Biol. Cybern. 51, 347–356 (1985)

Biological Cybernetics

A Theoretical Model of Phase Transitions in Human Hand Movements

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Abstract. Earlier experimental studies by one of us (Kelso, 1981a, 1984) have shown that abrupt phase transitions occur in human hand movements under the influence of scalar changes in cycling frequency. Beyond a critical frequency the originally prepared out-of-phase, antisymmetric mode is replaced by a symmetrical, in-phase mode involving simultaneous activation of homologous muscle groups. Qualitatively, these phase transitions are analogous to gait shifts in animal locomotion as well as phenomena common to other physical and biological systems in which new "modes" or spatiotemporal patterns arise when the system is parametrically scaled beyond its equilibrium state (Haken, 1983). In this paper a theoretical model, using concepts central to the interdisciplinary field of synergetics and nonlinear oscillator theory, is developed, which reproduces (among other features) the dramatic change in coordinative pattern observed between the hands.

1 Introduction

While researching voluntary oscillatory motions of the two index fingers, one of us (Kelso, 1981a) observed an interesting phenomenon[1]. Under instructions to increase the frequency of out-of-phase, antisymmetrical motion (involving simultaneous flexor and extensor muscle activities), the subject's finger movements shifted abruptly to an in-phase symmetrical mode that involved simultaneous activation of homologous muscle groups. This finding was not restricted to finger movements. In later work (Kelso, 1982, 1984) that employed similar experimental manipulations, modal transitions in hand motions around the wrist were also observed: the antisymmetrical phase relationship between the hands was replaced by symmetrical phasing. Moreover, although the phase transition occurred at very different frequencies of hand motion for different subjects, it was nevertheless predictable. When the transition frequency was expressed in units of preferred frequency, i.e., an independent measure of the rate at which each subject was content to cycle the hands "as if he/she were going to do it all day", the resulting dimensionless ratio or "critical value" was constant for all subjects. Introducing a frictional resistance to movement systematically changed both the preferred and transition frequencies for each subject, but did not change the critical value across all subjects (Kelso, 1984).

The most dramatic aspect of these simple experiments, addressed in detail in the present theoretical model, is the sudden and completely involuntary change in the ordering or phasing among muscle groups that occurs at a critical, intrinsically defined frequency (see Fig. 1). In this feature, the hand movement data share a likeness to gait transitions in locomotion[2]. For example, Shik et al. (1966) showed that a steady increase in electrical stimulation to the midbrain region of the decerebrate cat was sufficient not only to induce an increase in locomotion rate, but, above a certain value of current, gait shifts as well. Like the hand experiments in which "flipping" from one

1 In discussions of these experiments with Shapiro (1981, personal communication) it was learned that Cohen (1971) observed occasional involuntary shifts into the in-phase coordinative mode when out-of-phase motions at a single cycling frequency (3 Hz) were required. Cohen did not, to our knowledge, examine the phenomenon further. Similar experimental findings on bimanual finger movements have been reported by MacKenzie and Patla (1983) and by Baldiserra, Cavallari, and Civaschi (1982) on ipsilateral hand and foot movements

2 Indeed, it was the slogan of "... Let your fingers do the walking" promoted by advertisers of the Yellow Pages in U.S. telephone directories, that led to the idea behind the present experiments

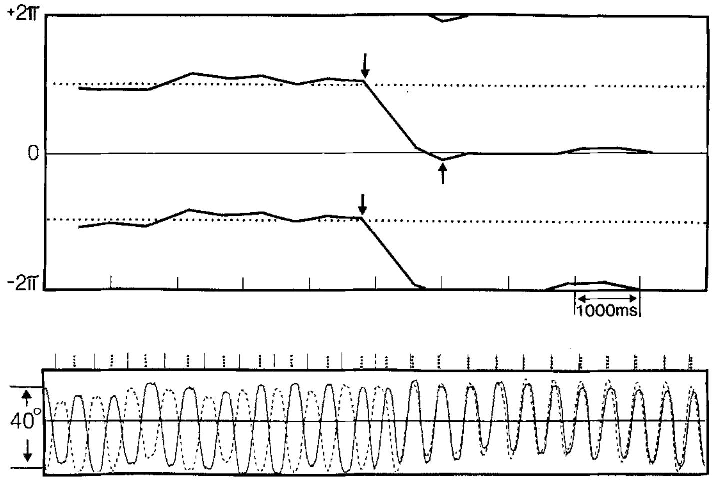

Fig. 1. *Bottom:* Displacements over time of left (solid line) and right (dashed line) hands. The subject is simply increasing cycling frequency in an antisymmetric mode in response to a verbal cue from the experimenter. *Top:* Phase relationship between the two hands. The peaks of one hand movement act as a "target" file and their phase position is calculated continuously relative to the peak-to-peak period of the other "reference" file. The graphic display repeats the phase curve so that phase lags and leads can be noted

mode to another occasionally occurred at higher movement frequencies, they too noted the presence of unstable regions in which the cat shifted from trotting to galloping and back again. Though the hand data as well as these findings on quadruped gait strongly suggest that changes in coordination may be ordered by changes in a single parameter, the neural processes underlying such motoric phase transitions are still poorly understood. As Grillner (1982, p. 224) notes for the case of quadruped gait transitions, the general conception is that there is a "switch mechanism" in which "coordinating fibers" serve to switch among hindlimb neural networks. But such coordinating fibers have yet to be identified neuroanatomically (Grillner, 1982) and their exact functional role in determining locomotor pattern remains to be explained.

