

Evolution of Behavioral Attractors With Learning: Nonequilibrium Phase Transitions

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Learning a bimanual coordination task (synchronization to a visually specified phasing relation) was studied as a dynamical process over 5 days of practicing a required phasing pattern. Systematic probes of the attractor layout of the 5 Ss' coordination dynamics (expressed through a collective variable, relative phase) were conducted before, during, and after practice. Depending on the relationship between the initial coordination dynamics (so-called *intrinsic dynamics*) and the pattern to be learned (termed *behavioral information*, which acts as an attractor of the coordination dynamics toward the required phasing), qualitative changes in the phase diagram occurred with learning, accompanied by quantitative evidence for loss of stability (*phase transitions*). Such effects persisted beyond 1 week. The nature of change due to learning (e.g., abrupt vs. gradual) is shown to arise from the cooperative or competitive interplay between behavioral information and the intrinsic dynamics.

Among the adaptive features of living things, learning is remarkable in two respects. First, learning results in durable and innovative modifications of behavior according to specific constraints. Second, such a process unfolds on a time scale compatible with its experimental study. It is little wonder that most "historical" theories in psychology are theories of learning. Nowhere is this more apparent than in the field of perceptual-motor behavior, in which a great deal of work has attempted to unravel the mechanisms and the principles of learning a new skill (e.g., Adams, 1987; Marteniuk & Romanow, 1983; Newell, Kugler, van Emmerik, & McDonald, 1989; Pew, 1974; R. A. Schmidt, 1987).

In a now-classic paper, Fitts (1964) defined skill as a highly organized behavior in both space and time and the central problem of skill learning as how such organization or patterning comes about. Understanding the formation of spatiotemporal patterns of behavior in systems of many interacting components is not unique to psychology but straddles all of the natural sciences (e.g., Haken, 1977/1983a; Kelso, Mandell, & Shlesinger, 1988; Nicolis & Prigogine, 1989; Prigogine, 1980). For example, in synergetics (Haken, 1977/1983b, 1983a), a physical theory of self-organization and pattern

formation in nonequilibrium systems, a central theme is the reduction of the number of degrees of freedom near critical values of a parameter (so-called *control parameters*), where patterns form or change spontaneously. Emerging patterns are characterized by only a few collective variables (or *order parameters*) whose dynamics (equations of motion) are low-dimensional but nonlinear and hence capable of displaying a rich variety of behaviors, including multiple patterns, bifurcations, intermittency, hysteresis, . . . and even so-called deterministic chaos.

That coordinated actions might be addressed in the language of self-organization was suggested some years ago (Haken, 1977/1983b; Kugler, Kelso, & Turvey, 1980). An explicit theoretical treatment of spontaneous pattern formation in human behavior followed the discovery of *phase transitions* in studies of rhythmic bimanual movement patterns (Kelso, 1984). In this situation, the relative phase, ϕ , among the components was identified as a relevant collective variable characterizing different ordered patterns (in-phase and anti-phase), bistable in one regime and monostable in another. Theoretically predicted features of nonequilibrium phase transitions (Haken, Kelso, & Bunz, 1985; Schöner, Haken, & Kelso, 1986), indicative of loss of stability, accompanied the shift from one pattern (anti-phase) to the other (in-phase), including enhanced fluctuations of relative phase (Kelso & Scholz, 1985; Kelso, Scholz, & Schöner, 1986) and growth in relaxation time, defined as the time it takes to return to the coordination pattern after a small perturbation (Scholz & Kelso, 1989; Scholz, Kelso, & Schöner, 1987). Predicted features of the transient switching process itself, such as switching time and its distribution, were also confirmed in experiments on spontaneous (Scholz & Kelso, 1989; Scholz et al., 1987) and intentional switching (Kelso, Scholz, & Schöner, 1988; Scholz & Kelso, 1990; Schöner & Kelso, 1988a).

The concepts and tools of nonequilibrium phase transitions have been demonstrated to provide a foundation for understanding behavioral pattern, its stability and change in a

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variety of experimental model systems on several levels of description (for recent examples, see Kelso, Delcolle, & Schöner, 1990; R. C. Schmidt, Carello, & Turvey, 1990; Tuller & Kelso, 1991). In this article we extend the approach to the experimental study of an essential feature of living things, namely, their ability to change behavioral pattern according to environmental requirements or tasks to be learned. For the present purposes, learning is defined as a relatively permanent change in behavior in the direction of a to-be-learned pattern specified by the environment.

In the dynamic pattern perspective, the key to understanding learning lies in the joint concepts of *intrinsic dynamics* and *behavioral information* (e.g., Schöner & Kelso, 1988b). The former construct applies to situations in which behavioral patterns arise spontaneously as a result of *nonspecific* changes in a control parameter (such as the movement frequency in the case of bimanual coordination). The nature of these intrinsic dynamics must be established in order to know what can be modified or what can be learned. The concept of intrinsic dynamics offers a way to operationalize an issue that learning theorists have historically emphasized but have not been able to do much about, namely, that organisms acquire new forms of skilled behavior on the background of already existing capacities. The initial state seldom, if ever, corresponds to a disordered random network but is already ordered in some way. The concept of intrinsic dynamics, basically the layout of attractors (or *phase diagram*) of the collective variable dynamics, thus allows (a) any initial patterned state to be defined prior to learning, and (b) a study of how these dynamics evolve in time as a new task is learned.¹ As we shall see, predictions regarding the evolution of an individual subject's learning behavior follow from knowledge of the collective variable dynamics, which constitute a kind of baseline signature. Note that the term *intrinsic dynamics* is not to be equated with innate biological constraints but rather reflects capacities that exist at the time a new task is to be learned.

In this sense, the present approach offers an interesting point of departure from the views of the ethologists (e.g., Tinbergen, 1951), who stressed that learning must be preceded by a study of innate mechanisms, expressions of which, called fixed action patterns, were difficult to measure objectively. Instead, we provide an operational means to identify patterns and their dynamics using phase transitions as an entry point. A strong point of conceptual agreement, however, is that learning involves a "secondary modification" (Tinbergen, 1951, p. 6) of these so-called intrinsic dynamics. Psychology, for the most part, equates for the initial state by adopting as arbitrary a learning task as possible but avoids a direct confrontation with the issue itself. At other levels of description, the idea of intrinsic dynamics is consistent with evidence for spontaneous movements in early embryonic development that coincide with rhythmical activity in spinal cord neurons (Hamburger, 1970), as well as with evidence for neuronal circuits for central pattern generation (Grillner, 1975).

The second cornerstone of the approach, *behavioral information*, constitutes the influence of *specific* parameters on the collective variable dynamics. As an expression of environmental or task requirements, for example, behavioral information is part of the dynamics attracting the order parameter

toward a required behavioral pattern. By definition, behavioral information is measured by the same type of collective variables that are used to characterize performed coordination patterns. Learning, in the dynamic pattern framework, is the process by which environmental behavioral information defining a pattern to be learned becomes memorized behavioral information. A coordination pattern is learned to the extent that the intrinsic dynamics are modified in the direction of the to-be-learned pattern. Once learning is achieved, the memorized pattern constitutes an attractor of the behavioral pattern dynamics (see Schöner, 1989; Schöner & Kelso, 1988c, 1988d).

To see the interplay between intrinsic dynamics and behavioral information consider two sets of experiments that provide the backdrop for the present research (Tuller & Kelso, 1989; Yamanishi, Kawato, & Suzuki, 1980). Both deal with the concrete case of coordination of bimanual rhythmic movement. Thus, the behavior is a coordination pattern defined by stable and reproducible timing relationships between the system's components, in this case homologous fingers. In the Tuller and Kelso study, two visual metronomes, one for each finger, served to specify a temporal order. Frequency was fixed and the relative phase between the metronomes varied, thereby constituting a continuously available, environmentally specified pattern for the subject to match. Yamanishi et al. had subjects practice several such phasing patterns until a criterion level of performance was reached. That is, Yamanishi et al. required subjects to produce a memorized relative phase, whereas Tuller and Kelso kept environmental information available at all times. Regardless of the procedure, two robust results emerged. First, the observed pattern (the actual relative phase produced) was performed best when the task requirement corresponded to one of the intrinsic patterns (in-phase or anti-phase). Moreover, when the task required other relative phasing values, systematic deviation in the direction of the intrinsic patterns occurred. Second, the variability of the performed phasing pattern was minimal in the two intrinsic patterns and larger at intermediate conditions (coined the "seagull effect" by Kelso, Schöner, Scholz, & Haken, 1987, because of the characteristic M-shaped curve, reminiscent of the seabird in flight). The main point, however, is that performance is not simply better

¹ The term *phase diagram* derives from thermodynamics. More generally, a phase diagram defines regions in parameter space that do not exhibit qualitative changes of the system's dynamics (hence, similar phases in the thermodynamic context), as well as the boundaries across which such changes occur (hence, phase transitions). Mathematicians typically describe such qualitative changes in terms of *bifurcations*, whereas physicists tend to stick to the term *phase transitions*. In this article we use these expressions interchangeably. In nonlinear dynamical systems, change can be continuous or qualitative depending on the region in parameter space occupied. We use the image of *attractor layout* synonymously with *phase diagram* in this article in order to avoid confusion with the collective variable of our experimental system, *relative phase*, ϕ , which is a relative timing variable expressing the coordination between active components. However, it is important to note that a typical attractor layout, or phase diagram, may contain attractive, repelling, and saddle points that occupy basins and "separatrices" (e.g., Abraham & Shaw, 1982).

