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Received 27 May 1986; accepted for publication 1 September 1986

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The movements of animals and people are ordered spatiotemporal structures even though they arise from microscopic sources (e.g. neuronal, skeleto-muscular, vascular) of huge dimensionality. This is reminiscent of the spontaneous formation of structure in open nonequilibrium systems (cf. e.g. [1]). It is not unreasonable therefore to consider the formation of such ordered states within a physical description. In coordinated biological motion the relative phasing among the limbs (or articulators, in the case of speech) may be a relevant order parameter characterizing different modes of coordination [2, 3]. For example, the phase relations among the limbs of a quadruped enable us to classify it various gaits, e.g. the near anti-phase, asymmetric pattern between the legs of the trotting horse or the near in-phase, symmetric pattern that is the signature of the gallop. Such phase relations are stably preserved over a range of locomotory speeds. Moreover, gait transitions occur when animals are forced to run faster on a treadmill [4] or when electrical stimulation to certain mid brain areas is systematically increased [5]. Around transition regions, unstable behavior – in which a cat will vacillate between trotting and galloping gaits – has also been observed.

Such movement transitions have been discovered also in human oscillatory movements. For instance, Kelso [6,7] performed experiments in which subjects were instructed to move their index fingers or hands rhythmically and the cycling frequency (corresponding to the control parameter) was varied. In such a situation subjects can stably and reproducibly perform in only two phase-locked modes, either in-phase (homologous muscle groups contracting simultaneously) or anti-phase (homologous muscle groups contracting in an alternating fashion). The finding that only two stable phase-lockings exist has been demonstrated quantitatively in experiments in which the relative phase between the two fingers was manipulated and the variability of the produced relative phase was measured. Much less variable performance was observed at relative phase $\phi=0°$ (in-phase) and $\phi=\pm 180°$ (anti-phase) than at any other specified relative phase [8,9]. In Kelso's experiments, when subjects, initially moving in the anti-phase mode, were instructed to increase cycling frequency, an involuntary abrupt shift to the in-phase mode was observed at a critical frequency. Beyond this critical frequency value only the in-phase mode was performed stably.

It seemed at least intuitive that the foregoing experimental observations were consistent with other bifurcation phenomena in nature [6,7,10]. Indeed, their essential features were succesfully modelled by

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0.375-9601/86/$ 03.50 © Elsevier Science Publishers B.V.
(North-Holland Physics Publishing Division)

Haken, Kelso and Bunz [3] introducing relaxational dynamics

$$\dot{\phi} = -\partial V/\partial \phi \qquad (1)$$

for the relative phase and mapping the observed modes onto point attractors. The potential

$$V(\phi) = -a \cos \phi - b \cos 2\phi \qquad (2)$$

complying with periodicity and symmetry requirements, captures the bifurcation diagram in that it has minima at $\phi=0°$ and $\phi=\pm180°$ for $a/b<4$ with the latter minimum turning into a maximum for $a/b>4$. The order parameter dynamics (1), (2) for ϕ were then derived from nonlinear oscillator equations for the two hands with a nonlinear couplings between them.

The foregoing modeling work inspired an attempt to explicitly test the phase transition character of the phenomenon. For example, a simple stochastic generalization of the above model [11] predicts certain characteristic features, including critical fluctuations of the hypothesized order parameter and critical slowing down. Although earlier experimental work hinted that critical fluctuations were present (evident, for example in the widening of Lissajous trajectories between the individual oscillatory components [7]), only in recently conducted experiments – reported here – have these fluctuations been quantified.