This problem of relating neuronal events to global patterns of behavior – in the present case abrupt macroscopic changes in the phasing of neuromuscular activities and changes in characteristic quantities such as frequency and amplitude – is somewhat reminiscent of a similar problem confronting physicists about 50 years ago. After it was discovered that matter consists of atoms and after the properties of atoms were understood theoretically, it may have seemed straightforward to derive the macroscopic properties of matter directly from the properties of the individual atoms. It turned out, however, that such a goal could not be reached immediately and it proved extremely fruitful to introduce macroscopic quantities for purposes of system description. Only later did it become possible to derive the equations governing the macroscopic quantities by means of a microscopic theory (for review and examples, see e.g., Wilson, 1979). It has been shown quite generally in the interdisciplinary field of synergetics (e.g., Haken, 1983) that in many cases the behavior of complex systems can be successfully modeled by means of a few macroscopic quantities in those situations where the behavior of the system changes qualitatively. Such macroscopic observables are called "order parameters" following a term first introduced by Landau (1936) to describe the "degree of order" (cf. Ter Haar, 1965, p. 208) of matter as it undergoes changes in phase. In synergetics, however, which deals with cooperative phenomena in non-equilibrium, open systems, the concept of order parameter has added significance: not only is it created by the cooperation of the individual components of a complex system, but the order parameter in turn governs the behavior of these components (for many examples, see Haken, 1975). Even in physical and chemical systems, finding the correct order parameter(s) is not always a simple matter. In the case of biological systems in general, and movement control and coordination in particular, the strategic approach of synergetics allows some license in selecting order parameters, an issue that we turn to next.

2 Initial Development of the Model: Order Parameters and the Potential Function

To summarize, the main features of the experiments described briefly above are: (i) the presence of only two stable phase (or "attractor") states between the hands (which one is observed is a function of how the system is prepared, i.e., an instruction to move the hands in the out-of-phase or in-phase mode); (ii) the abrupt transition from one attractor state to the other at a critical cycling frequency; (iii) beyond the transition, only one mode (symmetrical in-phase) is observed; and (iv) when cycling frequency is reduced, the system stays in the symmetrical mode, i.e., it does not return to its initially prepared state – a result that suggests coexistence of the basins of attraction for the symmetrical and antisymmetrical modes and the depletion of one of them. Taken together, these results as well as other findings in the motor control literature support the hypothesis that *phase* is a relevant macroscopic (or "essential") parameter of certain movement patterns[3]. For example, the internal phasing structure of activities as widely varied as chewing, locomotion, handwriting, and speech remains invariant across scalar changes in force or rate (Grillner, 1982; Kelso, 1981b; Schmidt, 1982; Tuller et al., 1982). Similarly, in the experiments described above, phase is preserved constant over a wide range of frequencies, even though the magnetitudes and durations of muscle activities and other kinematic variables change considerably. Only when frequency is scaled beyond a critical value does a phase shift occur.

In the present paper it seems reasonable to propose phase as an order parameter for at least two reasons. First, unlike many other possible candidates, phase is an accurate reflection of the *cooperativity* among the components of the system. Thus, we can say, in a manner consistent with synergetics, that the configuration of the subsystems (in the present context defined as the individual hand motions) specifies their phase relation, and conversely, that the phase variable specifies the spatiotemporal ordering of the subsystems. Second, it is phase that remains invariant across transformations in many motor activities that involve very different anatomical substrates. This highlights an important further feature of the order parameter concept, namely, that the order parameter (by hypothesis here, the relative phase) changes much more slowly than the variables describing the behavior of the individual components (e.g., velocities of each hand motion).

Our first step in the development of the present model is to provide a mathematically accurate description of the main qualitative features of the data. We therefore specify a potential function that corresponds to the layout of attractor states and how that layout is altered as a control parameter is changed. In a following section, we employ nonlinear oscillator theory to show how the model equations describing the potential function can be derived from the equations of motion of each hand and a (nonlinear) coupling between them.