(small error, low variability) for in-phase and anti-phase patterns, but that other nearby phasings are biased or attracted toward these stable states.

The foregoing results were modeled theoretically by Schöner and Kelso (1988c, 1988d) at the level of both the relative phasing patterns and the component oscillators. In the Schöner–Kelso model, behavioral information, a relative phase required by either the environment, ψ_{env} (as in Tuller & Kelso, 1989), or by memory, ψ_{mem} (as in Yamanishi et al., 1980), acts on the pattern dynamics attracting the order parameter toward the required pattern. The two main experimental findings are accommodated as follows: When the intrinsic dynamics and behavioral information cooperate (i.e., the required pattern corresponds to one of the attractors for in-phase and anti-phase), the resulting state is highly stable, whereas when they compete, fluctuations occur and the resulting state is much less stable. In other words, the extent to which behavioral information cooperates or competes with the intrinsic dynamics determines the behavioral patterns observed.

An intuitive way to observe cooperative and competitive effects between behavioral information and the intrinsic dynamics is provided in Figure 1. Implementing a mathematical model means mapping reproducibly observed patterns (i.e., those that occur independent of initial conditions) onto attractors of a dynamical model (i.e., the asymptotically stable solutions of the collective variable equation of motion). The concrete model of the intrinsic dynamics (Haken et al., 1985), that is, a dynamical description in terms of relative phase between the oscillatory components without specific behavioral information, is defined by a vector field (a differential equation) expressing the rate of change in relative phase, $\dot{\phi}$, as a function of the derivative of its potential, $V(\phi)$:

$$\dot{\phi} = -\frac{dV(\phi)}{d\phi} + \sqrt{Q}\xi_t, \quad (1)$$

where $V(\phi) = -a \cos(\phi) - b \cos(2\phi)$ and $\sqrt{Q}\xi_t$ is Gaussian white noise of strength Q . Noise is introduced in Equation 1 because all real systems described by low-dimensional dynamics are coupled to many subsystems at a more microscopic level (e.g., in the present case at a neuromuscular level), which act as stochastic forces on the collective variable, ϕ . One may view noise as a continuously applied perturbation that produces deviations from the attractor state. Such fluctuations are conceptually important in dynamical modeling of phase transition or bifurcation (see Footnote 1) phenomena and are essential in effecting transitions (Schöner et al., 1986). Intuitively, fluctuations test the stability of an attractive state and allow the discovery of new (or other) available states.

Complying with periodicity and symmetry requirements, Equation 1 captures the observed, so-called pitchfork bifurcation, namely, a bistable regime below the critical point and a monostable regime beyond it. Thus, for $0 < a < 4b$, two stable states $\phi = 0^\circ$ and $\phi = \pm 180^\circ$ exist, whereas for $a > 4b > 0$, only $\phi = 0^\circ$ remains stable. Local measures of the in-phase and anti-phase modes (Kelso & Scholz, 1985; Kelso et al., 1986; Scholz et al., 1987) allow for the easy determination of the a , b , and Q parameters in Equation 1 (Schöner et al., 1986).

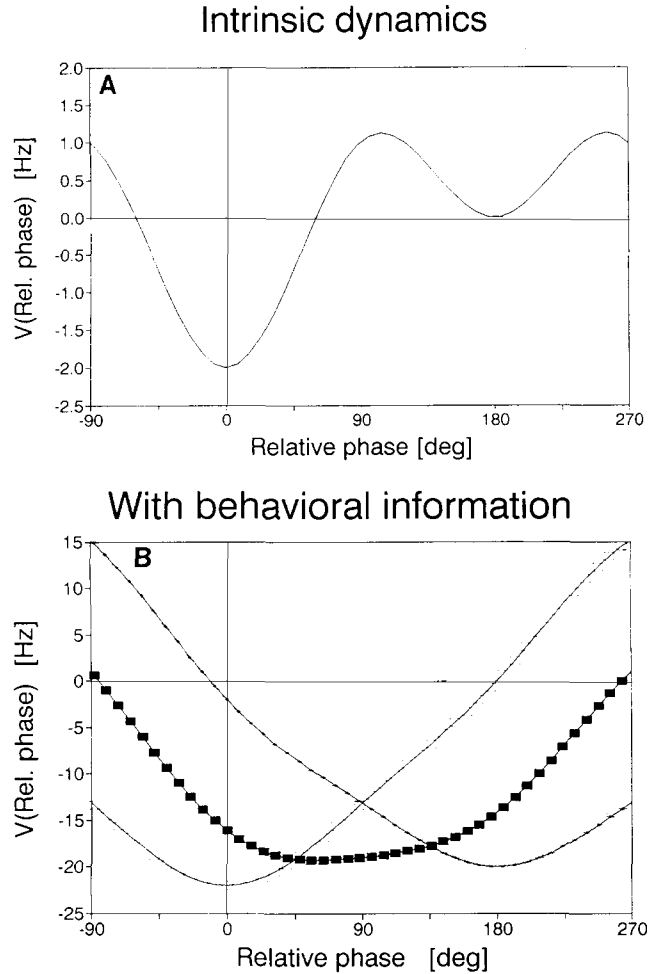


Figure 1. Visualization of the potential ($V(\phi)$) of the pattern dynamics. (In Panel A, the potential of the intrinsic dynamics is displayed in the bistable regime, using Equation 1 with a and $b = 1$ Hz. In Panel B, requiring a pattern introduces behavioral information acting at $\psi = 0^\circ$ [\square], $\psi = 180^\circ$ [$*$], and $\psi = 90^\circ$ [\blacksquare], using Equation 2 with a and $b = 1$ Hz and $c = 20$ Hz.)

Panel A of Figure 1 plots the potential corresponding to Equation 1 in the bistable regime of the intrinsic dynamics. The relative stability of the two attractors at 0° and 180° is reflected by the depth of each well, and their attraction is reflected by the slope at each point of the curve. Such a picture makes it clear how the system will eventually relax into one of the two attractors as long as the initial condition is in the basin of attraction of one of the modes. Note that $\phi = 90^\circ$ and its symmetry partner ($\phi = 270^\circ = -90^\circ$) are unstable fixed points of the intrinsic dynamics. Any small perturbation causes the system to relax to one of the stable patterns.

The model, when environmental information specifying a required relative phase, ψ , between the pacing stimuli is included, reads as follows:

$$\dot{\phi} = -\frac{dV_\psi}{d\phi} + \sqrt{Q}\xi_t, \quad (2)$$

where now $V_{\psi} = V(\phi) - c \cos((\phi - \psi)/2)$. $V(\phi)$ is the potential pertaining to the intrinsic dynamics given in Equation 1, and the second term is the simplest function (conforming with certain periodicity requirements, see Schöner & Kelso, 1988c) that attracts the relative phase toward the required phasing. Note that this new term breaks the $\phi \leftrightarrow -\phi$ symmetry just as the metronomic pacing does in the experimental model system. The parameter c represents the strength of environmental information on the intrinsic dynamics and can again be measured experimentally (Schöner & Kelso, 1988c). Panel B of Figure 1 plots the potential of Equation 2 for three required relative phases, 0° , 90° , and 180° (\square , \blacksquare , and $*$ curves, respectively). Using model parameters corresponding to the intrinsic dynamics and a value of the parameter c consistent with Tuller and Kelso's (1989) data, two features emerge clearly. On the one hand, when the required relative phase coincides with one of the stable intrinsic patterns—namely, $\psi = 0^\circ$ or 180° —the minimum of the potential is exactly at the required relative phase, and its shape is well-articulated (less so for $\phi = 180^\circ$ than for $\phi = 0^\circ$, reflecting the differential stability of these two states). This case represents the *cooperation* between extrinsic requirements and intrinsic dynamics. On the other hand, if the required relative phase does not correspond to one of the intrinsic patterns—for instance, $\psi = 90^\circ$ —a *competition* between the two forces pulls the minimum away from the required relative phase (see the \blacksquare curve of Figure 1, Panel B). The potential is deformed, and a wider, less articulated minimum results because of the competitive interaction between the intrinsic dynamics and the behavioral information.

