

## DYNAMICS GOVERNS SWITCHING AMONG PATTERNS OF COORDINATION IN BIOLOGICAL MOVEMENT

J.A.S. KELSO, J.P. SCHOLZ and G. SCHÖNER

*Center for Complex Systems, Florida Atlantic University, Boca Raton, FL 33432, USA*

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In new experiments on coordinated human movement we demonstrate that the process of intentionally switching from one pattern of coordination to another is governed by the dynamics of the patterns themselves. In particular, the stability of the patterns as established in earlier experiments on instabilities of these coordination patterns, determines the nature of the transient switching process. Measures such as the length of the transient (or switching time) and its distribution closely match theoretical predictions.

Nonequilibrium phase transitions are not only at the core of pattern formation in open physical (see e.g. ref. [1]) and chemical [2,3] systems but have recently been encountered also in several biological systems [4–7]. Among the dynamical features observed in such systems are the onset of oscillations, period doubling bifurcations and chaos. A central theme of the theory of nonequilibrium phase transitions is the reduction of the number of degrees of freedom that occurs near critical points where patterns form or change spontaneously. Emerging patterns may be characterized by only a few collective variables or order parameters whose dynamics are low dimensional [8]. In biological systems collective variables defining patterned states are not known *a priori*. Rather they have to be identified and their dynamics studied through a detailed stability analysis. Points of pattern change offer a useful departure point for implementing such an approach because they allow (1) a clear differentiation of one pattern from another; and (2) the study of stability and loss of stability. In nonequilibrium phase transitions, non-trivial predictions are associated with such loss of stability – including enhanced fluctuations and relaxation time of the order parameter – that may be subjected to direct experimental test.

Experiments by ourselves and others on coordination of rhythmic biological motion have found

spontaneous transitions in behavioral patterns when a relevant control parameter crosses a critical point [7,9,10]. We were able to identify the relative phase,  $\phi$ , among the rhythmically moving components as an essential collective variable, characterizing different temporal patterns (e.g. in-phase and anti-phase). As theoretically predicted [11,12] enhanced fluctuations of relative phase [13,14] and growth in relaxation time (the time it takes to return to the coordination pattern after a small perturbation [15,16] – both indicative of loss of stability – accompanied the transition from one (anti-phase) to the other (in-phase) pattern. Furthermore, details of the actual transient switching process, such as the mean duration, or so-called *switching time* and its distribution, were predicted [12] and found to be in striking agreement with theory [16].

Although the concepts and tools of nonequilibrium phase transitions provide a foundation for understanding behavioral pattern, its stability and change, on several levels of description [17,18] one may ask whether it is only the more physical aspects of pattern formation that have been addressed. Much of the research on biophysical and physiological systems (e.g. electrically stimulated neutral [4] or cardiac [6] tissue) deals with spontaneous pattern formation when the system is driven to its apparent limits of stability. From the point of view of a phys-

ical biology (see e.g. ref. [19]), it is relevant to ask whether the methods of low-dimensional dynamics may also allow us to address certain *essentially* biological aspects of pattern formation. For example, an essential feature of organisms is the ability to flexibly change behavioral pattern in an apparently purposeful fashion. Is the process of such intentional change from one pattern of coordination to another constrained (like spontaneous transitions) by the underlying pattern dynamics, in particular by the relative stability of the patterns? To answer this question, we report new experiments in which intentional changes among temporal patterns are characterized by the duration of the transient process, the switching time. We find that intentional behavioral change is governed by the underlying dynamics, i.e. by the different pattern stabilities. Our results are mapped onto a theoretical model [20,21] in which the intention to switch acts as a perturbation of the order parameter dynamics attracting them to the intended behavioral pattern.

The experimental task as rhythmic bimanual coordination in the transverse plane, in which the subject began either in the in-phase pattern (fingers moving toward and away from each other in unison) or the anti-phase pattern (fingers moving in parallel). A MacIntosh 512-E computer was programmed to produce an auditory metronome pulse (50 ms square wave) at a certain frequency which the subject was instructed to follow. Each trial began with a metronome signal that lasted for 10 movement cycles and was then turned off. Subjects were instructed to continue cycling their index fingers at the established frequency. After a further 10 cycles, an auditory tone occurred that was the signal for the subject to switch immediately to the other mode of coordination which the subject maintained until the end of the trial (an additional 20 cycles). The experimental paradigm is shown in fig. 1. The  $x$ - and  $y$ -coordinates of the two index fingers were recorded using the Watsmart<sup>TM</sup> motion analysis technique (Northern Digital Inc., Waterloo, Ontario, Canada). Light-weight, infrared light emitting diodes (IREDs) were mounted permanently in thimbles into which the subject's index fingers were inserted proximal to the distal interphalangeal joints. The thimble IREDs were placed so as to project toward two infrared sensitive cameras. IREDs were also at-