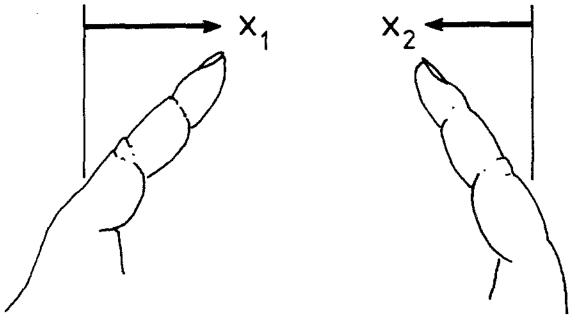

Fig. 2. The displacements of x_1 and x_2 of the finger tips of the left and right hand in the symmetrical (in-phase, homologous) mode

For sake of clarity we introduce the elongations of the finger tips x_1 and x_2 as shown in Fig. 2. In order to define the relative phase ϕ we assume that the motion of the hands is more or less harmonic (see Fig. 1) so that we put

$$x_1 = r_1 \cos(\omega t + \phi_1), \tag{2.1}$$

$$x_2 = r_2 \cos(\omega t + \phi_2), \tag{2.2}$$

where ω is the basic frequency of the hand movement, while the amplitudes r_1, r_2 and the phases ϕ_1, ϕ_2 are time dependent quantities whose time dependence is assumed to be much slower than that defined by the frequency ω. The relative phase is defined by

$$\phi = \phi_2 - \phi_1 . \tag{2.3}$$

In order to describe the change of phase we adopt basic ideas from synergetics. As shown in synergetics, in many cases the equations for order parameters are of the form

$$\dot{\phi} = \frac{\partial V}{\partial \phi}, \tag{2.4}$$

where V is the so-called potential function. In our search for a model we make a few rather obvious assumptions about V. Since ϕ occurs under cosine or sine functions [cf. (2.1) and (2.2)][4] the properties of the physical system must not change when ϕ is replaced by $\phi + 2\pi$. Consequently, we shall postulate that the potential V is periodic:

$$V(\phi + 2\pi) = V(\phi) . \tag{2.5}$$

We furthermore introduce the assumption that both hands play a symmetric role[5]. In such a case the behavior of the system must not depend on the way we

3 The reader must be warned that the word "phase" in the context of this paper has two different meanings:

1) "phase" as a temporal relationship whose precise definition is given in (2.1)–(2.3).

2) "phase" as a state of aggregation of matter (e.g. liquid or solid) or, more generally, different modes of behavior. Therefore, in physics, "phase transition" means transition from one state, e.g. fluid, to another one, e.g. solid. In synergetics, transitions between different dynamic states (e.g. behavioral modes) are also called phase transition.

Since in the present paper the behavioral modes are characterized by definition 1), the notion "phase transition" is unique – in spite of the double meaning of "phase"

4 This become obvious when we change the origin of time so that $\omega t + \phi_1 = \omega \tau$. In this case $x_1 = r_1 \cos(\omega \tau)$, $x_2 = r_2 \cos(\omega \tau + \phi_2 - \phi_1)$

5 Our model can easily be generalized to include asymmetries

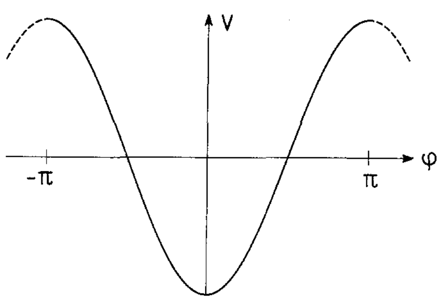

Fig. 3. The potential V (2.7) for $b=0$

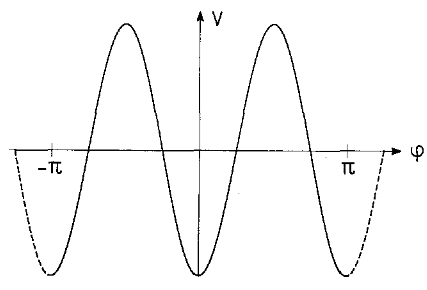

Fig. 4. The potential V (2.7) for $a=0$

label the right hand and the left hand. This means that V must remain unchanged when we exchange the indices 1 and 2 in Eq. (2.3). This in turn means that the potential V is symmetric:

$$V(\phi)=V(-\phi). \tag{2.6}$$

We assume that V obeys the conditions (2.5) and (2.6) in the simplest form which explains the above mentioned experimental results. To this end we write V as a superposition of two cosine functions:

$$V=-a\cos\phi-b\cos2\phi. \tag{2.7}$$

As is known from synergetics, the behavior of the system obeying the Eq. (2.4) can be easily described by identifying ϕ with the coordinate of a particle which moves in an overdamped fashion in the potential V.

To illustrate this let us consider Fig. 3 where b is put equal to 0. There is only one stable equilibrium position, namely at $\phi=0$. When we taken $a=0$, $b\neq0$, the potential function looks like the one shown in Fig. 4.

Here we have two equivalent positions, namely at $\phi=0$ and $\phi=\pi$ (which is equivalent to $\phi=-\pi$). When we take the total superposition (2.7) but change the ratio b/a we run through a series of potential fields shown in Fig. 5. When we initially prepare the system in a state shown by the black ball and increase the frequency, and likewise assume that b/a decreases with increasing frequency we obtain a critical value ω_c where the ball falls to the lower minimum belonging to $\phi=0$.

This means that the hand movement made a transition from the antisymmetric ($\phi=-\pi$ state) into the symmetric state with $\phi=0$. The hand movement stays in that state when ω is further increased. When we decrease ω starting from high values, the system remains all the time in the $\phi=0$ state even if ω drops below ω_c. This "hysteresis" phenomenon is well known in many physical and biological systems.