This conceptualization opens a window into learning. Consider the case where a subject must learn a phasing pattern specified environmentally (e.g., $\psi_{\text{env}} = 90^\circ$) that does not correspond to either of the intrinsically stable patterns. As this new relative phase is learned, the influence of the initially bistable dynamics attracting the system to in-phase or anti-phase patterns dwindles, because of the progressively overwhelming attraction by the pattern being memorized (ψ_{mem}). Thus, with the passage from environmental to memorized information, a *phase transition in learning* is predicted. In particular, the least stable of the two intrinsic patterns, the anti-phase state, should lose stability as the strength of memorized information increases. This should take the form of a qualitative change in the pattern dynamics and the emergence of a new behavioral attractor corresponding to the learned pattern (Schöner, 1989; Schöner & Kelso, 1988c).

We may summarize the present approach to learning in the form of a set of questions and their proposed answers.

1. What is learned? Here we provide a means for evaluating the existing structure (initial state of the behavioral pattern dynamics) before exposure to a new task. Each individual possesses his or her own intrinsic dynamics, which may reflect contributions from ancestry and prior experience. By determining the phase diagram prior to any practice, it is possible to identify individual constraints that may exist *before* the learning process begins. By the same token, the dynamics of learning itself may be evaluated (e.g., continuous versus abrupt transitions, multistability, loss of stability) by probing the phase diagram in time *as practice proceeds*. Thus, the evolution of the learning process, seen as a specific modifica-

tion of the intrinsic dynamics, may be studied directly, not simply as improvements in performance in a single task.

2. What form does the learning process take? By probing the behavioral pattern dynamics, a full view is provided of how an already organized structure evolves toward new (or different) forms of behavior, informing as to how such structural alterations are at the origin of the observed change in behavior. Learning, in the present model system, may involve an order-to-order transition, a qualitative change in the phase diagram. This is a far cry from the "acquisition" of habits and associations through repetition that have tended to dominate, in one way or another, theories of learning. More modern information-processing and feedback models of skill acquisition that incorporate storage and retrieval stages (e.g., Welford, 1976) assume that gradual changes occur in an underlying mental schema. The present approach may be interpreted as an operationalization of the schema concept in terms of the interplay between dynamical processes (e.g., competition and cooperation between behavioral information and intrinsic dynamics), the consequence of which defines the nature of change.

3. What mechanisms and principles govern changes due to learning? Whether some tasks are learned more easily than others (e.g., in terms of rate of learning and performance efficiency) depends on the extent to which behavioral information cooperates or competes with the intrinsic dynamics.² If for some reason the pattern to be learned coincides with one of the intrinsically stable patterns, then cooperative processes dominate, performance will improve rapidly, and no phase transition is initially predicted. If the behavioral requirements conflict with the initial pattern intrinsic dynamics, then, as the strength of memorized information increases, the less stable pattern will lose stability, and a phase transition will be seen.

The following experiment constitutes an effort to study learning in the context of this deductive, dynamic pattern approach. The acquisition process of the behavior in question, learning a single relative phase that may or may not correspond to one of the intrinsic patterns, is evaluated as it proceeds in real time. Probes of the phase diagram are conducted periodically to look for predicted qualitative (and corresponding quantitative) evidence for changes in the pattern dynamics. Other issues, such as the reason for persistence of learning over time and the system's ability to generalize to other unpracticed patterns, are addressed in the General Discussion section.

Method

The learning procedure entailed five consecutive daily sessions in which the same required pattern was practiced repeatedly, with knowledge of results given after every trial. In between learning trials, the phase diagram (a set of relative phasing patterns between 0° and 180°) was systematically probed, providing an image of the individ-

² This is the reason why the concept of intrinsic dynamics is so central to the present approach. Without knowledge of the system's initial pattern dynamics, change due to cooperative or competitive processes is impossible to interpret.

ual's intrinsic dynamics at that moment in time. One week later, a follow-up session was given in order to investigate the expected long-term effects of practice.

Subjects

Five subjects (4 women and 1 man, mean age = 22.3 years) participated in the experiment. All were right-handed for writing and were paid \$50 after completion of the entire experiment. Two subjects (B.A. and J.T.) did not complete the entire session on Day 1 because of compelling time constraints.

Apparatus

Subjects were seated in front of a black board displaying a "visual metronome" similar to that used by Yamanishi et al. (1980) and Tuller and Kelso (1989). It consisted of two light-emitting diodes (LED) that were placed 8 cm apart at gaze height, forming a visual angle of about 5°. The onset of each LED was individually controlled through a microcomputer (a single light pulse lasted 40 ms), so that different relative phases (RP) between LED onsets were possible. To define RP in this experiment, the right LED onset served as the reference; thus, a positive RP meant that the left LED onset lagged the right LED onset in time, and conversely. The subject's hands were slipped into a bimanual finger apparatus, which allowed flexion-extension movements of the index fingers about the metacarpophalangeal joint to be monitored through the rotation of two coaxial potentiometers. The fingers could freely oscillate in the horizontal plane within their natural anatomical boundaries (i.e., no abutment and negligible friction). The visual metronome signals and the output from the potentiometers were digitized in real time through a mini-computer (sampling frequency: 200 Hz per channel). A connected workstation returned knowledge of results to the subject on a screen located beside the visual metronome.

Procedure

The specific task requirements were similar to those imposed in the experiments by Yamanishi et al. (1980) and Tuller and Kelso (1989). Subjects were instructed to flex each finger in temporal coincidence with the onset of the ipsilateral LED. No other constraint on motion was imposed, such as a required amplitude, but subjects were asked to produce movements as smoothly and regularly as possible.

On the first day, prior to any experimental practice trial, subjects were acquainted with the task and the apparatus through informal familiarization, performing various finger movements according to the metronome. However, these patterns were different in both phasing and frequency from those used in the actual experiment.

A typical daily session comprised three blocks of five *learning trials*, in which a required RP of 90° was practiced. Each learning trial lasted 20 s, and the metronome frequency was set to 1.75 Hz. This frequency was chosen as a value at which multistability of finger patterns is observed (i.e., above about 2.2 Hz, only the 0° pattern is stable). Moreover, the frequency was high enough to prevent subjects from responding reactively to each LED pulse by an independent finger flexion; rather, it induced them to perform the task by coupling the fingers with the metronome. In other words, subjects had to generate a coordinated phasing pattern that eventually matched the required RP. After each learning trial, qualitative and quantitative knowledge of results about produced RP and pattern synchronization were provided to the subjects, and their performance was described and discussed accordingly.

At the beginning and end of each daily session, as well as between training blocks, a *scanning run* was carried out in order to probe the current phase diagram (i.e., there were four scanning runs per day). During each scanning run, the required RP was progressively increased from 0° (simultaneous blink of the two LEDs) to 180° (alternate blink) by 12 discrete steps of 15°. The plateau duration for each required RP was 20 s. Each step in required RP was signaled to the subject by an auditory tone. The metronome frequency was identical to that of the learning trials, namely, 1.75 Hz. It is important to emphasize that no knowledge of results about performance was given during or after the scanning runs.

In the follow-up session (7 days after the last learning session), two *recall trials* were administered, separated by a conventional scanning run. In a recall trial subjects had to reproduce from memory the pattern required in the learning trials (i.e., RP = 90°) for 1 min. A central LED was blinked at a frequency of 1.75 Hz for pacing purposes. No information pertaining to the required RP or actual performance was provided. The longer trial duration was to increase chances of detecting any drift in performance with time, that is, to assess pattern stability over a reasonable time span.

Measures

The main dependent variable was a point estimate of the actually produced RP, as illustrated in Figure 2. The time difference between the occurrence of maximal flexion of the left finger (t_{target} on the lower curve) and that of the right finger (t_o on the upper curve) closest in time was first calculated. This duration was expressed in degrees relative to the period of the right finger cycle ($t_{\text{reference}} - t_o$; see complete formula in Figure 2). This method yields an RP that ranges between -180° and 180° , where a positive value indicates that the left finger lags with respect to the right finger, and vice versa. Although such a point estimate does not reflect the average RP over a complete cycle because of probable asymmetries and irregularities in actual motion, it precisely assesses the effects of the task requirements on behavior—namely, to flex each finger synchronously with the respective LED. Moreover, it can be shown (e.g., Kelso & Schöner, 1988) that such a measure adequately captures the instantaneous relative timing between the moving components.