The basic experiments described below have been run on a sizeable number of subjects (a total of 10 using movements around the wrist joints, and 7 using movements of the index fingers). As we shall show, in spite of a variety of differences between the experiments, e.g. different anatomical components, paradigmatic modifications, data handling procedures etc., the qualitative features of the results are remarkably consistent and reproducible. For experiments involving oscillatory wrist flexion/extension, the subject's forearms were fixed in a comfortable posture while each hand grasped a vertical handle attached to the experimental apparatus (described in detail in ref. [12]) that rested on a table top. The axes of the wrist joints were colinear with the axes of the handles. The latter incorporated potentiometers for conversion of wrist rotation angle to dc voltages. The finger movement experiments used a similar experimental set-up except that the forearms were stabilized to restrict movements to the index fingers alone. (It is important to note in each case that in order to reproduce the phenomenon precisely, movements must be restricted to the relevant degrees of freedom (wrists and fingers respectively).) On a given run subjects oscillated the index fingers bilaterally in the transverse plane of motion (i.e. abduction–adduction). The continuous x, y coordinates of the tip of each finger were measured using infra red light emitting diodes attached to the finger tips. All data were digitized with a 12-bit A–D converter at 200 samples/s and stored on magnetic tape for later computer analysis.

There were two kinds of experiments. In each the subjects' task was to rhythmically oscillate the wrists or the fingers either in an in-phase or an anti-phase mode of coordination as she/he increased the frequency of movement in a step-wise manner. In the wrist movement experiments the "control parameter", the driving frequency F, was not precisely controlled. Every 3 or 4 s the subject was instructed by the experimenter to increase slightly the cycling rate. In the finger movement experiments, which will be our primary focus, the frequency of oscillation was systematically increased in 0.25 Hz steps at 4 s intervals according to a metronome pacing stimulus. Data from the finger experiments could therefore be time-averaged for each driving frequency.

First we show the wrist data focusing on the hypothesized order parameter, relative phase. In this case the estimate of relative phase (which we call a point estimate) was based simply on the phase of one wrists' oscillatory peak (maximum displacement) relative to the other.

An example from one run is presented in fig. 1 which shows that an abrupt transition occurs at a critical frequency from an antiphase ($\phi\approx180°$) to an in-phase pattern ($\phi\approx0°$) in which the wrists flex and extend in a near synchronous fashion. The mean phase modulus $\langle|\phi|\rangle$ and its $\mathrm{SD} \doteq (\langle\phi^2\rangle - \langle|\phi|\rangle^2)^{1/2}$ averaged over 30 separate runs on four subjects are presented in fig. 2. In order to facilitate comparison among subjects and runs, nine segments were defined for each run for analysis purposes. Each segment includes an average of the relative phase measure over four cycles of oscillation. The origin of time was defined as 8 cycles prior to the transition onset (see fig. 1). The nine segments were obtained

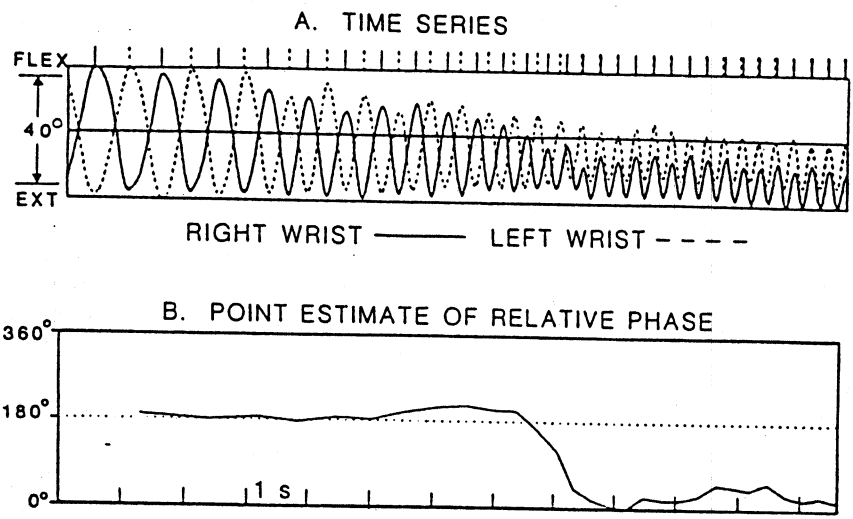

Fig. 1. (A) Representative time series showing position over time of right (solid line) and left (dashed line) wrist flexion and extension movements as the control parameter, frequency, is scaled every 3–4 s according to instruction. (B) The corresponding point estimate of relative phase based on the phase of one wrist's oscillatory peak (maximum displacement) relative to the other (see text for details).

