NONEQUILIBRIUM PHASE TRANSITIONS IN COORDINATED BIOLOGICAL MOTION: CRITICAL SLOWING DOWN AND SWITCHING TIME

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In new experiments on coordinated biological motion we measure relaxation times and switching times as the system evolves from one coordinated state to another at a critical control parameter value. Deviations from the coordinated state are induced by mechanical perturbations and relative phase is used as an order parameter to monitor the dynamics of the collective state. Clear evidence for critical slowing down, a key feature of nonequilibrium phase transitions, is found. The mean and distribution of switching times closely match predictions from a stochastic dynamic theory. Together with earlier results on critical fluctuations these findings strongly favor an interpretation of coordinative change in biological systems as a nonequilibrium phase transition.

How do complex, biological systems containing very many microscopic components generate ordered behavior or macroscopic, spatiotemporal patterns? Faced with complexity, the conventional approach is to unravel the material substrate (e.g., neural circuitry) – component by component – in order to explain the underlying basis of pattern generation. On the other hand, in the last decade or so it has been frequently demonstrated that in open physical, chemical and biological systems, dynamic patterns can spontaneously emerge in a so-called self-organized fashion. Indeed, there is growing evidence that even though the material substance that can realize such patterns is quite variable, the underlying principles may be the same (see ref. [1] for review).

In living systems, the path from the miroscopic dynamics to the collective order parameter(s) describing macroscopic patterns is not readily accessible to theoretical analysis. An understanding of biological order may still be possible, however, via an alternative strategy (see ref. [2]), namely one in which the essential (collective) variables defining macroscopic patterns are first empirically determined, and their equations of motion studied. Next, the relevant subsystems and their dynamics can be identified, a suitable coupling of which may give rise to macroscopic patterns.

A key idea behind the foregoing strategy is to map reproducibly observed patterns onto attractors of a dynamical model. The *stability* of these patterns can then be evaluated, using, for example, fluctuations of the collective variables, relaxation rates, and so on. Changes of pattern are associated with *loss of stability* resulting in non-trivial predictions for such nonequilibrium phase transitions (e.g., critical fluctuations, critical slowing down), that can be subjected to experimental test.

Certain experimentally accessible ordering phenomena in biology appear open to the present approach in which stability and loss of stability play a key role in the understanding of biological order (see e.g., refs. [3–6]). Here we report new experimental evidence from observations of an instability in coordinated biological movement that further support this view [7–10]. Briefly, in earlier studies of human bimanual coordination, it was shown that when subjects – initially moving their wrists or index fingers rhythmically in an anti-phase mode of coordination (homologous muscle groups contracting in an alternating fashion) – were instructed to increase

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cycling frequency, an involuntary abrupt shift to an in-phase coordinative pattern (homologous muscle groups contracting simultaneously) occurred at a certain critical frequency. Beyond this critical point, only the in-phase mode was performed stably [3,4,9,10]. Similar results have been obtained by other investigators using slightly different paradigms [11] and/or anatomical components [12]. Using the relative phase ϕ between the oscillatory components as a suitable collective variable and assuming relaxational dynamics, Haken, Kelso and Bunz [7] provided an explicit model of the dynamics of ϕ that reproduced the observed bifurcation, i.e., bistable below the critical point with minima at $\phi = 0°$ and $\phi = \pm 180°$ and monostable beyond it. Later, Schöner, Haken and Kelso [8] incorporated fluctuations into this model, a step that led to several quantitative predictions regarding the transition. First, as the critical frequency was approached from below, the enhancement of fluctuations (as measured by the SD of relative phase) was calculated. Second, the corresponding increase in relaxation time was predicted. Third, for the actual transient switching process, a switching time distribution was calculated.