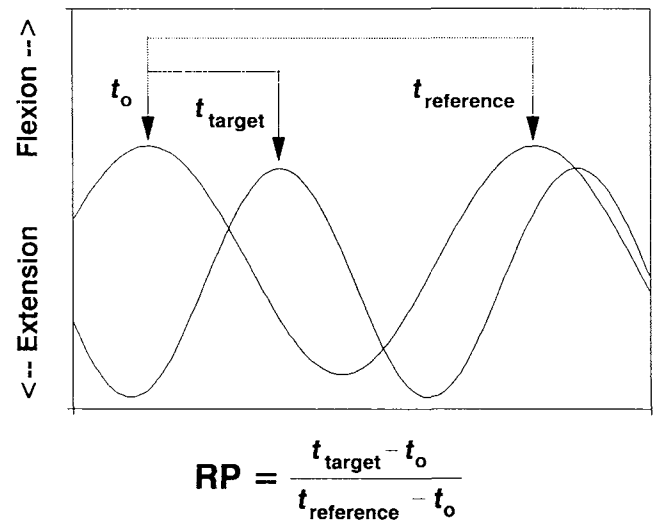


Figure 2. Calculation of the point-estimated relative phase (RP; see text for details).

To assess synchronization of the produced phasing pattern with the metronome, the same formula as in Figure 2 was applied to compute the RP between LEDs and fingers, namely, lag. Lag was arbitrarily defined with respect to the leading events of both patterns, the right LED onset and the maximal flexion of the right finger being the reference events for the metronome and the finger patterns, respectively. Accordingly, a positive lag indicates that the finger pattern lags behind the metronome, and vice versa. Note that the left finger lag with respect to its LED is easily computed using lag and between-finger RP.

Figure 3 reproduces an actual knowledge-of-results display after a learning trial. In the bottom window of the screen, the time series of both finger motions are drawn, along with the onsets of the right metronome LED (i.e., the leading LED used for lag calculation). In the upper window, the produced relative phase and lag are displayed as a function of time. At the bottom of the screen, some relevant statistics of these cycle-by-cycle measurements over a trial were also furnished in order to quantify improvement in performance across trials. In the instance illustrated in Figure 3, the subject produced a fairly stable pattern at about 104° of RP, with synchronization in-

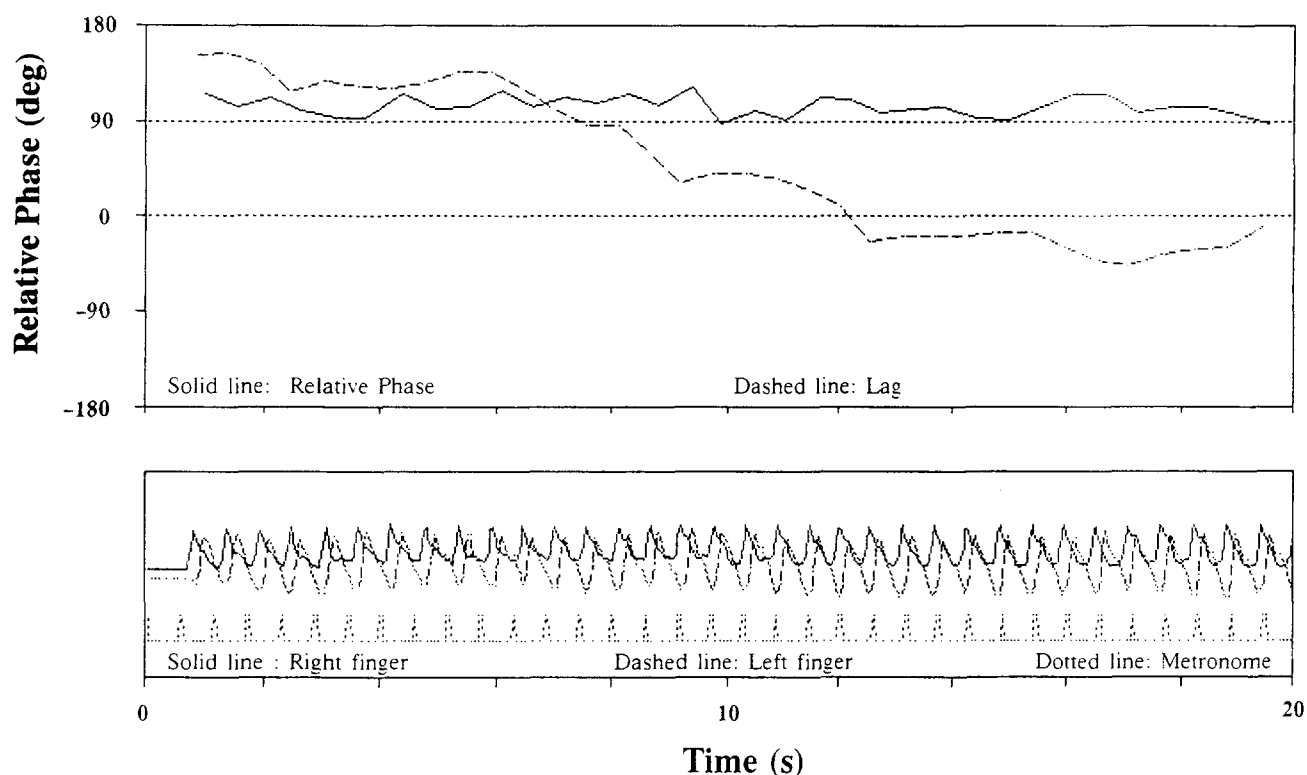
creasing from about 130° of lag to a small lead of about 40° at the end of the trial.

Results and Discussion

We first present the data on practice, scanning, and recall. Then we try to establish the relationship between these results in terms of learning as a long-term modification of the intrinsic dynamics. Finally, we provide more support for this contention by focusing on specific features pertaining to individual differences among subjects.

Learning Task

A picture of changes in performance with practice is provided in Panel A of Figure 4. The upper curves (solid lines) and lower curves (dotted lines) represent the mean RP within a trial and its standard deviation, respectively, collapsed across subjects. The scores are plotted as a function of practice trials



0 phase		Abs phase		Lag		# Cycles
104.2	9.13	104.2	9.13	48.14	67.35	0

Figure 3. Display for knowledge of results after a learning trial. (In the bottom window, the time series of the right [solid line] and left [dashed line] finger movements and of the right LED level [dotted line] are displayed for a typical run. In the top window, the corresponding cycle-by-cycle relative phase [solid line] and lag [dashed line] are plotted as a function of time. The mean and standard deviation of relative phase [ranging from -180° to 180°] are given under "0 phase," those of its absolute value [ranging from 0° to 180°] under "Abs phase," and those of lag under "Lag." Because of the wrapping of lag around the 0° - 360° span, "# Cycles" displays the final number of cycles that the produced pattern lags or leads with respect to the metronome.)

and are joined together within each day of training. In both graphs, the vertical bars indicate the variability across subjects (i.e., ± 1 SD). The graphs displayed in Panel A of Figure 4 present several characteristic features of classical "learning curves" as practice of the 90° pattern proceeds from Day 1 through Day 5. Mean produced RP (upper curves) progressively reaches the required RP of 90° with practice, although some fluctuations still remain across trials after 5 days of practice. Mean within-trial SD (lower curves) gradually decreases by an average amount of 50%. Meanwhile, the between-subject SD (denoted by the vertical bars) diminishes substantially for both scores, suggesting that a decrease in pattern variability occurs for all subjects. Very roughly, both the mean RP and its SD have stabilized by the first 2 days of practice.

Over successive days, decreases in within-trial variability go along with a reduction in fluctuations across trials for both mean RP and SD. Such fluctuations are presented in Table 1, operationalized by the SD of within-trial mean RP and SD

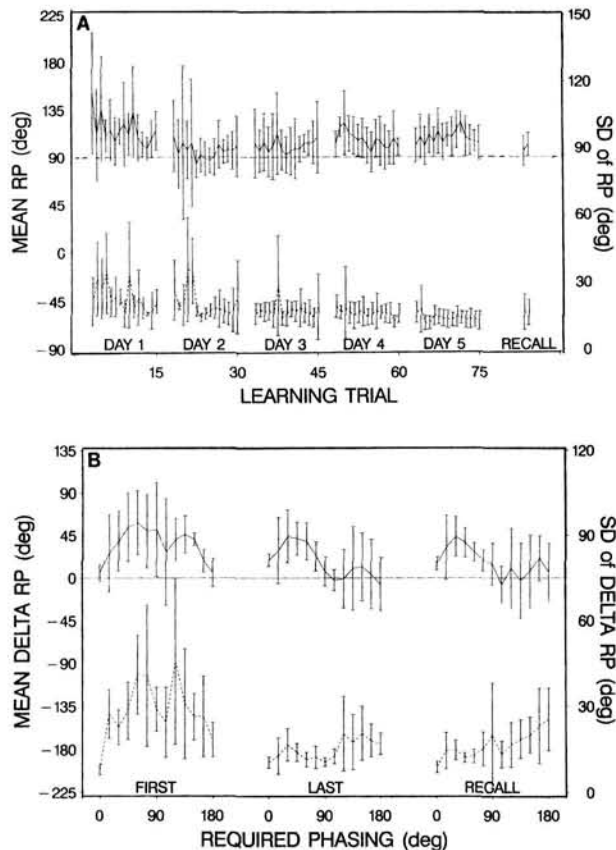


Figure 4. Effects of learning in the learning and scanning tasks over the 5 days of practice, averaged across subjects (vertical bars encompass ± 1 between-subject SD). (Panel A presents the average within-trial mean [upper solid line] and SD [lower dotted line] of produced relative phase [RP] as a function of practice and recall trials. Panel B displays the average first, last, and recall phase diagrams. Within-plateau mean [upper solid line] and SD [lower dotted line] of delta RP [error between produced and required relative phase] are plotted as a function of the required relative phase, stepped by 15° between plateaus.)