In order to study at which value of b/a the transition occurs, we seek the extrema of V which are defined by

$$\frac{dV}{d\phi}=0. \tag{2.8}$$

Using (2.7), (2.8) reads:

$$-a\sin\phi-2b\sin2\phi=0. \tag{2.9}$$

The second term can be transformed by means of:

$$\sin2\phi=2\sin\phi\cos\phi, \tag{2.10}$$

so that (2.9) can be cast into the form:

$$-a\sin\phi-4b\sin\phi\cos\phi=0. \tag{2.11}$$

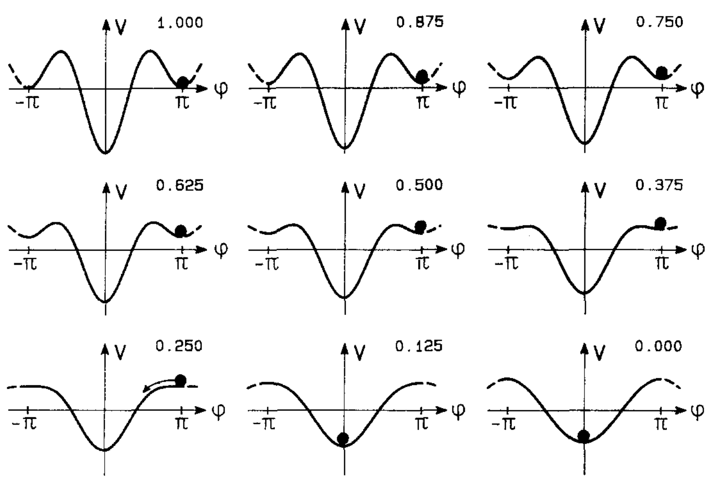

Fig. 5. The potential V/a for the varying values of b/a. The numbers refer to the ratio b/a

One set of roots is given by:

$$\sin\phi = 0, \tag{2.12}$$

namely

$$\phi = 0,\ \phi = \pm\pi. \tag{2.13}$$

The other set of roots is given by:

$$-a - 4b\cos\phi = 0, \tag{2.14}$$

or, when we solve for $\cos\phi$, by:

$$\cos\phi = -\frac{a}{4b}. \tag{2.15}$$

This value of $\cos\phi$ corresponds to the inner maxima of V. The transition occurs when these maxima vanish which is the case if (2.15) can no more be fulfilled by a real ϕ. This happens provided:

$$\left|\frac{a}{4b}\right| > 1, \tag{2.16}$$

or

$$|b| < |a|/4, \tag{2.17}$$

i.e., the transition occurs if $|b|$ drops below the critical value $b_c = |a|/4$. On the other hand, we know from experiments that the amplitudes r_1, r_2 decrease with increasing ω. This suggests that b can be expressed by means of the amplitude $r = r_1 = r_2$ and a critical amplitude r_c so that we may write the potential function in the form:

$$V = -a\left(\cos\phi + \frac{1}{4}\frac{r(\omega)^2}{r_c^2}\cos 2\phi\right), \tag{2.18}$$

where r_c is defined as that value of r where the transition occurs.

3 Further Development of the Model

In the next step of our analysis we want to show how the model equations derived in the previous section can be derived from equations for the movements of the individual hands and a coupling between them. We write the corresponding equations in the form:

$$\ddot{x}_1 + f_1(x_1, \dot{x}_1) = I_{12}(x_1, x_2), \tag{3.1}$$

$$\ddot{x}_2 + f_2(x_2, \dot{x}_2) = I_{21}(x_1, x_2). \tag{3.2}$$

The left hand sides describe the motion of the individual hands with amplitudes x_1 and x_2, respectively, while the right hand sides describe the coupling. Of course, the coupling is achieved via the nervous system and in this way the Eqs. (3.1) and (3.2) describe a complex system composed of the mechanical motions of the hands generated, in large part by neuromuscular input. It is our goal to derive a minimal model for the macroscopic observables which are now the amplitudes and phases of the hand motion. Since the motion is basically oscillatory, we need at least a second order differential equation so that the terms $\ddot{x}_1$, $\ddot{x}_2$ occur. With respect to the restoring and damping forces we have a certain repertoire at hand and in all likelihood the choice of f_1 and f_2 is not unique. Since the hand movement has a more or less stable amplitude the equations must be nonlinear. We study several different examples. The first is well known from the operation of vacuum tube oscillators. Here, of course, we shall use only its mathematical properties. Let us consider the Van der Pol equation of the form:

$$\ddot{x} + \varepsilon(x^2 - r_0^2)\dot{x} + ax = 0, \tag{3.3}$$

where ε, r_0 are adjustable, but then fixed parameters, while a serves as a control parameter. In order to solve this equation for not too high amplitudes and in order to cast it into a form convenient for our later purposes we put:

$$x = Ae^{i\omega t} + A^* e^{-i\omega t}, \tag{3.4}$$

where $\omega^2 = a$ and the complex amplitude A can be time dependent. It is assumed, however, that its time dependence is much slower than that of $e^{i\omega t}$. One can then perform two approximations well known in the theory of nonlinear oscillators (e.g. Haken, 1984). The "slowly varying amplitude approximation" means that we neglect terms $\dot{A}$ compared to terms ωA. The "rotating wave approximation" means that we may neglect terms containing $e^{3i\omega t}$ and $e^{-3i\omega t}$ compared to $e^{i\omega t}$ and $e^{-i\omega t}$. By means of these approximations (3.3) is transformed into:

$$e^{i\omega t} i\omega(2\dot{A} + \varepsilon(A|A|^2 - Ar_0^2)) = 0. \tag{3.5}$$

In the steady state the amplitude A is a constant and the only non trivial solution reads $|A|^2 = r_0^2$. Thus the amplitude becomes frequency independent.