In recent papers [9,10] we reported experimental results on the mean relative phase and its SD as frequency was scaled systematically in each of the two coordinative modes. When parameter scaling began in the in-phase mode, both variables remained roughly constant (see ref. [10], figs. 2 and 4). In contrast, a clear enhancement of fluctuations was observed for the anti-phase mode both before and during the transition. Thus the first major prediction of the stochastic dynamic model – the presence of *critical fluctuations* – received striking experimental confirmation.

In the present paper we report experimental evidence pertaining to the second and third predictions. In these new experiments, relaxation times and switching times were measured. As we shall show, both critical slowing down and a switching time distribution closely matching the one predicted were found.

The experimental set-up required considerable modifications from that used to study critical fluctuations [9,10]. In particular, special allowance was made to incorporate the injection of perturbations. Subjects ($N = 5$) inserted their index fingers into the metal sleeves of manipulanda whose axes of rotation coincided with those of the first metacarpophalangeal joints. The manipulanda restricted finger motion to flexion and extension at this joint in the horizontal plane. Finger movement trajectories were transduced by 0.1% linear potentiometers mounted over the respective axes of rotation. These data were recorded on FM tape and later digitized with 12-bit resolution at 250 sample/s for subsequent computer analysis. The latter involved: (1) Numerical differentiation of finger position (with a symmetric five sample window to avoid phase shifts) in order to obtain velocity; (2) calculation of each finger's oscillation phase in the phase plane (position x and velocity $\dot{x}$ normalized for each cycle to the square $[-1, 1] \times [-1, 1]$) defined as $\phi = \arctan(\dot{x}_i / x_i)$ where i is left or right; (3) calculation of a continuous estimate (i.e. at the sampling rate) of relative phase ϕ defined as $\phi = \phi_{\text{left}} - \phi_{\text{right}}$. The subject's task was to oscillate both fingers rhythmically at the same frequency in one of the two modes of coordination. The movement was paced by an auditory metronome pulse with the instruction to perform one complete movement cycle per pulse. The initial pacing frequency was determined individually for each subject based on a series of 10 scaling test trials that determined the frequency of movement at which the subject switched spontaneously from the anti-phase to the in-phase mode of coordination with highest incidence. The initial pacing frequency was then chosen to be five 0.2 Hz steps below that most frequently occurring transition frequency. In the actual experimental runs the pacing frequency was increased every 10 s in nine 0.2 Hz steps. Trials began either in the in-phase or in the anti-phase modes of bimanual coordination.

In order to estimate the system's relaxation time, the pattern of bimanual coordination was disturbed by perturbing the right index finger with a 50 ms torque pulse that was generated by a dc torque motor mounted above the finger's axis of rotation. The torque pulse was timed to the peak velocity of finger flexion movement using a servo-control circuit. The size of the torque pulse was adjusted individually to produce approximately comparable displacements of the right index finger. The range of applied torque across subjects was 0.028 to 0.039 Nm. In each trial, movement perturbation occurred on up to four non-