Table 1

Across-Trial Fluctuations of the Mean and the Standard Deviation of Relative Phase as a Function of Day and Subject

Subject	Day	n	M	SD
B.A.	1	10	15.29	15.22
	2	15	21.63	13.72
	3	15	13.87	14.37
	4	15	7.09	2.91
	5	15	7.64	1.89
J.T.	1	10	54.20	20.56
	2	15	40.08	11.93
	3	15	19.41	7.86
	4	15	19.79	9.38
	5	15	12.76	6.58
M.S.	1	15	22.39	11.89
	2	15	16.46	3.89
	3	15	13.94	2.74
	4	15	9.27	3.37
	5	15	22.57	28.38
			9.45 ^a	5.88 ^a
S.B.	1	15	48.72	18.88
	2	15	14.49	15.85
	3	15	12.75	4.29
	4	15	12.08	3.14
	5	15	6.05	3.29
T.M.	1	15	24.46	8.92
	2	15	7.86	3.54
	3	15	9.63	3.16
	4	15	12.10	3.45
	5	15	13.03	2.73

^a If Trial 11 is suppressed.

over the 15 trials constituting each daily session. Results in Table 1 indicate that for all subjects, fluctuations of mean and SD within a day diminish with practice by more than 70% between Day 1 and Day 5. Contrasting with this general tendency, the large fluctuations exhibited by Subject M.S. on Day 5 are mostly due to a single trial (i.e., Trial 11), in which the finger oscillations were not frequency-locked (right finger frequency = 1.84 Hz; left finger frequency = 1.72 Hz). As a result, a highly variable RP was produced, ranging between -180° and 180°. If this trial is omitted from the calculations, the across-trial fluctuations of mean RP and its SD are more in keeping with those of the other subjects. This trial was thus omitted from all subsequent analyses, because RP makes no sense without frequency-locking between the two components. A one-way multivariate analysis of variance (MANOVA) with repeated measures on day confirmed the decrease in across-trial fluctuations for mean RP and SD, $F_{(4, 16)} = 5.25$ and 6.34 , respectively, $p < .01$. For both dependent measures, post hoc analyses revealed significant differences between Day 1 and Days 4 and 5, $F_{(1, 4)}$ ranging between 8.91 and 40.67 , $p < .05$.

However, the foregoing results deserve a careful look. First, as indicated earlier, most of the improvements in performance take place in the first 2 days. Changes in mean RP and SD occur mainly during this interval (see Panel A of Figure 4), along with a sharp reduction in within-day fluctuations for

both variables (see Table 1). Second, large differences among individuals are obviously downplayed in this overall analysis. A MANOVA (Subject \times Day \times Trial) with repeated measures on day and trial showed that the three-way interaction was significant for both mean RP and *SD*, $F_s(144, 550) = 13.48$ and 6.69, both $ps < .01$, respectively. We shall dissect this interaction when we examine individual subjects' performance later.

Scanning Task

By gradually varying required RP from 0° to 180°, we aimed to establish the phase diagram of the underlying dynamics. In order to sketch changes over the entire experiment that were due to practice, Panel B of Figure 4 displays results, averaged across subjects, obtained during the first and last scanning probe (i.e., before and after practice), along with those pertaining to the recall session (left, middle, and right parts of Figure 4, Panel B, respectively). Each part contains two series of curves. The upper group (solid lines) plots the mean delta RP as a function of the required RP. Delta RP is the difference between the actually produced RP and the required RP. One can interpret delta RP as an error variable that takes on a systematic structure depending on the required RP. When required RP is overestimated (i.e., produced RP is larger than required RP), delta RP has a positive value, and conversely. Note that if the intrinsic dynamics do not come into play, actual RP would perfectly match required RP; thus, mean delta RP would be a flat curve lying on the zero (dashed) line. The lower graphs (dotted lines) in Figure 4, Panel B, display the corresponding *SD* of delta RP as a function of required RP, collapsed across subjects. In both curves, the vertical bars encompass ± 1 between-subjects *SD*.

For the first scanning run (left part of Panel B), mean delta RP exhibits a humped curve as a function of required RP; that is, it is lowest when required RP is 0° or 180°. Between-subject variability (vertical bars) is also lowest around these two values of required RP. The negative slope between 135° and 180° of required RP reflects attraction to the anti-phase pattern, because intermediate RPs are overshoot in the direction of 180°. Relative phase variability (bottom curves) is lowest at 0° and 180° and increases markedly at intermediate values, indicating that in-phase and anti-phase patterns are the most stable, with the latter more variable than the former. Also, between-subject variability is smallest at these required phasings. The picture concerning the first phase diagram is in keeping with the so-called "seagull effect." However, the apparent absence of attraction (a negative slope) of nearby phasing patterns toward 0° results partly from the averaging across subjects and partly from the experimental design. Because the required phasing was always increased in an ascending order, with an auditory tone signaling each step, subjects may have been induced to escape the in-phase pattern as soon as a difference in required RP was perceived or cued. By contrast, in both the Tuller and Kelso (1989) and Yamanishi *et al.* (1980) studies, in which a negative slope at 0° was observed, the required RP was assigned randomly in separate experimental runs.

An altogether different phase diagram emerges in the last probe performed at the end of Day 5 (middle part of Figure 4, Panel B). Mean delta RP is still low around 0° and 180°, but now also around 90°. Moreover, attraction to the 90° pattern is clearly demonstrated by the negative slope of curves in the interval from approximately 60° to 105° of required RP. At higher required RPs, the larger variability across subjects (vertical bars) suggests a more differentiated behavior, which we will discuss in a following section. The corresponding bottom curves show that the 0° pattern is still stable, because the *SD* is low. Between 60° and 105° of required RP (while the 90° pattern is actually being performed), *SD* is equally low. For required phasings greater than 105°, however, *SD* becomes larger for all subjects, along with an enhancement in the variability across subjects. This finding suggests partial loss of stability of the anti-phase pattern, leading to erratic performance (i.e., inconsistent across trials and subjects) when the required RP is above 120°.

Our theoretical interpretation of the results in Figure 4, Panel B, is that the initial intrinsic dynamics underwent a dramatic change over days of practice: From initially bistable dynamics, in which the 0° and 180° patterns constitute behavioral attractors, tristable dynamics emerge, in which the 90° pattern becomes an attractor as well. This qualitative alteration of the phase diagram constitutes a *phase transition* on the time scale of the experiment. Such an interpretation is corroborated by statistical analysis. Delta RP scores within the plateaus closest to the 0°, 90°, and 180° patterns were pooled into three intervals, from 0° to 30°, from 75° to 105°, and from 150° to 180°, respectively, representing, as it were, the basins of attraction surrounding the patterns.³ Day \times Pattern MANOVAs with repeated measures on day and pattern were carried out for the mean and the *SD* of delta RP. The results for mean delta RP show a significant Day \times Pattern interaction, $F(2, 28) = 5.88, p < .01$. Post hoc contrasts revealed that mean delta RP is different between days for the 90° pattern, $F(1, 14) = 6.25, p < .02$, whereas no significant difference is revealed for the other patterns. The Day \times Pattern interaction is also significant for the *SD* of delta RP, $F(2, 28) = 5.45, p < .01$, in addition to the main effect of day, $F(1, 14) = 25.36, p < .01$, which reflects the general decrease in pattern variability. Post hoc analysis of the interaction revealed a significant day effect only for the 0° and the 90° patterns, $F_s(1, 14) = 21.16$ and 4.57, $ps < .05$, respectively, supporting the interpretation that an attractor emerged at the 90° pattern between the first and last day of practice. Small group differences in mean and *SD* of delta RP between the first and last probes for the 0° pattern, $F_s(1, 4) = 12.07$ and 10.19, $ps < .05$, are not readily interpretable. Here again, however, we are temporarily postponing consideration of differences among subjects.

