qualitative behavior from antisymmetric to symmetric modes.

6.3 Theoretical Underpinnings

If the bimanual phase transition constitutes a critical instability far from equilibrium then certain specific predictions can be generated regarding the system's behavior near the transition. In particular, the hypothesized order parameter (relative phase) should exhibit at least two major properties: 1) critical slowing down as the transition is approached, i.e., the relaxation time of the order parameter to any perturbation should diverge at the transition. In general, the system exhibits a symmetry breaking instability, i.e., a constraint arises during the transition that restricts the future configuration of the system; and 2) enhanced fluctuations of the order parameter in space and time near the transition. The data presented next represent a preliminary attempt to explore the degree to which these theoretical predictions may or may not apply to phase transitions in hand movements.

6.4 New Experiments

Two kinds of experiment were performed. In each, subjects were seated comfortably with pronated forearms, supported up to the metacarpal heads of the hand. The forearm was stabilized to restrict movement to the fingers alone. On each trial, the subject oscillated the index finger bilaterally in the transverse plane (i.e., abduction-adduction). Continuous finger displacement in the transverse and parasagittal (i.e., flexion-extension) planes was measured using a modified Selspot camera system. The electromyographic (EMG) activity of the right and left first dorsal interosseous (FDI) muscle was obtained with platinum fine-wire electrodes (see Fig. 4). All data were recorded on 12-channel FM-magnetic tape recorder for later off-line computer analysis.
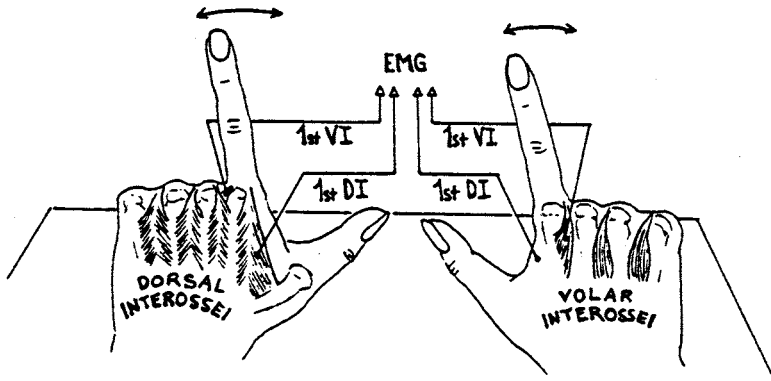
Fig. 4. General experiment set-up for recording EMG.   Support splints not shown (drawing by C. Carello).

Initially, subjects were instructed to move in one of two ways: oscillation of the right (R) and left (L) index fingers in either 1) the symmetrical mode or 2) the antisymmetrical mode, at their preferred rate. The frequency of oscillation was gradually increased to a maximum of approximately 3.5 Hz. In Experiment 1, the frequency of oscillation was increased every 2-3 sec by asking the subject to slightly increase his rate. Thus, the rate of increase was not strictly controlled. In Experiment 2, the frequency of oscillation was systematically increased in 0.25 Hz steps every 4 seconds paced by a metronome. Data from trials in this experiment could therefore be averaged in time. Averages for Experiment 1 required alignment of trials by similar frequencies of oscillation. However, despite the lack of exact frequency equivalence, results from the two experiments are surprisingly consistent.

6.5 Order Parameter Behavior

6.5.1 Critical Slowing Down

The time series of one trial of finger oscillation, when the system is prepared initially in the antisymmetrical

mode, is depicted in Fig. 5a (note: the figure shows only a portion of the trial in the vicinity of the phase transition). Here, one can clearly see the transition to the symmetrical mode with an increase in the frequency of oscillation. In Fig. 5b a point estimate of relative phase for the same sample record, based upon the peak displacement of the R and L fingers, is shown. A slow oscillation in phase, particularly before the transition, is evident. As the transition is approached the frequency of this phase oscillation slows; the system takes longer and longer to return to its stationary state from a small deviation. This finding is a consistent feature of the experiments and is taken as preliminary evidence for the phenomenon of critical slowing down. Future work will calculate the relaxation time of the hypothesized order parameter explicitly using correlation techniques and perturbation experiments.

A. TIME SERIES

ABD.