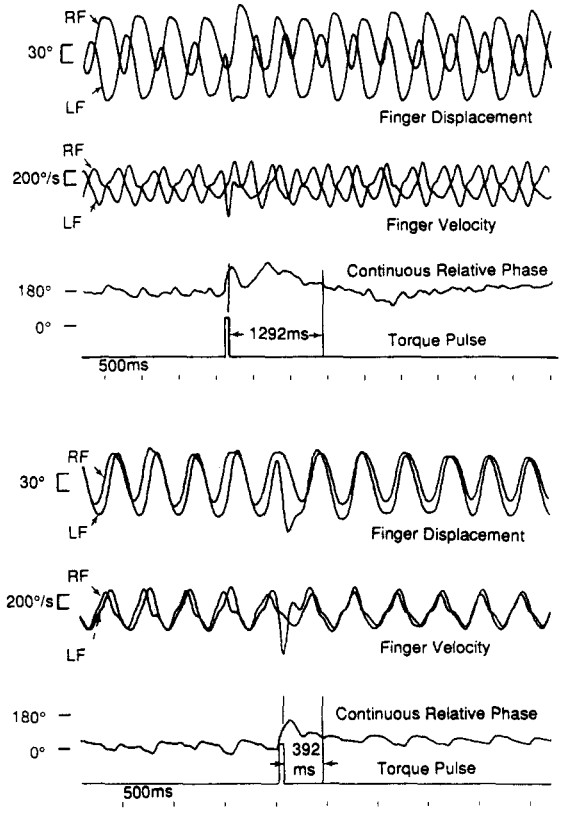

Fig. 1. Sample relaxation time estimates in the anti-phase (top) and the in-phase (bottom) mode. In each part are shown (from above): the finger displacements (RF: right finger, LF: left finger), the finger velocities, the continuous estimate of relative phase and the torque pulse.

adjacent frequency plateaus. Perturbations were randomly distributed over a block of trials such that each of the nine frequency plateaus was perturbed a total of ten times.

Using interactive computer displays, an estimate of the relaxation time was obtained from the time of torque pulse offset until the relative phase time series stabilized at its pre-perturbation mean value. Fig. 1 illustrates this procedure for two typical runs – at the same pacing frequency (2 Hz) – in the two modes of coordination.

Interactive computer displays were also used to measure the switching time on frequency plateaus in which a transition occurred. Here the estimate was determined as the time from the beginning of the frequency plateau to the point where the relative phase time series stabilized at a 0° (or 360°) mean value corresponding to the completion of the transition.

The results of these experiments for the relaxation time estimate are shown in fig. 2 for all five subjects. We note the following features: (1) Except for the lowest frequencies, the relaxation time in the anti-phase mode is consistently higher than in the in-phase mode. (2) As the frequency approaches the transition frequency, the relaxation time in the anti-phase mode increases yet remains constant or decreases in the in-phase mode. A mode by pacing frequency analysis of variance performed individually for each subject's data showed that this difference was statistically significant in all but one case. Even for this subject (BK), who showed an overall decrease of relaxation time in both modes, a sharp increase occurs in the anti-phase mode immediately prior (2.2 Hz) to the transition.

Overall pre-transitional increases in relaxation time thus prove the presence of critical slowing down in this biological coordination problem and are consistent with earlier theoretical predictions [7,8] and experimental studies of relative phase fluctuations [9,10] showing that: (1) The anti-phase mode is dynamically less stable than the in-phase mode; and (2) the transition from anti-phase to in-phase mode is connected with a loss of stability. Specifically, in the theoretical model for the stochastic dynamics of relative phase ϕ [7,8]:

$$\dot{\phi} = -a\sin(\phi) - 2b\sin(2\phi) + \sqrt{Q}\,\xi_t\,, \qquad (1)$$

with ξ_t as gaussian white noise of unit variance, and model parameters a, b and Q. The relaxation times, τ_{rel}, were predicted as:

$$\tau_{\mathrm{rel},0} = \frac{1}{4b+a}\,, \quad \tau_{\mathrm{rel},\pi} = \frac{1}{4b-a}\,, \qquad (2)$$

where 0 refers to the in-phase mode and π to the anti-phase mode. When we determine the parameters a and b from the measured relaxation times in the two modes, we find that $a/4b \approx 0.39$ on the last pre-transition frequency plateau for all subjects. This is much further from the critical point ($a/4b = 1.0$) than found in earlier studies of relative phase fluctuations (in ref. [10]: $a/4b \approx 0.64$). Consequently the critical fluctuations predicted [8]

$$\frac{\mathrm{SD}_\pi}{\mathrm{SD}_0} = \left(\frac{\tau_{\mathrm{rel},\pi}}{\tau_{\mathrm{rel},0}}\right)^{1/2} \approx 1.50 \qquad (3)$$