Recall

To test whether changes in performance persist, we considered the results of the recall session, administered 1 week after

³ We thank an anonymous reviewer for suggesting this analysis.

the last day of practice (i.e., Day 5). In the right-hand part of Panel A of Figure 4, the within-trial mean and *SD* of produced RP during the two trials of the recall session are plotted, slightly separated from the rest of the graph. The scores seem quite similar between the 15 learning trials of Day 5 and the 2 recall trials. A repeated measures MANOVA revealed a significant day effect for both dependent variables, $F_s(5, 95) = 10.06$ and 4.57 , $p < .01$, respectively. Post hoc analysis indicated that the mean RP was significantly different between Day 1 and the following days, $F_s(1, 19)$ ranging between 12.89 and 23.40 , $p < .01$, and between Day 1 and recall, $F(1, 19) = 17.68$, $p < .01$. Thus, there were no significant differences across days, including recall, after Day 1. The *SD* followed along similar lines. Variability decreased across days, with Day 5 different from Day 1 and Day 2, $F_s(1, 19) = 11.11$ and 17.31 , $p < .01$, respectively. Recall was not significantly different from the last day of practice. To sum up, the long time interval between learning and recall sessions did not entail changes in performance beyond the normal fluctuations during the preceding days. Practice therefore led to fairly long-lasting changes in performance, consistent with the interpretation that the required RP of 90° was learned.

In the right-hand side of Figure 4, Panel B, the last scanning probe on Day 5 (middle graphs) can be compared with the probe carried out during the recall session (right graphs). Globally, no major changes can be detected after an interval of 7 days. The main features of the typical layout on Day 5 are still present in the recall session: stability of the 0° pattern (low *SD*); attraction of produced RP to 90° for the mid-range required RPs (negative slope); stability of the 90° pattern itself (low *SD*); and relative instability of the 180° pattern (high *SD* and large between-subject variations). Statistical analysis confirms this picture. Day \times Pattern MANOVAs with repeated measures on both factors were carried out for delta RP and its *SD*. Both dependent measures showed the trivial one-way effect of pattern, $F_s(2, 28) = 6.66$ and 9.63 , $p < .01$. Notably, the Day \times Pattern interaction was not significant. Hence, there is no suggestion of any change in the produced RP as a function of the variation in the required phasing between Day 5 and the recall session. We may interpret this result to mean that the attractor layout following extended practice remains unaffected over time. Indeed, post hoc contrasts failed to show any significant difference in mean delta RP and *SD* between probes for all three patterns, and the pattern of contrasts between the recall and the first probes is exactly the same as that described previously for the probe on Day 5. These results strongly suggest that the 5 days of practice led to a modification of the dynamics that was not temporary, but persisted over a fairly long time span.

Comparison Between Learning and Scanning

If both tasks involved the same underlying dynamics, we would expect the large relative phase (RP) fluctuations produced across trials and days during the learning trials to correspond to comparable changes in performance when 90° RP was required in the scanning trials. Such a comparison is drawn in Panel A of Figures 5–7 for 3 prototypical subjects, T.M., M.S., and J.T., respectively (the performances of Sub-

jects B.A. and S.B., which are not reported, are similar to that of M.S.). In each panel, upper curves (solid lines) and lower curves (dotted lines) display mean produced RP and its *SD*, respectively. Performance in the learning trials is coded by a star (\star). The squared curves (\square) correspond to the mean and *SD* produced within the 90° required RP plateau of a probe. Each probe is plotted at the same position on the abscissa as the learning trial closest in time. Panel A of Figures 5–7 indicate a close covariation between learning and scanning scores across trials and days. In particular, the large jumps in produced RP between days in the learning task tend to coincide with similar variations in the scanning task. Thus, within-day as well as across-day fluctuations, which unfold on two separate time scales, are captured coherently, suggesting that both tasks are tapping into the same dynamics. Such an interpretation is also supported by a regression analysis performed on the mean RP and *SD*, collapsed across subjects, $R^2 = .342$, $p < .01$, and $R^2 = .291$, $p < .01$, respectively. In a subject-by-subject analysis, the covariation for the mean and the *SD* was significant for all subjects except B.A.

Another feature of the comparison between learning and scanning performance is the difference among subjects during the first 2 days. Roughly speaking, M.S., S.B., and B.A. (see Figure 6, Panel A, for an illustration) were able to execute a 90° pattern in a fairly precise manner quite early in practice. In contrast, T.M. and J.T. (Figure 5, Panel A, and Figure 7, Panel A, respectively) did so only during Day 2. If we assume the existence of common dynamics for both tasks, the various behaviors exhibited on the very first learning trial must reflect differences in the initial intrinsic dynamics. We examine this issue next.

Individual Differences in Learning: Cooperative and Competitive Effects

One central theme of our approach is that all observed behavioral patterns and their dynamics emerge ultimately from the interplay between competitive and cooperative processes. In particular, the outcome of learning is in large part determined by competitive processes. That is, behavioral information—whether environmental (before much practice of the required pattern has occurred) or memorized (following practice)—“wins out” over preexisting tendencies to produce preferred phase relations (intrinsic dynamics). In each case, the alteration may take the form of a phase transition, or bifurcation, although the reasons for the phase transition are different.

Complete representations of the evolution of the attractor layout with learning is provided for the 3 typical subjects S.B., M.S., and J.T. in Panels B and C of Figures 5, 6, and 7, respectively. In Panel B, mean delta RP (i.e., produced minus required RP) and the related *SD* are plotted as a function of required RP on the first two (left graphs) and last two (right graphs) scanning runs. In Panel C, the evolution of the attractor layout with practice is rendered in a more flowing fashion. Mean RP within a plateau is plotted for each probe as a function of the total number of probes. Actually, the abscissa roughly matches the ordinal scale of the learning trials used in Panel A. A cubic polynomial interpolation of