In order to find a decrease of the amplitude with frequency we adopt a new model equation, namely:

$$\ddot{x} + \varepsilon(\dot{x}^2 - \omega_0^2 r_0^2)\dot{x} + ax = 0. \tag{3.6}$$

Making again the rotating wave approximation and the slowly varying amplitude approximation and using the hypothesis (3.4) we readily obtain for (3.6):

$$e^{i\omega t} i\omega(2\dot{A} + \varepsilon(3A|A|^2\omega^2 - A\omega_0^2 r_0^2)) = 0. \tag{3.7}$$

In the steady state where $\dot{A} = 0$, (3.7) has the nontrivial solution

$$|A| = \frac{\omega_0 r_0}{\sqrt{3}\omega}. \tag{3.8}$$

Thus the amplitude indeed drops with ω^{-1}, giving us, therefore a model equation which describes both the oscillatory motions of the hand and a drop in amplitude with increasing ω.

The experimental results suggest a superposition of a constant amplitude function [corresponding to ε_1 in Eq. (3.9)] and a function that decreases with ω [corresponding to ε_2 in Eq. (3.9)]. That is, there is an intercept as well as a slope to the observed relationship between amplitude and frequency of hand movement. Such a behavior can be modelled by a superposition of (3.3) and (3.6):

$$f_i=[\varepsilon_1(x_i^2-r_0^2)+\varepsilon_2(\dot{x}_i^2-\omega_0^2r_0^2)]\,\dot{x}_i+ax_i\,. \tag{3.9}$$

This leads in the steady state to:

$$|A|^2=\frac{(\varepsilon_1+\varepsilon_2\omega_0^2)r_0^2}{(\varepsilon_1+3\varepsilon_2\omega^2)}\,. \tag{3.10}$$

As we shall see, however, the main features of the phase transition can be modelled by choosing 3.6 as a basic equation.

We now come to the central problem, namely to derive a suitable coupling between the two macroscopic quantities, i.e. the amplitudes x_1 and x_2. The simplest hypothesis would be a linear coupling of the form:

$$I_{12}=\alpha(x_1-x_2)\,. \tag{3.11}$$

However, as we shall see below such a coupling will not lead to the required potential V for the relative phase. Rather we have to add a *nonlinear* coupling. Requiring that this coupling term has the same symmetry properties as (3.11) we are led to a coupling term of the following kind:

$$I_{12}=\alpha(x_1-x_2)+\beta(x_1-x_2)^3\,. \tag{3.11a}$$

A detailed analysis reveals that such a coupling term still lacks an important feature, namely, it does not produce the correct phase relation between the motion of the individual hands. We have to introduce the coupling term either via a time delay or by using time derivatives. We first study the coupling by a time delay. This can be achieved by averaging over past values of (3.11a) so that we can replace (3.11a) by:

$$I_{12}=\int_{-\infty}^{t}[\alpha(x_1-x_2)_\tau+\beta(x_1-x_2)_\tau^3]\,e^{-\gamma(t-\tau)}d\tau\,. \tag{3.11b}$$

An equivalent formulation is obtained by the requirement that I_{12} obeys the differential equation:

$$\dot{I}_{12}+\gamma I_{12}=\alpha(x_1-x_2)+\beta(x_1-x_2)^3\,. \tag{3.11c}$$

In order to facilitate the subsequent calculation we shall assume that γ is much smaller than ω. This assumption is not all that crucial, however, since it does not change the basic structure of the equations. In order to proceed further we differentiate Eqs. (3.1) and (3.2) with respect to time. Making use again of the slowly varying amplitude approximation and the rotating wave approximation, Eq. (3.1) acquires the form

$$\begin{aligned}&-\omega^2(2\dot{A}_1+\varepsilon(3A_1|A_1|^2\omega^2-A_1\omega_0^2r_0^2))\\&\quad=\alpha A_1+3\beta A_1|A_1|^2+K_{12}\,.\end{aligned} \tag{3.12}$$

The first two terms on the right hand side of (3.12) can be absorbed into the terms on the left hand side containing the factor ε and do not alter qualitatively the behavior of the system. The term K_{12} specifies the coupling influence of oscillator 2 on oscillator 1, corresponding to the motions of the two hands. In the above mentioned approximation K_{12} reads:

$$\begin{aligned}K_{12}=&-\alpha A_2-3\beta(A_1^2A_2^*+2|A_1|^2A_2)\\&+3\beta(2A_1|A_2|^2+A_1^*A_2^2)-3\beta A_2|A_2|^2\,.\end{aligned} \tag{3.13}$$