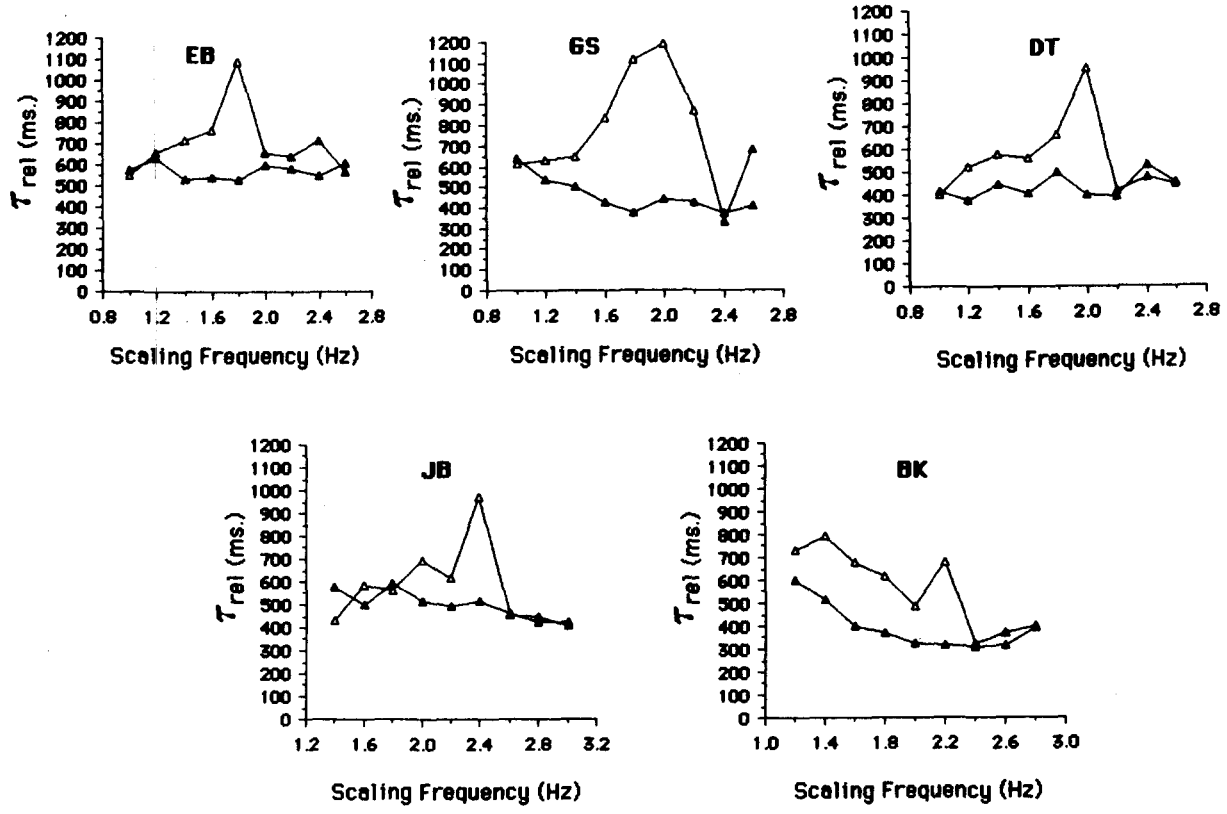

Fig. 2. The mean relaxation times as a function of pacing frequency for the five subjects (EB, GS, DT, JB and BK). The open triangles refer to the anti-phase mode, the closed triangles to the in-phase mode. The mean transition frequencies for the five subjects were: EB: 2.02 ± 0.15 Hz ($N=34$), GS: 2.27 ± 0.15 Hz ($N=33$), DT: 2.21 ± 0.17 Hz ($N=30$), JB: 2.56 ± 0.19 Hz ($N=26$) and BK: 2.35 ± 0.19 Hz ($N=28$). In these means, transitions that were induced by a mechanical perturbation were discarded. Note that beyond the transition frequency trials started in either mode are in-phase.

are comparatively small (cf. ref. [10], where this ratio is 2.13). Indeed in the present data the fluctuation enhancement on the pre-transition plateau in the anti-phase mode was not statistically significant. The SDs in both modes are at a level of 20°, except for a transient enhancement on the transition plateau in the anti-phase mode. The parameter Q was estimated from these data as 0.47 Hz.