ADD.

—— Position of Right Index Finger
····· Position of Left Index Finger

B. POINT ESTIMATE OF RELATIVE PHASE

360°

180°

0°

| sec |

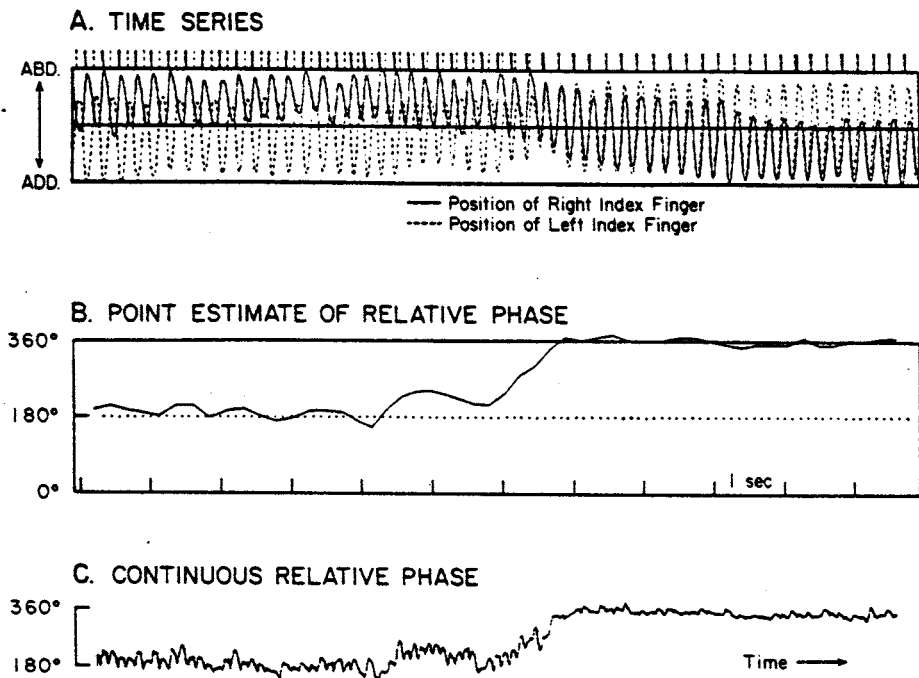## C. CONTINUOUS RELATIVE PHASE

360°

180°

Time ⟶

Fig. 5. Time series (A) and relative phase (B & C) of R and L finger oscillation (see text for details).

A continuous estimate of relative phase may be found in Fig. 5c, based upon the continuous phase angle difference between each oscillator. Note that this estimate reveals some of the microscopic details of the phase fluctuations, while preserving the slow modulations in phase described above. A clear reduction in these fluctuations occurs following the transition. All remaining data on relative phase to be reported are based upon this continuous estimate.

6.5.2   Enhancement of Fluctuations

An important feature of critical phenomena is the increase in variance of the order parameter near the phase transition. The system is said to become "soft" and thus unable to suppress critical fluctuations. The variance of the order parameter in the finger experiment is presented in
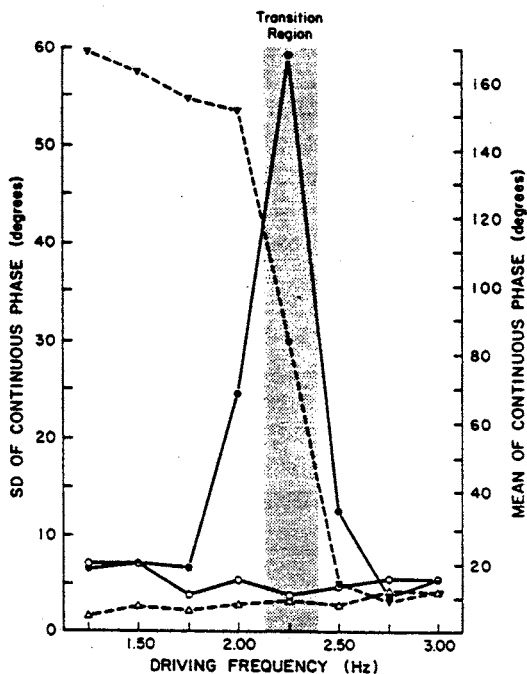

Fig. 6. Mean (▼ AMS, △ SMS) and standard deviation (● AMS, ○ SMS) of continuous relative phase at each driving frequency (n=10). AMS = antisymmetrical mode scaled. SMS = symmetrical mode scaled.