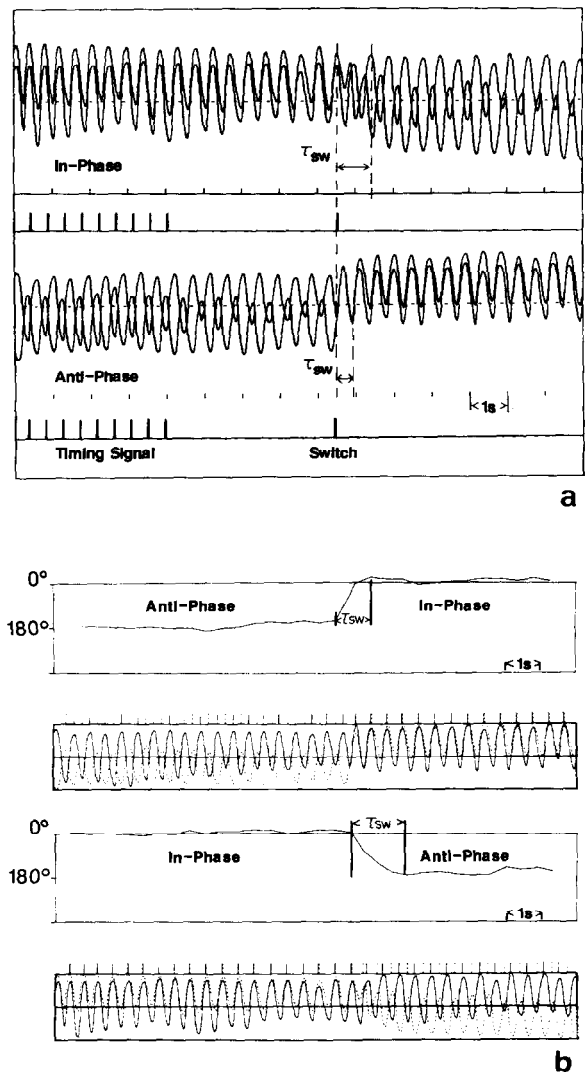


Fig. 1. Experimental paradigm for studying intentional switching among behavioral patterns. (a) The trajectories of the left and right index fingers are shown for two typical experimental runs with different initial conditions, in-phase (top) or anti-phase (bottom). The 10 metronome pulses (e.g. frequency = 2.25 Hz) establish the required oscillation frequency and are followed 10 cycles later by a single pulse that cues the intentional switching process. For the in-phase initial condition, the frequencies of the two hands are locked at 2.24 Hz before the transition and 2.18 Hz after the transition. The corresponding frequencies for the anti-phase initial condition are 2.19 Hz (before) and 2.16 Hz (after).  $\tau_{sw}$  is the estimated switching time in the two examples. (b) Sample switching time estimate ( $\tau_{sw}$ ) obtained from kinematic data of left (dashed) and right (solid) index fingers and the relative phase between them.

tached to the knuckles which acted as rigid segment monitors in relation to the finger movement. Before each experimental session, the calibration error of the cameras' position and direction in relation to the experimental field of view was calculated. To calibrate the cameras, a 30 mm cubic steel frame containing 24 IREDs and three permanently attached strober units were placed in the field of motion. These IREDs were pre-surveyed by computer (IBM PC/AT) to a resolution of 0.1 mm in 3 dimensions, thus allowing the frame to serve as a permanent reference point across experimental sessions. Once the frame and cameras were adjusted, a calibration program updated the mathematical 3D reconstruction constants and produced a calibration conversion of the raw 2D to 3D data trajectories. Calibration error for all sessions was less than 2 mm.

The IRED data were digitized in real-time at 200 Hz and stored on disk for later processing and analysis of the movement trajectories. In addition, electromyographic (EMG) recordings from the first dorsal interosseus muscles of the left and right indexed fingers were obtained using silver-silver chloride electrodes. These signals were preamplified on-site and dc coupled to an active high pass filter ( $-3$  dB cut-off of 75 Hz). The root mean square waveforms were sampled at 400 Hz.