We can use these parameter estimates to test the consistency of our stochastic-dynamic modelling (1). As discussed in refs. [2–8], the system is predicted to switch as soon as the time scales relation:

$$\tau_{rel,\pi} \ll \tau_p \ll \tau_{equ} , \qquad (4)$$

is violated. Here τ_{equ} is the equilibration (or global relaxation) time of (1) and τ_p is the time scale of parameter change which is identical here to the observed time scale, and is given by $\tau_p = 10$ s. An estimate of τ_{equ} can be obtained from the mean first passage time (MFPT) for the passage from $\phi = \pm 180°$ to $\phi = 0°$. Using model parameter estimates for the frequency plateau immediately before the transition we calculated the MFPT numerically from a standard formula (cf. ref. [8], eq. (4.26)) and found MFPT = 13.0 s. For critical parameters ($a = 1.6$ Hz, $b = 0.40$ Hz, $Q = 0.47$ Hz) we found MFPT = 5.35 s. Thus switching indeed occurs as τ_{equ} becomes shorter than τ_p, entirely consistent with the stochastic theory. In earlier experiments [9,10] which found critical fluctuations, τ_p was smaller (4 s) allowing the system to come closer to the critical point before (4) was violated (MFPT = 9.62 s pre-transitional and 5.28 s critical there). As we have emphasized [2,8], and as the present observations clearly

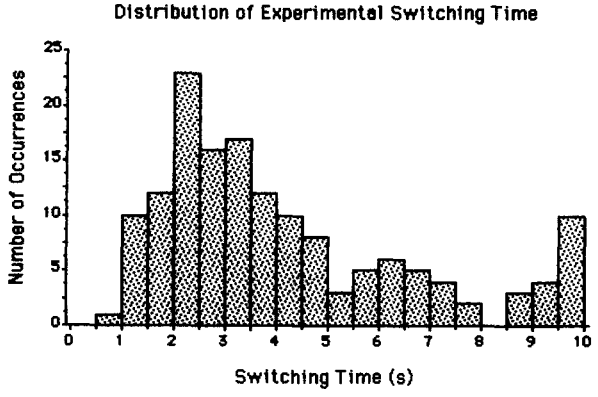

Fig. 3. The distribution of switching times (time from last change of control parameter frequency to the completion of switching) from all subjects and trials. Again we discarded trials in which the transition was induced by one of the torque pulse perturbations.

indicate, time scales relations are crucial to the interpretation of pattern stability and change in biological systems.

The final theoretical prediction from (1) that we test here concerns the switching time. On the transition plateau one may calculate from the transient probability distribution of relative phase, the probability mass of the peak at $\phi=0$ (in-phase mode). Its change in time is the probability that switching occurs in a given time interval (ref. [8], eq. (4.24)). In ref. [8] this distribution was calculated for very similar parameter values to the present ones (see fig. 11 in ref. [8]). The histogram shown in fig. 3 presents the experimentally determined switching times for the present experiment. A quite astounding agreement with the theoretical curve is observed, both in terms of the mean switching time and the shape of the distribution. Hence yet another feature of the dynamics of biological coordination is shown to follow in detail a simple stochastic-dynamic equation (1) for the collective variable ϕ. In particular we find that noise is qualitatively and quantitatively relevant for the switching behavior studied here, closely paralleling similar features in physical switching processes [13].

In summary, from previous experimental observations of critical fluctuations, and now the present research confirming critical slowing down and switching time predictions, we have shown that the present biological coordination problem may be understood – in considerable detail – as a nonequilibrium phase transition. The key concepts of stability and loss of stability shown here to play a central role, may also be crucial to understanding other biological ordering phenomena at both macroscopic (e.g. locomotor gait patterns and transitions) and microscopic (e.g. neuronal patterns) levels of description.

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