Fig. 6. The SD of continuous phase was calculated in the stable regime with the transient removed, i.e., over the last 3 seconds (= 600 data points) of oscillation at each frequency. Each point on the graph represents an average of 10 trials from Experiment 2. Mean phase is presented as well.

Consideration of trials in which the system was initially prepared in the antisymmetrical mode reveals a clear increase in relative phase fluctuations as the transition is approached. The phase variance maximum at the transition is somewhat artifactual, since the phasing <u>must</u> change in order for a new mode to be exhibited. Note also that after the transition the variance eventually stabilizes at a lower level (corresponding to the symmetrical mode) than before the transition. So-called control trials in which the system is initially prepared in the symmetrical mode, exhibit no such fluctuational amplification with increasing driving frequency. These findings are therefore consistent with theoretical predictions and the results of the nonlinear oscillator modeling shown earlier.

Order parameter dynamics can be further explored by examining the spectral content of relative phase. Each sample record of continuous relative phase was divided into eight segments corresponding to the increments in driving frequency. The power spectral density function (PSDF) of each segment was then determined by Fast Fourier Transform. Average PSDFs were obtained for trials in which subjects were initially prepared in the antisymmetrical mode, as well as those prepared in the symmetrical mode. The results are displayed in Fig. 7. The DC component has been removed from each plot, since it represents the mean phase value, and overwhelms the other components, particularly in the anti-phase mode.

Fig. 7a displays the average PSDF for trials initially prepared in the antisymmetrical mode. Note that as the driving frequency (ω) increases, a gradual increase in the frequency of the dominant spectral peak occurs. This increase appears to represent, in part, the influence of the driving frequency. Just prior to the transition, at 2.25 Hz, a dramatic increase occurs in the amplitude of the low-
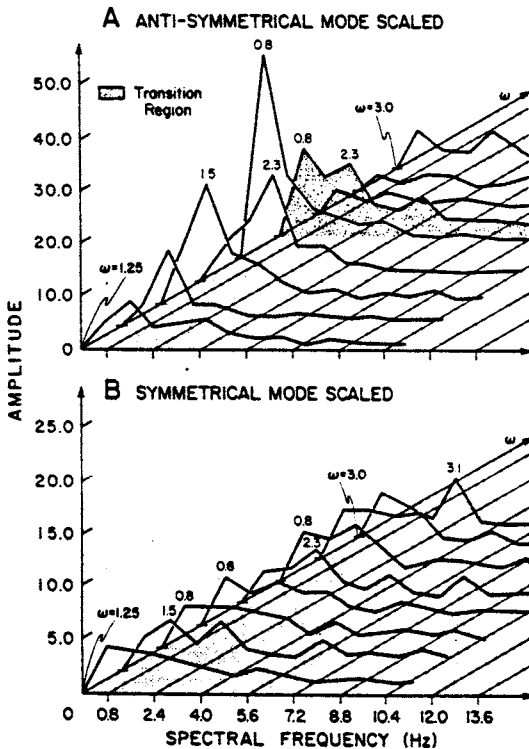
Fig. 7. Average PSDF of continuous measure of relative
phase computed at each driving frequency (ω) for
trials prepared in A. antisymmetrical and
B. symmetrical modes.

est frequency band, 0.8 Hz, along with the disappearance of
higher frequency components. The stippled PSDF represents
the transition region alone and reveals spectral broaden-
ing. With further increases in driving frequency the spec-
trum remains relatively broad and 0.8 Hz remains as a
strong harmonic.

The average PSDF of trials initially prepared in the
symmetrical mode is shown in Fig. 7b. While higher spec-
tral components are present as the driving frequency is in-
creased, the 0.8 Hz component is always strong, even at low
driving frequencies. Driving frequency appears to have
relatively less effect on the PSDF of the symmetrical mode
than that of the antisymmetrical mode. The dramatic in-

crease in the amplitude of the 0.8 Hz component in the antisymmetrical mode just prior to the phase transition may represent the "swamping" of this mode's energy by that of the more stable symmetrical mode. That is, the longest lasting mode--symmetrical, in-phase--appears prominently before the transition itself. Though this interpretation is speculative at present, there does seem to be evidence that the antisymmetrical mode "feels" the driving frequency move strongly than its in-phase counterpart condition. In the language of synergetics, the order parameter is "slaving" its components less strongly in the former case than the latter.