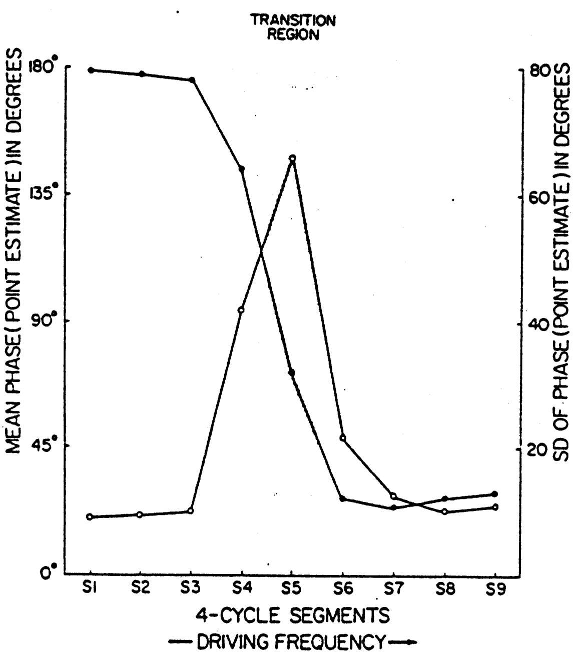

Fig. 2. The mean phase modulus $\langle|\phi|\rangle$ (solid circles) and its SD$=(\langle\phi\rangle^2-\langle|\phi|\rangle^2)^{1/2}$ (open circles) averaged over 30 experimental runs. Each segment includes a temporal average of relative phase over 4 oscillatory cycles (see text for details).

by using a moving window over the data, adjacent windows overlapping by two cycles. From S1 through S3 (encompassing 8 cycles of oscillation) the mean relative phase remains stable at around 180°, decreasing only slightly. A change in relative phase is apparent by S4 and continues until S6 where a new steady state, $\langle|\phi|\rangle=25°$ is observed. Note also in fig. 2 that further increases in oscillation frequency produce no further changes in the relative phasing between the wrists. Fig. 2 also shows the pattern of fluctuations in relative phase. Here for an individual run the SD of ϕ was determined for each four cycle frequency segment, then averaged across all runs and all subjects. Fluctuations in the steady state (anti-phase pattern) are relatively low and nearly constant for the first three segments. A significant increase in the magnitude of relative phase variation occurs at S4, immediately prior to the transition region, a finding consistent with the enhancement of order parameter fluctuations evident in second-order nonequilibrium phase transitions (see e.g. ref. [1], sect. 6.7). As expected in the transition region the SD reaches a maximum; thereafter phase fluctuations decrease to a constant level. Stability is attained in the new, symmetrical pattern even though oscillation frequency itself continues to increase. Across subjects the driving frequency ranged between 2.41

and 2.88 Hz at the pre-transition segment, S4. By S9 (the end of the run) the frequency range was between 2.99 and 4.04 Hz.

Increases in fluctuations immediately before the transition appear to reflect an instability of the anti-phase coordinative pattern. However, the experimental and analysis procedure in the wrist experiment still leaves doubts about the evidence for critical fluctuations in two respects: (1) The point estimate of relative phase necessarily produces a relatively low number of data points within each segment for the temporal averages. (2) A possible non-stationarity in the data is introduced due to the lack of exact control over the rate of frequency scaling. To alleviate these problems we performed more refined experiments on finger movements. In these the relative phase was measured continuously, i.e. at every 5 ms sample. In this case, each sample estimate was determined on the basis of the individual phase of each finger's motion defined by $\phi_R = \tan^{-1}(\dot{X}_R / X_R)$ where X_R is the position of the right index finger normalized to the cycle extrema and $\dot{X}_R$ is its normalized instantaneous velocity. Continuous relative phase is just $\phi_R - \phi_L$ at each sample. In fig. 3 it is possible to compare the continuous estimate of relative phase (fig. 3C) and the point estimate of relative phase (fig. 3B) for a representative experimental run (fig. 3A).