Subject TM

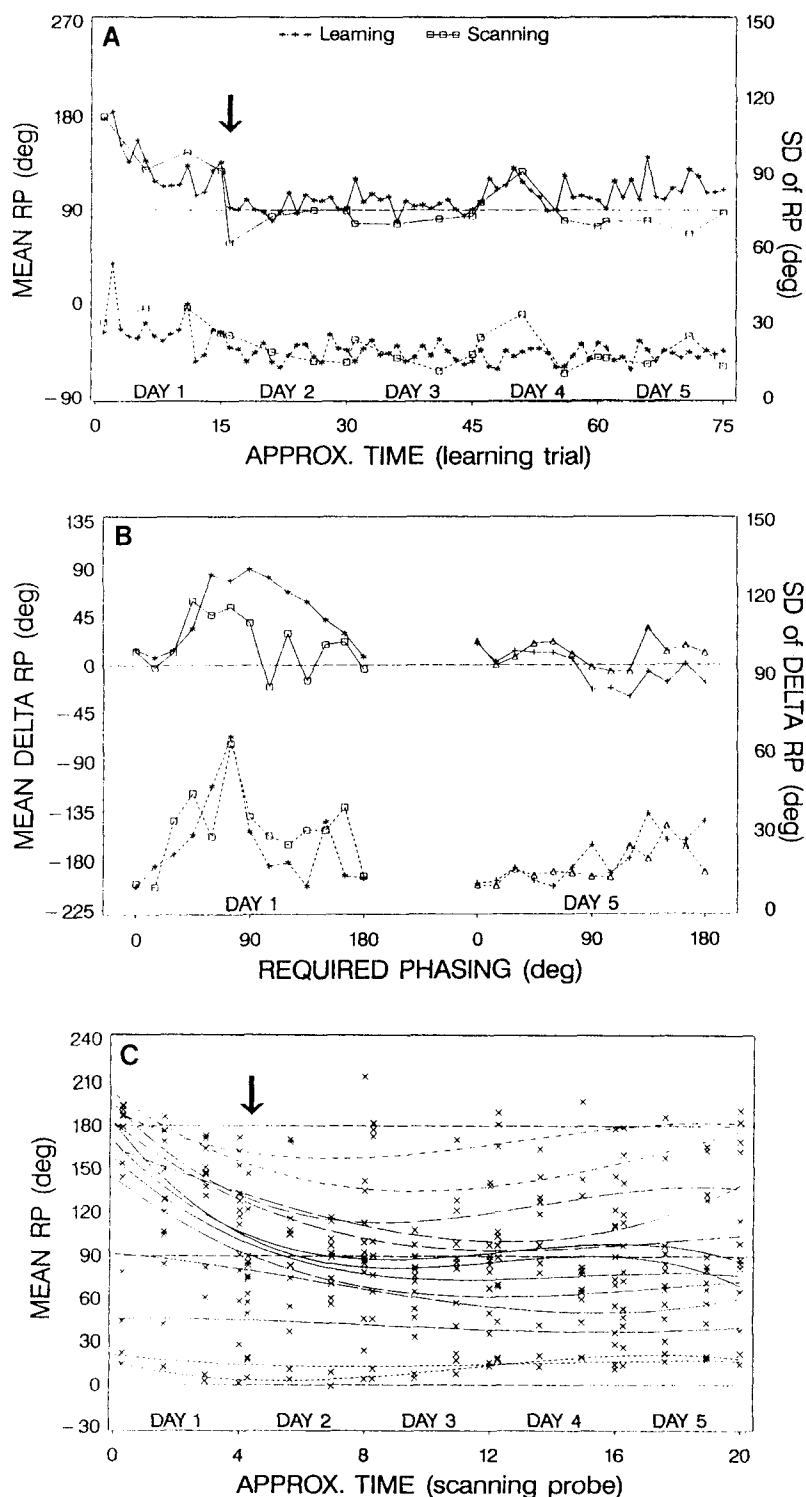


Figure 5. Individual performance for Subject T.M. (Panel A draws a comparison between learning and scanning performance when a 90° phasing is required: within-trial [\star] and within-plateau [\square] mean [upper solid line] and SD [lower dotted line] of produced relative phase [RP] when 90° RP is required in the learning and scanning trials, respectively. The scanning scores are plotted at the same position on the approximate time abscissa as the learning trial closest in time. Panel B presents the phase diagram on the first two [Day 1] and the last two [Day 5] scanning probes. [For Day 1: Probe 1 = \star , Probe 2 = \square . For Day 5: Probe 3 = $+$, Probe 4 = \triangle .] Within-plateau mean [upper solid line] and SD [lower dotted line] of delta RP are plotted as a function of the required relative phase. Panel C illustrates the “flow” of the attractor layout as learning proceeds. The 13 within-plateau relative phase means are plotted for each scanning probe as a function of the total number of probes, along with the respective cubic interpolation [see text for details].)

Subject MS

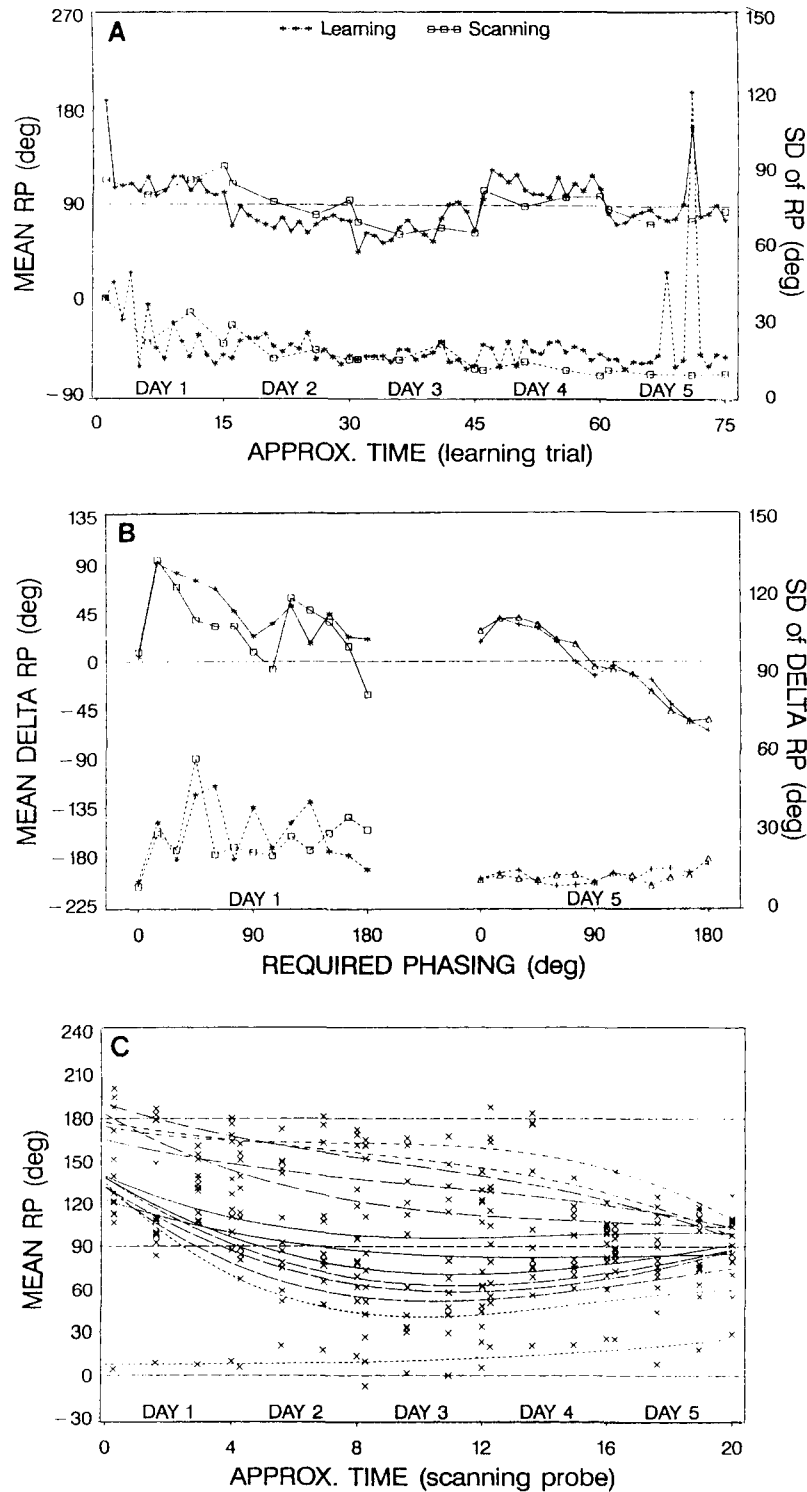


Figure 6. Individual performance for Subject M.S. (Panel A draws a comparison between learning and scanning performance when a 90° phasing is required: within-trial [★] and within-plateau [□] mean [upper solid line] and SD [lower dotted line] of produced relative phase [RP] when 90° RP is required in the learning and scanning trials, respectively. The scanning scores are plotted at the same position on the approximate time abscissa as the learning trial closest in time. Panel B presents the phase diagram on the first two [Day 1] and the last two [Day 5] scanning probes. [For Day 1: Probe 1 = ★, Probe 2 = □. For Day 5: Probe 3 = +, Probe 4 = △.] Within-plateau mean [upper solid line] and SD [lower dotted line] of delta RP are plotted as a function of the required relative phase. Panel C illustrates the “flow” of the attractor layout as learning proceeds. The 13 within-plateau relative phase means are plotted for each scanning probe as a function of the total number of probes, along with the respective cubic interpolation [see text for details].)