6.6 Exploring the Neuromuscular Basis of the Transition

6.6.1 The η Parameter

In order to determine the extent to which changes in EMG activity map onto those of the hypothesized order parameter already described, the parameter η was calculated. Fig. 8a shows how this was done. R_0 and L_0 were obtained for each cycle of a sample record by determining the percent of to-tal mean rectified EMG of one FDI that overlapped in time with that of the contralateral FDI. Note that η is thus a sample estimate of the total energy of motor unit activity within a time interval defined by the phase between the fingers. It therefore constitutes a way of observing how the "microscopic" quantities relate to the macroscopic phasing parameter. A plot of η vs. time (and increasing frequency) for one representative trial is provided in Fig. 8b. The change in η maps quite nicely onto the change in the kinematic order parameter, as might well be expect-ed. The η parameter change appears to occur more abruptly as compared to the change in relative kinematic phase, how-ever.

6.6.2 EMG Autocorrelograms

One question concerns the nature of the neuromuscular reorganization underlying these phase transitions. In a
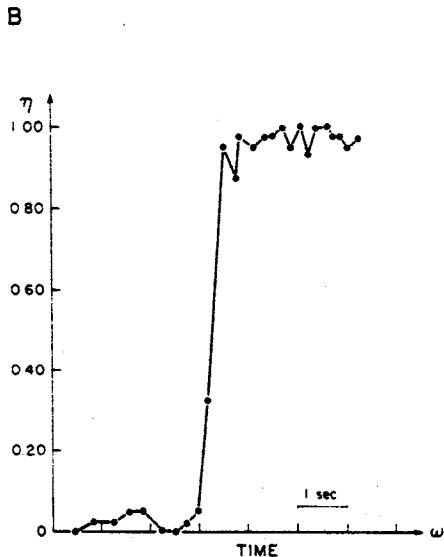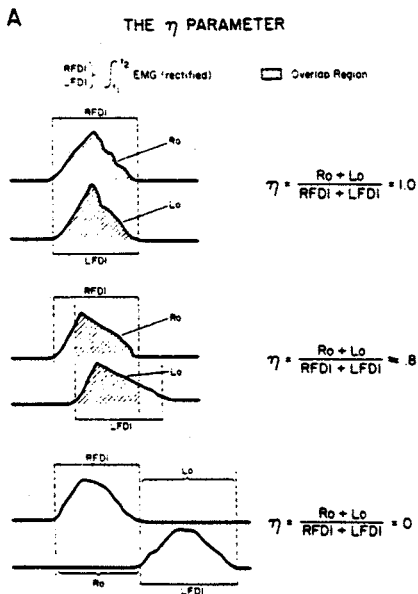
Fig. 8. The η parameter. A. Method of calculation from mean rectified, integrated EMG. B. Plot of η vs. time (and increasing oscillation frequency ω) for one representative trial.

preliminary attempt to examine this issue we looked at the autocorrelograms of mean rectified EMG for RFDI and LFDI, assuming they provide a measure of the temporal coherence of an individual muscle's activity. Two second segments of sample records prior to, during, and immediately following the transition were analyzed. The calculation of each sample autocorrelogram was adjusted according to the oscillation frequency of the fingers so that the same number of peaks occurred in each function. The mean value of the peaks in each function and their coefficient of variation were calculated as measures of temporal coherence. Both measures yielded similar results.