Using interactive computer graphic displays, the main measure of interest – the length of the actual transient between the two modes of coordination – was determined, i.e., the total amount of time from where the relative phase,  $\phi$ , first diverged from its previous mean state ( $\phi \approx 0^\circ$  or  $\phi \approx 180^\circ$ ) to when the relative phase stabilized ( $\pm 15^\circ$ ) for two consecutive cycles. Both the time series of the two index fingers (fig. 1a) and the calculated relative phase,  $\phi$ , of their motions (fig. 1b, see refs. [7,14]) were used to estimate the experimental switching time,  $\tau_{sw}$ . The mean of these durations, averaged across trial runs (6) and subjects (4), the mean switching time, is shown in fig. 2 for each of the initial conditions (in-phase or anti-phase) as a function of the metronome frequencies used. Clearly, switching from the in-phase to the anti-phase mode is slower by approximately a factor of two than switching in the opposite direction. Analysis of variance of the switching time bears this difference out. Each subject exhibited a highly significant condition effect,  $F_s(1,60) = 52.5$  (JB),

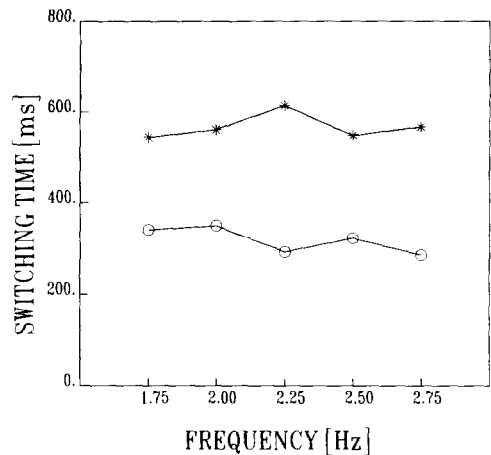


Fig. 2. The mean switching time (mean duration of transient from one mode of coordination to the other) collapsed over subjects and experimental trials as a function of the required oscillation frequency for switching from anti- to in-phase (circles) and from in- to anti-phase (asterisks).

20.7 (JD), 27.3 (JJ) and 100.4 (JS),  $P_s < 0.0001$ . Fig. 3 shows a histogram of the experimental distributions of switching times in the two directions. Note the longer tail and larger mean of the switching time in the in- to anti-phase condition.

Intuitively, these results are highly consistent with the differential stability of the two coordination pat-

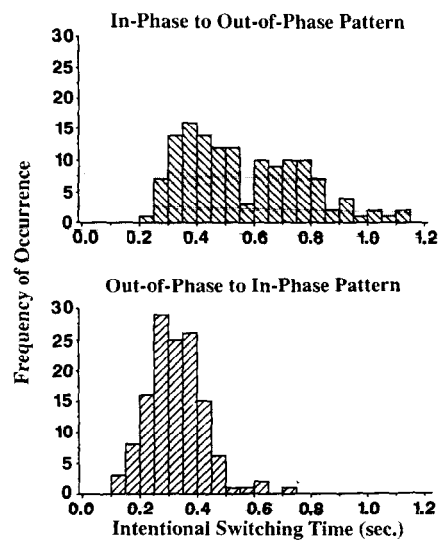


Fig. 3. The experimentally obtained frequency distributions of switching times collapsed over subjects and trials for both directions of switching.

terns established in studies of spontaneous transitions [7,13,14]. Within the theoretical framework of dynamic patterns [17,18,20,21] we can provide an explicit model that corroborates this intuition. Choosing relative phase as the relevant collective variable or order parameter we map observed patterns of coordination onto fixed point attractors of the dynamics of relative phase. In the theory for spontaneous transitions among modes of coordination, relative phase dynamics of the form

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

(where  $\xi_t$  is gaussian white noise of variance  $Q$ ) were identified, that accounted for differences in stability between the two basic patterns and the observed phase transition [11,12]. We assume that these so-called *intrinsic* dynamics are still valid in the presence of an intention to change behavioral pattern. This intentional information is assumed to be part of the relative phase dynamics such that it attracts relative phase to the intended relative phase. Neglecting hypothesized physiological processes associated with intentional acts [22] and being concerned only with intentional influences on the performed coordination patterns we assume, for the time being, that the intention becomes instantaneously effective. The onset time  $t_0$  of intention is therefore equated to the onset of the transient observed experimentally. The simplest functional form of the contribution of intentional information to the relative phase dynamics is

$$f_{\text{int}}(\phi, t) = -\theta(t - t_0) c_{\text{int}} \sin(\phi - \psi), \quad (2)$$

where  $\psi$  is the intended relative phase,  $c_{\text{int}} > 0$  is a parameter that measures the strength of this part of the dynamics and  $\theta$  is a Heaviside step function that is zero for negative arguments and one for positive arguments. The complete dynamics,

$$\dot{\phi} = f(\phi) + f_{\text{int}}(\phi), \quad (3)$$

describes both the initial and final stationary state as well as the transient switching process, similar to the case for spontaneous transitions [12]. We characterize the switching process by the switching time which is the length of the transient from one state to the other. This switching time is a random variable whose distribution can be determined from the time-dependent probability distribution of relative phase.