The slow component of phase fluctuations is apparent in both figs. 3B and 3C, though a finer fluctuational structure emerges from the continuous estimate. Because of the anharmonicities present in the individual finger movement trajectories, the continuous relative phase also contains an oscillatory component. Due to the controlled, stepwise increase of cycling frequency explicit stationarity checks could be made by averaging over a 0.5 s window that was moved through the 4 seconds of data at each frequency. Stationarity was guaranteed less than 1 s after

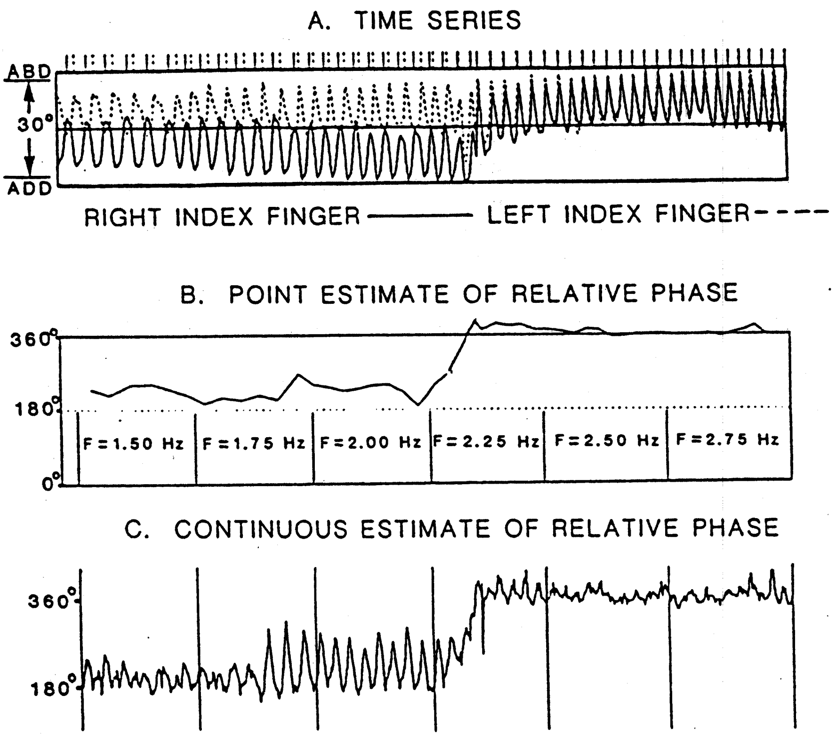

Fig. 3. (A) Representative time series showing position over time of right (solid line) and left (dashed line) finger abduction–adduction movements as the control parameter F is systematically scaled every 4 s. (B) The corresponding point estimate of relative phase, i.e. the phase of one finger's oscillatory peak relative to the other. (C) The continuous estimate of relative phase measured every 5 ms (see text for details) of the same time series data.