We are now in a position to show how our model Eqs. (3.1), (3.2) with the specific choice (3.11b) allow us to derive the order parameter Eq. (2.4). To this end we make the hypothesis:

$$A_j=r_je^{i\phi_j},\quad j=1,2\,, \tag{3.14}$$

where r_j and ϕ_j may be time-dependent, which transforms (3.12) into:

$$\begin{aligned}&e^{i\phi_1}[-\omega^2\{2\dot{r}_1+2i\dot{\phi}_1r_1+\varepsilon(3\omega^2r_1^3-\omega_0^2r_0^2r_1)\}\\&\quad-\alpha r_1-3\beta r_1]=K_{12}\,.\end{aligned} \tag{3.15}$$

K_{12} acquires the form:

$$\begin{aligned}K_{12}=&-\alpha r_2e^{i\phi_2}-3\beta r_1^2r_2(2e^{i\phi_2}+e^{2i\phi_1-i\phi_2})\\&+3\beta r_1r_2^2(2e^{i\phi_1}+e^{2i\phi_2-i\phi_1})-3\beta r_2^3e^{i\phi_2}\,.\end{aligned} \tag{3.16}$$

Similarly the equation for the oscillator 2 contains the coupling term

$$\begin{aligned}K_{21}=&-\alpha r_1e^{i\phi_1}-3\beta r_2^2r_1(2e^{i\phi_1}+e^{2i\phi_2-i\phi_1})\\&+3\beta r_2r_1^2(2e^{i\phi_2}+e^{2i\phi_1-i\phi_2})-3\beta r_1^3e^{\phi_1}\,.\end{aligned} \tag{3.17}$$

We divide Eq. (3.15) by $-\omega^2re^{i\phi_1}$ and consider its imaginary part,

$$\dot{\phi}_1=-\frac{1}{g(r)}\mathrm{Im}(e^{-i\phi_1}K_{12})\,, \tag{3.18}$$

where $g(r)=2\omega^2r_1$.

Applying an analogous procedure to oscillator 2 and taking the difference of the two equations for ϕ_1,ϕ_2 we obtain after a small intermediate calculation:

$$\dot{\phi}=-\frac{2}{g(r)}[(\alpha r+6\beta r^3)\sin\phi-3\beta r^3\sin2\phi]\,. \tag{3.19}$$

We have assumed $r=r_1=r_2$ and is well stabilized, so that r is practically time independent. If the assumption $\gamma \ll \omega$ is dropped, then $g(r)$ is replaced in Eq. (3.19) by $\hat{g}(r)=2(\omega^2+\gamma^2)r$. As we shall see β must have a sign opposite to α in order to obtain agreement with experimental findings. Therefore we put:

$$\beta=-\hat{\beta}. \tag{3.20}$$

Thus we are left with our final equation:

$$\dot{\phi}=-\frac{2}{g(r)}[(\alpha r-6\hat{\beta}r^3)\sin\phi+3\hat{\beta}r^3\sin 2\phi], \tag{3.21}$$

which indeed has the required structure of the order parameter Eq. (2.4) with (2.7). However, we are now in a position to relate the coefficients a and b to the amplitude r. The phase transition takes place for:

$$|b|=\frac{|a|}{4}\begin{cases}\text{if} \quad 4|b|>|a| & \text{bistable}\\ \text{if} \quad 4|b|<|a| & \text{monostable}\end{cases} \tag{3.22}$$

[cf. (3.16)]. Comparing the coefficients a and b with those occurring in (3.21), enables us to cast (3.22), into the form:

$$\frac{3}{2}\hat{\beta}r^2=\frac{1}{4}(\alpha-6\hat{\beta}r^2) \tag{3.23}$$

or, after a little algebra, into

$$r_c^2=\frac{\alpha}{12\hat{\beta}}. \tag{3.24}$$

We thus find that bistable operation, particularly in the antisymmetric mode, occurs when r^2 fulfills (3.24). In the other case, with decreased amplitude the system becomes monostable and operates in the symmetric mode.

As mentioned above, there is still another possibility of defining K_{12}, namely by means of time derivatives. In the sense of a minimal model we choose:

$$K_{12}=(\dot{x}_1-\dot{x}_2)\cdot(\alpha+\beta(x_1-x_2)^2). \tag{3.25}$$

Again to the same degree of approximation as used in Eqs. (3.11)–(3.21) we obtain the equation for the phase:

$$\dot{\phi}=(\alpha+2\beta r^2)\sin\phi-\beta r^2\sin 2\phi. \tag{3.26}$$

The critical amplitude is then given by:

$$r_c^2=\frac{\alpha}{4\beta}. \tag{3.27}$$

In the transitions generally studied in synergetics, fluctuating forces play an important role. Extrapolating to the present case, a transition, say from $\phi=\pi$ to $\phi=0$ can be initiated only if fluctuating forces, F are present. To this end we enlarge the Eqs. (3.1) and (3.2) to include such forces, so that these equations now read:

$$\ddot{x}_1+f_1(x_1,\dot{x}_1)=I_{12}(x_1,x_2)+F_1(t), \tag{3.28}$$

$$\ddot{x}_2+f_2(x_2,\dot{x}_2)=I_{21}(x_1,x_2)+F_2(t). \tag{3.29}$$

In the context of the present paper it suffices to assume F_j, $j=1,2$ as a random small variable, which can be easily mimicked on a digital computer. At present, we cannot say much about the source of these fluctuations from existing experimental data. However, ongoing experimental work in which fine-wire electrodes are inserted into the finger muscles involved, is exploring their possible neuromuscular origin [see also Goodman and Kelso (1983) for evidence pertaining to the relationship between physiological tremor "fluctuations" and voluntary movement].