The mean peak autocorrelation of seven trials (Experiment 1) is presented in Fig. 9. The striking finding is the similarity between the coherence measures of the RFDI and LFDI before and after the transition, and their divergence at the transition. In the former two cases, even when the temporal coherence of one muscle is low, the contralateral FDI exhibits similar behavior. The correlation between the temporal coherence measures before and after the transition was above 0.90. This presumably indicates a tight coupling of their activity patterns, even when operating antisymmetrically. By contrast, one muscle always becomes more or less coherent in the transition region. Here, correlation of the R and L coherence measure was low, negative and non-significant. Note also that the muscle showing the lowest coherence, and the direction of coherence change (compare with pre-transition measures) is never the same from trial to trial. Therefore, the underlying neurophysiologial mechanisms do not appear to be strictly deterministic as one might assume from a programming model of phase transitions.
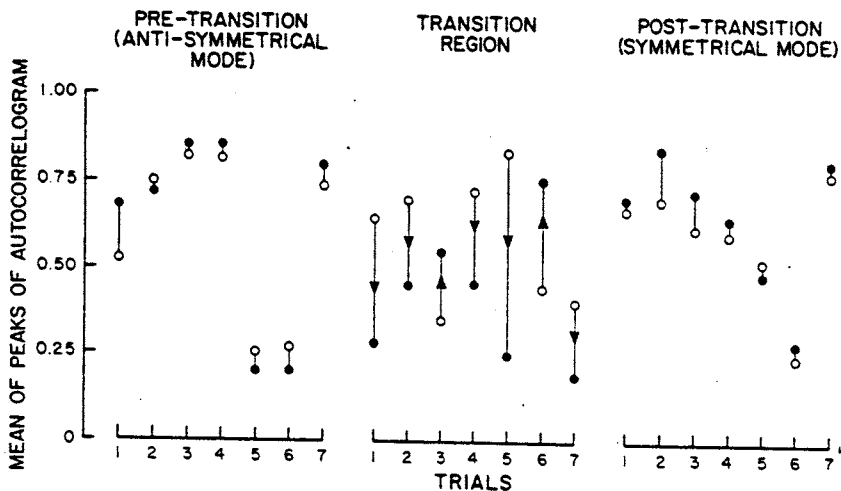

Fig. 9. Measure of temporal coherence of right FDI (●) and left FDI (O) 2 sec before, during, and 2 sec after phase transition (see text for details).

6.7 Second Kinematic Phase Transition

As subjects move toward the upper extremes of oscillation frequency used in these experiments (~3.25-3.5 Hz) we have observed that a second instability occurs irrespective of the initial mode in which the subjects are prepared. In-phase modal behavior in the horizontal plane becomes unstable and gives way to a similar pattern in the vertical plane. A sample record of such an event is shown in Fig. 10 in which the displacement of each finger in both horizontal and vertical planes is plotted versus time (and, therefore, increasing oscillation frequency). Motion frequently becomes rotary in nature before simultaneous flexion-extension occurs. Further analysis, using comparable procedures to those described above, is underway.
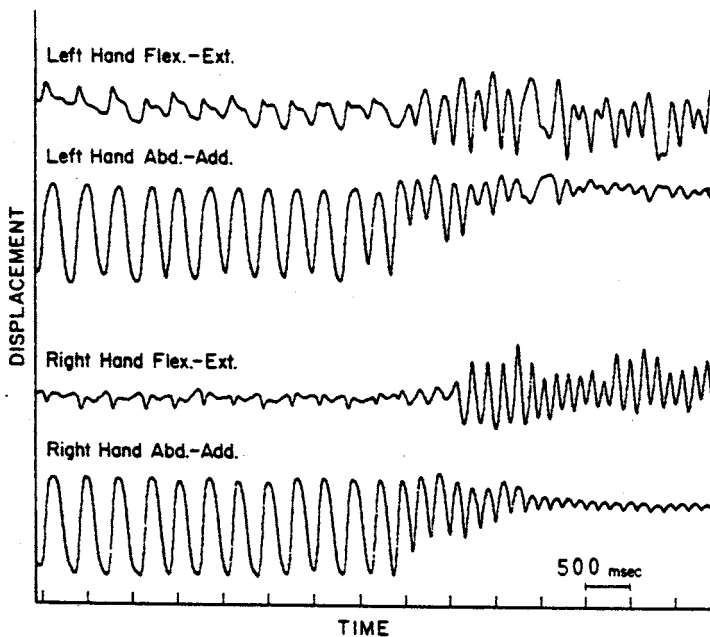
SECOND KINEMATIC PHASE TRANSITION

Fig. 10. Time series of oscillation of R and L index finger in horizontal (abduction-adduction) and vertical (flexion-extension) planes for oscillation frequency above 3 Hz. See text for details.