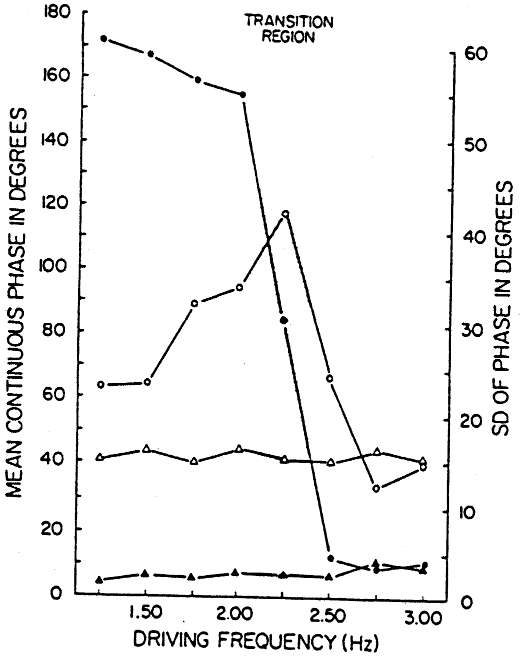

Fig. 4. The average mean relative phase modulus $\langle|\phi|\rangle$ for the in-phase (closed triangles) and anti-phase (closed circles) modes of coordination and the average SD (in-phase = open triangles, anti-phase = open circles) as a function of driving frequency (in Hz) for a set of 10 experimental runs. On a given run, the mean and SD were calculated for the last 3 s (600 samples) at a given frequency (see text for details).

the parameter change. The mean phase modulus $\langle|\phi|\rangle$ and the SD were therefore calculated on a given run for the last 3 seconds at a given frequency (i.e. 600 data points).

Fig. 4 presents the average mean relative phase modulus (triangles) and the average SD (circles) of the continuous relative phase across a set of 10 experimental runs for a representative subject. Several points are worth noting in fig. 4. (1) As in the wrist experiments, at a critical value of F there is an abrupt transition in $\langle|\phi|\rangle$ from an asymmetrical to symmetrical pattern. No such shift in $\langle|\phi|\rangle$ occurs in the symmetrical pattern (open triangles). (2) The continuous estimate of relative phase reveals more clearly (than the point estimate of fig. 2) the enhancement of fluctuations (SD) in the asymmetrical pattern as the transition is approached. Given the elimination of problems associated with the wrist experiments, we believe this observation provides strong evidence for the presence of critical fluctuations. No such fluctuational growth occurs in the symmetrically prepared pattern even though the control parameter continues to increase. (3) Relatedly, below the transition, the stability of the two coordinative patterns is clearly differentiated even at frequencies as low as 1.25 Hz. At all pre-transition control parameter values the symmetrical pattern exhibits a lower level of phase variance than the asymmetrical pattern. (4) Above the transition the data for asymmetric and symmetrically prepared patterns coincide. (5) In the transition region itself, the SD reaches a maximum while $\langle|\phi|\rangle=85°$, a value that almost corresponds to an equidistribution for which $\langle|\phi|\rangle=90°$.

To summarize, the experiments reported here have documented, for the first time in the context of coordinated biological motion, one of the key features of a nonequilibrium phase transition, namely the presence of critical fluctuations. Obviously, the fluctuational data are very similar for the two experiments reported even though they involved different anatomical systems, different experimental paradigms and even different measures of relative phase. Further exploration, however, is necessary to evaluate the extent to which the identity between the present phenomenon and other nonequilibrium phase transitions in nature holds. For example, in addition to enhancement of fluctuations, critical slowing down should be observed. That is, the time it takes the system to reach the stationary anti-phase state from a state nearby (e.g. after a slight perturbation) should increase as the frequency of oscillation is scaled toward the transition [11]. The same prediction does not hold for the symmetrically prepared mode, i.e. its relaxation time should not be affected to the same degree. This predicted strong increase in local relaxation time of the anti-phase mode can be observed in the line shape of the power spectrum of relative phase. Recently, very preliminary evidence has been obtained that line narrowing does in fact occur [13]. However, longer frequency plateaus are required to adequately resolve spectral properties to our satisfaction and these – as well as direct measures of relaxation times using perturbation methods – are incorporated into new experiments that we hope to report soon.

This research was supported by Contract No.

N00014-83-K-0083 from the U.S. Office of Naval Research (H. Hawkins, Scientific Officer), NINCDS Grant NS-13617 and BRS Grant RR-05596. G. Schöner was supported by a Forschungsstipendium of the Deutsche Forschungsgemeinschaft, Bonn, FRG.

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