4 Numerical Results

In this section we present some numerical results that correspond to the analytical treatment provided above. We solve the minimum model given by Eq. (3.6) along with the coupling (3.25) on a digital computer using a fourth order Runge-Kutta method. To test the stability of a stationary solution small random fluctuations of finite amplitude are introduced. The resulting simulation shown in Fig. 6 compares quite favorably with the experimental data (e.g. Fig. 1). In Fig. 6a the displacements x_1, x_2 are plotted over time and in Fig. 6b the corresponding phase difference between the oscillators is plotted for the same motions. As in the bimanual experiments, the coupled oscillation is prepared in the state $\phi=\pi$ and the frequency ω is increased monotonously. A transition from the out-of-phase mode to the in-phase mode is observed, when ω exceeds a critical value. However, the frequency of the oscillation changes rather quickly so that stationary oscillations are not reached. Thus the exact form of the curves depends strongly on the noise level and the rate of changing ω.

The steady state amplitudes for the in-phase mode and the out-of-phase mode are shown in Fig. 7. The unstable branch of the out-of-phase mode is shown by dotted lines. The ω^{-1} dependence of the amplitudes is quite clear. This feature is exhibited only by the simplified model equations and will change if Eq. (3.9) is used. As shown in Fig. 7 for ω smaller than ω_c, the in-phase mode and the out-of-phase mode are both stable. Due to the coexistence of two basins of attraction, the particular mode observed depends on the initial conditions, i.e. which coordinative state is prepared.

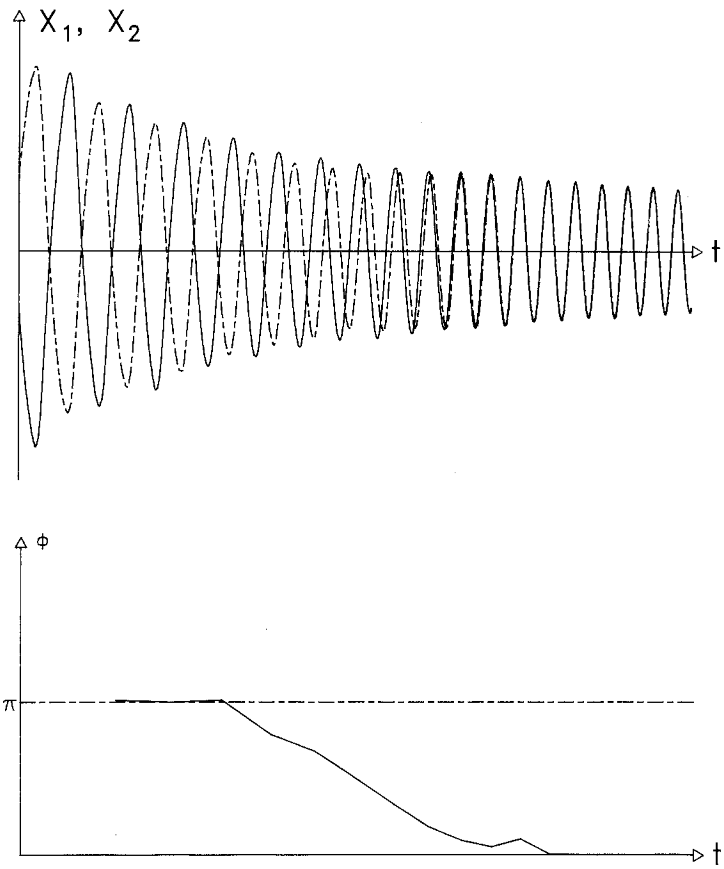

Fig. 6a and b. A numerical simulation of the phase transition in voluntary cyclical hand movement. In **a** the displacements of the oscillators and in **b** the corresponding phase difference between the oscillators is plotted over time. The parameters of the Eqs. (3.6) and (3.25) were fixed at $\varepsilon = 1$, $\omega_0^2 r_0^2 = 1$, $\alpha = -0.2$, $\beta = 0.2$. From the left to the right of the displays, ω changes from $\omega = 1.17$ to $\omega = 3.05$