Eq. (3) defines a Fokker-Planck equation for this probability distribution that can be solved numerically. The initial distributions of relative phase are determined as locally stationary solutions around  $\phi=0$  or  $\phi=\pm\pi$  depending on the direction of switching (see refs. [12,21] for details).

Consistent with the assumptions stated above we obtain all parameter values for the intrinsic part of the dynamics,  $f(\phi)$ , from our experiments on spontaneous transitions [12-16]. Typical numerical values were  $a=1$  Hz,  $b=0.5$  Hz and  $Q=0.25$  Hz for which the two states at  $\phi=0$  and  $\phi=\pm\pi$  differ in their stability, and the relative phase fluctuations and relaxation times are of the correct order of magnitude. The only new adjustable parameter is  $c_{\text{int}}$  which in comparison to  $a$  and  $b$  measures the strength of the intentional influence on the dynamics. When  $c_{\text{int}}$  is chosen as  $c_{\text{int}} \approx 10$  Hz the correct order of magnitude for the switching times is obtained. The theoretical result for the probability density of switching times is displayed in fig. 4. Note the longer tail and larger mean of the distribution for switching from the more stable (in-phase) to the less stable (anti-phase) state,

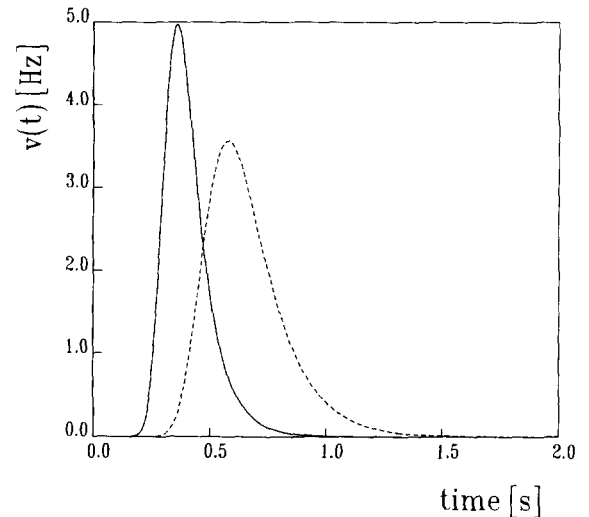


Fig. 4. The probability density of switching time for both directions of switching as obtained theoretically from the stochastic dynamic theory (eq. (3)) by numerically integrating the corresponding Fokker-Planck equation. The only adjusted parameter,  $c_{\text{int}}$ , was chosen to account roughly for the observed order of magnitudes of the mean switching times. The solid line is the anti-to in-phase distribution; the dashed line is the in-to anti-phase distribution.

in remarkable agreement with the experimental result (fig. 3). The mean switching times from these distributions are 0.41 s for switching from anti-phase to in-phase and 0.85 s for switching from in-phase to anti-phase, which should be compared to the data in fig. 1. More qualitatively, the theory can account for the ability of the system to sustain a pattern that is intrinsically unstable, because an intention (as part of the dynamics) can change the stabilities of the intrinsic dynamics. However, the presence of the intrinsic dynamics in eq. (3) is still felt as a difference in stability between the two patterns. We note in passing that a theoretical model can also be formulated on the level of the component oscillators [21].

In summary, we have shown experimentally that intentional switching among patterns of coordination is strongly influenced by the underlying behavioral pattern dynamics, i.e., by the different stabilities of the patterns. The match between these new experimental results and a theoretical model based on a generalization of dynamic pattern theory is quite satisfactory. The strategic step of identifying collective variables for behavioral patterns proves to be crucial in establishing a theory-experiment relation in this biological system, making it possible to define precisely those aspects of behavior that can be intentionally modified. More generally our findings suggest that the language and tools of stochastic dynamics are quite adequate to address inherently biological and even psychological questions.

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