Note that in this situation there is an additional degree of freedom available for energy dissipation. Thus a new (or different) configuration among the oscillatory components can occur--an additional basin of attraction appears spontaneously. The basis for this second transition is not altogether clear and requires further exploration. It may be determined, in large part, biomechanically, linked to the relaxation times of the participating muscles (i.e., FDI and first palmar interosseous, FPI). As the frequency of oscillation increases the relaxation times begin to exceed the 1/2 period of each cycle, resulting in maximum agonist-antagonist coactivity [38]. Energy can no longer be dissipated through motion in the transverse plane. However, because the experiment left open an additional degree of freedom, parasagittal motion, the system adopts this new configuration, apparently in order to dissipate the increasing energy. Both the FPI and FDI have lever arms which provide contribution to finger flexion. The extent to which the long finger flexors and extensors are also facilitated cannot be determined by the present data.

7 Concluding Remarks

Neuroscience has not looked seriously to contemporary physical theory for ways to think about brain-behavior relationships. And, with few notable exceptions (this conference being one, see also [39]), physics has made little contact with organic phenomena. Here we have shown in a very preliminary fashion--how some of the tools and concepts of nonequilibrium phase transitions may offer insight into the emergence of space-time order at a macroscopic level. In our simple experiments we have begun to identify some of the main features of non-equilibrium transitions, including symmetry breaking, critical slowing down, and enhancement of fluctuations. Further work--both theoretical and experimental--will be necessary to converge on these and other characteristics, e.g., identification of the system's time scales and especially measurement of mode relaxation times using correlation functions and perturbation techniques, classification of the stochastic nature of fluctuations, exploring the system's sensitivity to parameter change, etc.

The central thrust here, of course, is to understand co-ordination in the multi-degree-of-freedom motions of animals and organisms. Even if we knew all the microscopic details about the system's components we would still need a lawful description of how the components relate among them-selves. An attraction of synergetics is that it deals with the formation of functional structures based on the cooperation among the system's many individual components. The theory achieves its full rigor when the system's behav-ior changes qualitatively, when newly emerging patterns are defined solely in terms of a few characteristic quantities, the so-called order parameters. A chief mechanism for the emergence of order lies in the competition between energy flowing into the operational components (i.e., a scaling influence) and the ability of those components to absorb the energy flow in their current configuration. As we have shown here (see e.g., Section 6.7) in the case of certain biological motions, higher bifurcations are possible if the system has available additional degrees of freedom, i.e., when a given configuration can no longer absorb the energy input. Moreover, fluctuations may permit the system's dis-covery of new modes or phasing structures.

If nature operates with ancient themes, as we suspect, then the same laws/strategies should appear at every level of description, and despite differences in material struc-ture. Thus, the reductionism advocated here is not to any privileged scale of analysis, but rather to a minimum set of principles. The present treatment, preliminary though it is, may be just as pertinent to the mysteries of bac-terial locomotion (see [40]) as it is to the coordinative patterns among the limbs and the abrupt transitions between them.

References

1. I. Procaccia, this volume.

2. R. Shaw: in Order and Chaos in Nature, ed. by H. Haken (Springer, Berlin, Heidelberg, New York 1981)

3. H. Haken: Rev. Mod. Phys. 47, 67 (1975)

4. H. Haken: Synergetics: An Introduction (Springer, Berlin, Heidelberg, New York 1983)

5. J.A.S. Kelso and B. Tuller: in Handbook of Cognitive Neuroscience, ed. by M. S. Gazzaniga (Plenum Press, New York 1984)