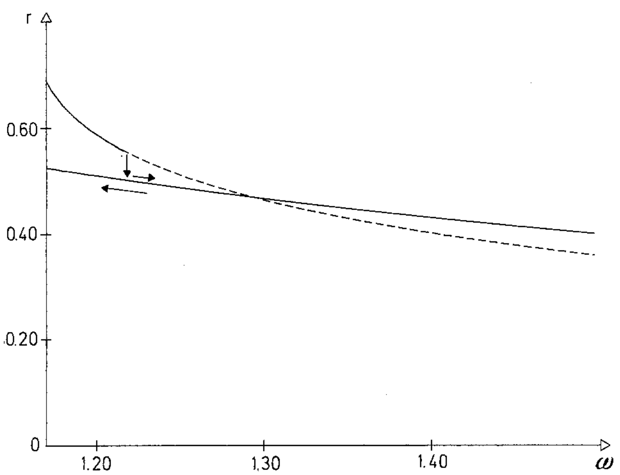

Fig. 7. The steady state amplitudes of the in-phase mode (1) and the out-of-phase mode (2) are shown as a function of ω. The other parameters are fixed at the same values as in Fig. 6. Stable branches of the oscillations are shown by the solid lines, while the unstable branch by the dotted line

If one starts in the antisymmetric phase and increases ω slowly, the oscillation remains in this mode until the solution becomes unstable. At this point a jump in amplitude occurs and the only stable stationary solution revealed by the system corresponds to the in-phase mode. Such is the case when ω is increased further. On the other hand, if ω is decreased slowly the system stays within the basin of attraction of this solution even when ω drops below ω_c. As we mentioned earlier, this hysteresis phenomenon is typical for such bistable situations. To summarize, it is quite clear that the main features of the experimental data described at the beginning of Sect. 2 are captured by the present mathematical formulation as illustrated by these numerical results.

5 Concluding Remarks

In this paper we have introduced a minimal theoretical model that reproduces a number of the observed facts. The hand movements are described by two nonlinearly coupled oscillators which are self-sustained, i.e., not driven from the outside. The assumption of autonomous limit cycle oscillators is quite consistent with pertubation studies of two-handed cyclical movements, showing that an unexpected pertubation to *one* hand does not disrupt the phasing relation *between* the hands. The perturbed hand returns to its limit cycle almost immediately (see Kelso et al., 1981; Yamanishi et al., 1980). Similar results in very different preparations (e.g. Cohen et al., 1982; Willis, 1980 for reviews) have also led to limit cycle models of neutral pattern generation.

In the present model the frequency ω is defined as a control parameter via the coefficient, a, of the restoring force. The model describes not only the observed decrease in hand movement amplitudes with increasing frequency ω, but, more importantly, the phase transition, i.e., the change of qualitative behavior from antisymmetric to symmetric hand movement. A relation which automatically results from the equations is that the transition takes place at a critical frequency via the amplitudes. This prediction is now open to further experimental test. In future studies a number of phenomena known to acccompany phase transition in synergetic systems (e.g., critical slowing down; critical fluctuations) will also be analyzed.

For the moment, any speculation on the origin of the coupling between the two hands is certainly premature. One coupling may be established via the corpus callosum, the well-known band of fibers that joins the two hemispheres of the brain. On the other hand, recent experiments (Tuller and Kelso, 1984) with patients whose corpus callosum has been severed, effectively cutting off communication between the left and right cerebral hemisphere, show that even in this case, control of the two index fingers in cyclical tasks is not independent. When asked to follow two pacing lights whose phase was varied between synchrony and alternation, split-brain subjects produced predominant synchrony or alternation even when paced at intermediate phase values. This bias in intermanual phase toward temporal symmetry is extremely powerful (see e.g., Kelso et al., 1979; Yamanishi et al., 1980, for evidence in normal populations) and suggests that the neural coupling for the voluntary hand movements may be established subcortically.

In conclusion, although we have shown here how a transition from one modal configuration to another is possible in our model, it remains for further theoretical and experimental research to address how it is that only two stable modes emerge in the first place from a wealth of possibilities, i.e. how these *particular* cooperativities arise. What is clear, however, from the present analysis, borne out by our numerical results, is the need to characterize the individual oscillators as nonlinear. But more important the coupling *between* oscillators must be nonlinear for the phase transition to occur. Although the present formulation clearly points to the important role of nonlinearities in certain basic motor behaviors (i.e. the frequency – amplitude relation in individual hand movements, modal transitions between the hands), the physiological underpinnings of such nonlinearities remain an open issue.

On the other hand, though their physiological basis may be obscure at present, it is entirely reasonable to enquire how a complex neuromuscular system might exploit these nonlinearities. Why are they important attributes for a neural control system to possess? What are they for? First, nonlinearity affords a stable coupling between the fundamental physical variables of space and time (i.e., the amplitude-frequency relation). In a linear system no such preferred coupling exists between these variables. Second, nonlinearity provides a means by which switching among coordinative states is possible (though other properties, e.g. fluctuations, play a key role also). In principle, there is no reason to limit this conclusion to the two phasing relations studied here. Thus, both of these attributes, we hypothesize, guarantee – in the present context – stability and flexibility of motor function.

Acknowledgements. The authors wish to thank the Volkswagenwerk foundation for financial support of the synergetics project. JASK was also supported by contract No. N0014-83-K-0083 from the U.S. Office of Naval Research, NIH grant NS-13617 and Biomedical Support Research Grant RR-05596.

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Received: November 17, 1984

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