6. V. Weisskopf: Frontiers and Limits of Science (Alexander von Humboldt, Stiftung, Marz 1984)

7. N.A. Bernstein: The Coordination and Regulation of Movements (Pergamon Press, London 1967)

8. J.A.S. Kelso, B. Tuller, E. V.-Bateson and C.A. Fowler: J. Exp. Psych.: Hum. Perc. Perf. 10, 812 (1984)

9. G.M. Edelman, and V.B. Mountcastle: The Mindful Brain (MIT Press, Cambridge, MA 1978)

10. M.M. Merzenich and J.H. Kaas: Trends Neurosci. 5, 434 (1984)

11. J.A.S. Kelso: in Attention and Performance (IX), ed. by J. Long and A. Baddeley (Erlbaum, Hillsdale, NJ 1981)

12. S. Grillner: Physiol. Rev. 55, 247 (1975)

13. M.L. Shik and G.N. Orlovskii: Physiol. Rev. 56, 465 (1976)

14. D.C. Shapiro and R.A. Schmidt: in The Development of Movement Control and Coordination, ed. by J.A.S Kelso and J. Clark (Wiley, New York 1982)

15. B. Tuller, J.A.S. Kelso and K. Harris: J. Exp. Psych.: Hum. Perc. Perf. 8, 460 (1982)

16. B. Tuller and J.A.S. Kelso: J. Acoust. Soc. Am. 76, 1030 (1984)

17. J.A.S. Kelso and B. Tuller: J. Acoust. Soc. Am. Suppl. 1 77, S53 (1985)

18. J.A.S. Kelso and B. Tuller: in Sensory and Motor Processes in Language, ed. by E. Keller and M. Gopnik (Erlbaum, Hillsdale, NJ in press)

19. E. von Holst: in The Behavioral Physiology of Animals and Man: The Collected Papers of Erich von Holst (Univ. of Miami Press, Coral Gables, Fl 1937/1973)

20. M.A. Sleigh and D.I. Barlow: in Aspects of Animal Locomotion, ed. by H.Y. Elder and E.R. Trueman (Cambridge Univ. Press, Cambridge, London, New York, Sydney 1980)

21. T.A. Easton: Amer. Sci. 60, 591 (1972)

22. C.A. Fowler: Timing Control in Speech Production (Indiana University Linguistics Club, Bloomington, IN 1977)

23. J.A.S. Kelso, D.L. Southard and D. Goodman: Sci. 203, 1029 (1979)

24. M.T. Turvey: in Perceiving, Acting and Knowing: Toward an Ecological Psychology, ed. by R. Shaw and J. Bransford (Erlbaum, Hillsdale, NJ 1977)

25. W.A. MacKay: Trends Neurosci. 3, 97 (1980)

26. S. Grillner: Sci. 228, 143 (1985)

27. T.H. Bullock: in Simple Networks and Behavior, ed. by J.D. Fentress (Sinauer Assoc., Sunderland, MA 1976)

28. T.H. Bullock: in Information Processing in the Nervous System, ed. by H.M. Pinsker and W.D. Willis (Raven Press, New York 1980)

29. A.I. Selverston: Behav. Brain Sci. 3, 535 (1980) .

30. G.E. Loeb and W.B. Marks: Behav. Brain Res. 3, 556 (1980)

31. J.A.S. Kelso, K.G. Holt, P.N. Kugler and M.T. Turvey: in Tutorials in Motor Behavior, ed. by G.E. Stelmach and J. Requin (North-Holland, Amsterdam, New York 1980)

32. P.N. Kugler, J.A.S. Kelso and M.T. Turvey: in Tutorials in Motor Behavior, ed. by G.E. Stelmach and J. Requin (North-Holland, Amsterdam, New York 1980)

33. M.L. Shik, F.V. Severin and G.N. Orlovskii: Biophys.

$\underline{11}$, 1011 (1966)

34. D.F. Hoyt and C.R. Taylor: Nature $\underline{292}$, 239 (1981)

35. J.A.S. Kelso: Am. J. Physiol.: Reg. Integr. Comp. $\underline{246}$, R1000 (1984)

36. H. Haken, J.A.S. Kelso and H. Bunz: Biol. Cyber. $\underline{51}$, 347 (1985)

37. J. Yamanishi, M. Kawato and R. Suzuki: Biol. Cyber. $\underline{37}$, 219 (1980)

38. H.-J. Freund: Physiol. Rev. $\underline{63}$, 387 (1983)

39. Synergetics of the Brain, ed. by E. Basar, H. Flohr, H. Haken and A. J. Mandell (Springer, Berlin, Heidelberg, New York 1983)

40. L. Janos: Smithsonian $\underline{14}$, 127 (1983)