Subject JT

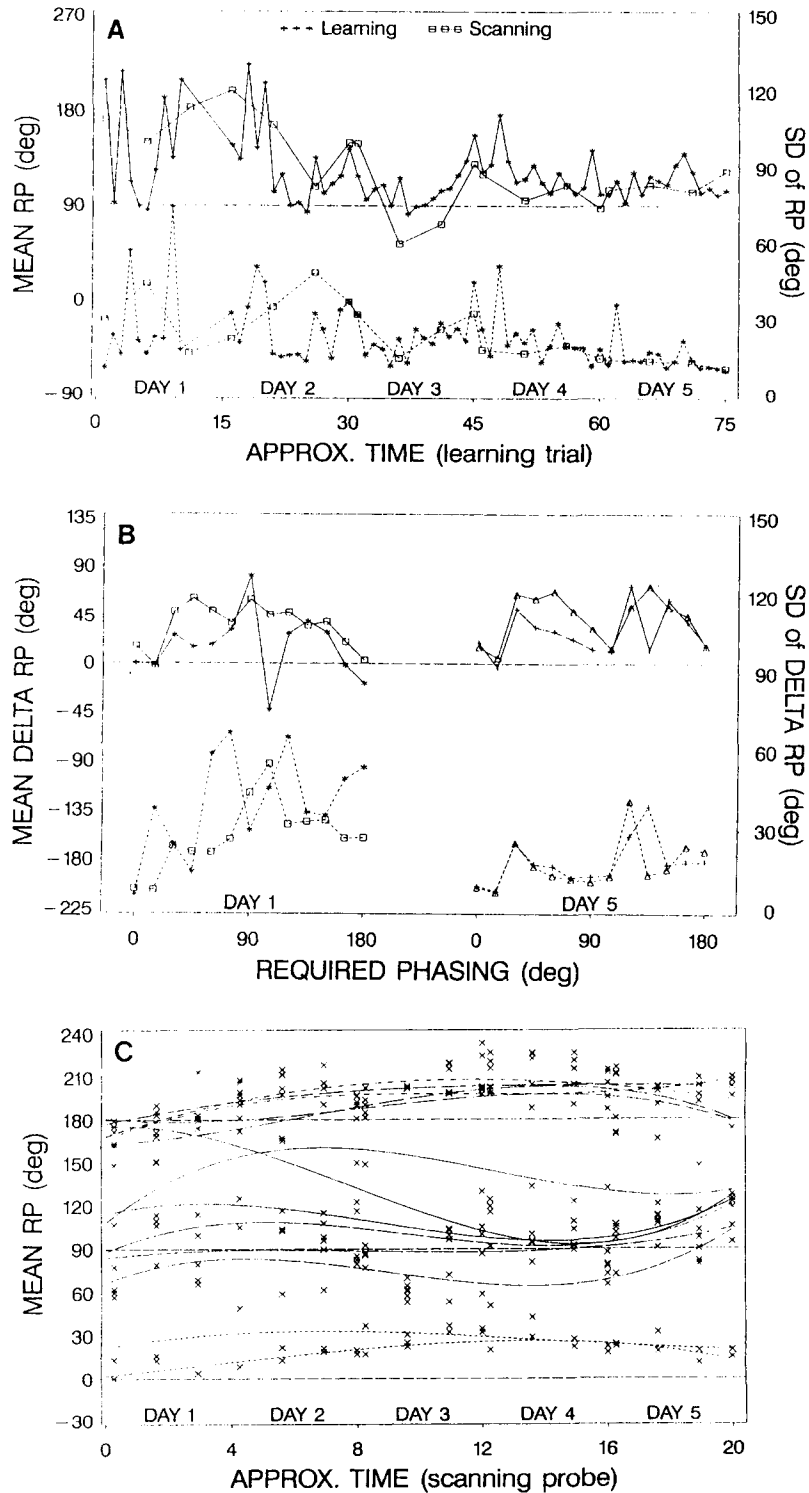


Figure 7. Individual performance for Subject J.T. (Panel A draws a comparison between learning and scanning performance when a 90° phasing is required: within-trial [★] and within-plateau [□] mean [upper solid line] and SD [lower dotted line] of produced relative phase [RP] when 90° RP is required in the learning and scanning trials, respectively. The scanning scores are plotted at the same position on the approximate time abscissa as the learning trial closest in time. Panel B presents the phase diagram on the first two [Day 1] and the last two [Day 5] scanning probes. [For Day 1: Probe 1 = ★, Probe 2 = □. For Day 5: Probe 3 = +, Probe 4 = △.] Within-plateau mean [upper solid line] and SD [lower dotted line] of delta RP are plotted as a function of the required relative phase. Panel C illustrates the “flow” of the attractor layout as learning proceeds. The 13 within-plateau relative phase means are plotted for each scanning probe as a function of the total number of probes, along with the respective cubic interpolation [see text for details].)

the mean RP produced in response to each required RP is drawn so that the trend may be followed across scanning runs. These interpolation curves are coded by their line type within adjacent phasing-requirements intervals (i.e., 0° – 15° , 30° – 60° , 75° – 105° , 120° – 150° , and 165° – 180°) to contrast the trends. If performance were perfect (i.e., no influence of the intrinsic dynamics), the mean produced RPs for a given probe would precisely match each phasing requirement. Thus, if no change in the dynamics occurred with practice, 13 equidistant horizontal lines would be plotted. Conversely, the clustering of produced RPs suggests the presence of a basin of attraction. Changes with time in the attractor layout may then be observed, such as drift of an attractor (fluctuation of a bunch of curves) and broadening or narrowing of its basin (convergence or divergence of curves, respectively). Although we recognize that such a procedure is statistically dubious because of the fake abscissa, it nevertheless provides a useful and insightful glimpse into how the attractor layout evolves over the time scale of the experiment.

Individual subjects can be classified roughly according to whether they display predominantly cooperative or competitive dynamics in the first practice trials. Subjects T.M. and M.S. belong to the latter category, although they exhibit qualitatively different initial intrinsic dynamics. For Subject T.M., the first probe (\star curves in Figure 5, Panel B) suggests the presence of two attractors at 0° and 180° , whereas Subject M.S. (Figure 6, Panel B) exhibits tristable dynamics, with a middle stable pattern located at about 115° . In both subjects, enhanced variability in the first scan as well as the first learning trials reflects competition between environmental information requiring a phasing of 90° and a bias to produce higher relative phases than required (see Panel A of Figures 5 and 6). With practice, T.M. is already showing evidence of an attractor at 90° (negative slope and reduced *SD*) on the second probe (\square curves in Figure 5, Panel B), so that by the end of learning (right curves), this pattern has become an attractor of the dynamics, and the 180° pattern is destabilized. Such a phase transition from bistable to tristable dynamics stems from competition between environmental behavioral information and the intrinsic dynamics. For Subject M.S., such competition involves the rapid shift of the middle pattern toward the task requirement, as indicated already in the second probe (cf. \star and \square graphs in Figure 6, Panel B). From then on, environmental behavioral information and the pattern dynamics cooperate to stabilize the 90° pattern. With further practice, the final dynamics become almost monostable, with delta RP showing a negative slope and a minimal *SD* all the way across the interval between 45° and 180° and intersecting the zero axis at 90° (right graphs in Figure 6, Panel B). The positive and negative shifts in delta RP for, respectively, 0° and 180° , suggest also that these intrinsic patterns are less attractive than before. Such a transition now results from competition between the waning influence of initially stable patterns (0° and 180°) and the growing influence of memorized information (i.e., 90°).

The “flow” of the dynamics (Panel C of Figures 5 and 6) is consistent with the foregoing interpretation. Both subjects exhibit quite dramatic modification of the phase diagram with learning, the actual form depending on the interplay between

task requirements and the preferred patterns. Theoretically, the removal (M.S.) or addition (T.M.) of an attractor is due to competition between behavioral information (environmental or memorized) and the initial intrinsic dynamics.

A glimpse into how learning affects the pattern dynamics in “real time” is afforded by comparing scanning and learning tasks. For T.M., the first time at which a substantial cluster is formed around 90° in a scanning run, accompanied by a near disappearance of the 180° pattern, coincides exactly with the first time at which the 90° pattern is produced in the learning task (cf. the arrows in Figure 5, Panels A and C). The simultaneous drop in variability (see lower curves in Figure 5, Panel A) may reflect the new cooperation developed between environmental behavioral information and the pattern dynamics.

For Subjects S.B. and B.A. (data not given), the initial dynamics are similar to those of M.S., whereas the final dynamics are comparable to those of T.M., that is, roughly speaking, always exhibiting attractors at 0° , 90° , and 180° (see left curves in Figure 5 and right curves in Figure 6, respectively, for an illustration). However, S.B. and B.A. appear to arrive at these final dynamics through a slightly different mechanism. For both subjects, practice bolsters the stabilization of the 90° pattern, which eventually becomes equivalent to the 0° and 180° patterns. Because the departure between required and initially available behavioral patterns is small, there is strong cooperation between behavioral information and the intrinsic dynamics.

Although Subject J.T. eventually displays tristable initial dynamics (see left part of Panels B and C of Figure 7), performance in the learning task is extremely variable over the first 2 days. Most produced RPs sit around 90° and 190° , with fewer scores at intermediate values. Closer examination shows that intermediate RPs are not produced as stable patterns, but rather result from the relative number of cycles produced at 90° and 180° during a given trial. In Figure 8, Panel A, we show the frequency distribution of produced RP binned in adjacent intervals of 15° for three groups of trials on Day 1. Trials with intermediate produced RP values (i.e., about 135°) and large *SD* (i.e., Trials 4, 7, and 9) constitute a first group. The second pool contains Trials 1, 3, 8, and 10, which exhibit a mean RP of about 90° . The last pool comprises the other trials, whose mean produced RP is about 190° . The bimodal distribution of trials with intermediate RP values (solid line) overlaps with the two unimodal distributions of the other groups. This suggests that whatever the actual within-trial mean, a large proportion of the produced RPs are centered about 90° or 180° – 200° . In Figure 8, Panels B and C are displayed two examples of such switching behavior over a similar 20-s period. Each presents the time series of produced RP and the angular displacements of the fingers over time in the bottom curves (the right finger corresponds to the dotted line). Note that in the top curves, the vertical axis scales RP between -360° and 360° , so that RP over time is drawn twice, avoiding wrapping about the 0° value. Panel B shows learning Trial 9 on Day 1, whereas Panel C displays part of the first scanning run on Day 3 for a required RP of 90° . Both panels reveal a coherent picture, the RP jumping between 90° and 180° and sitting there for a while (about 4–5 s), with rare visits

Subject JT

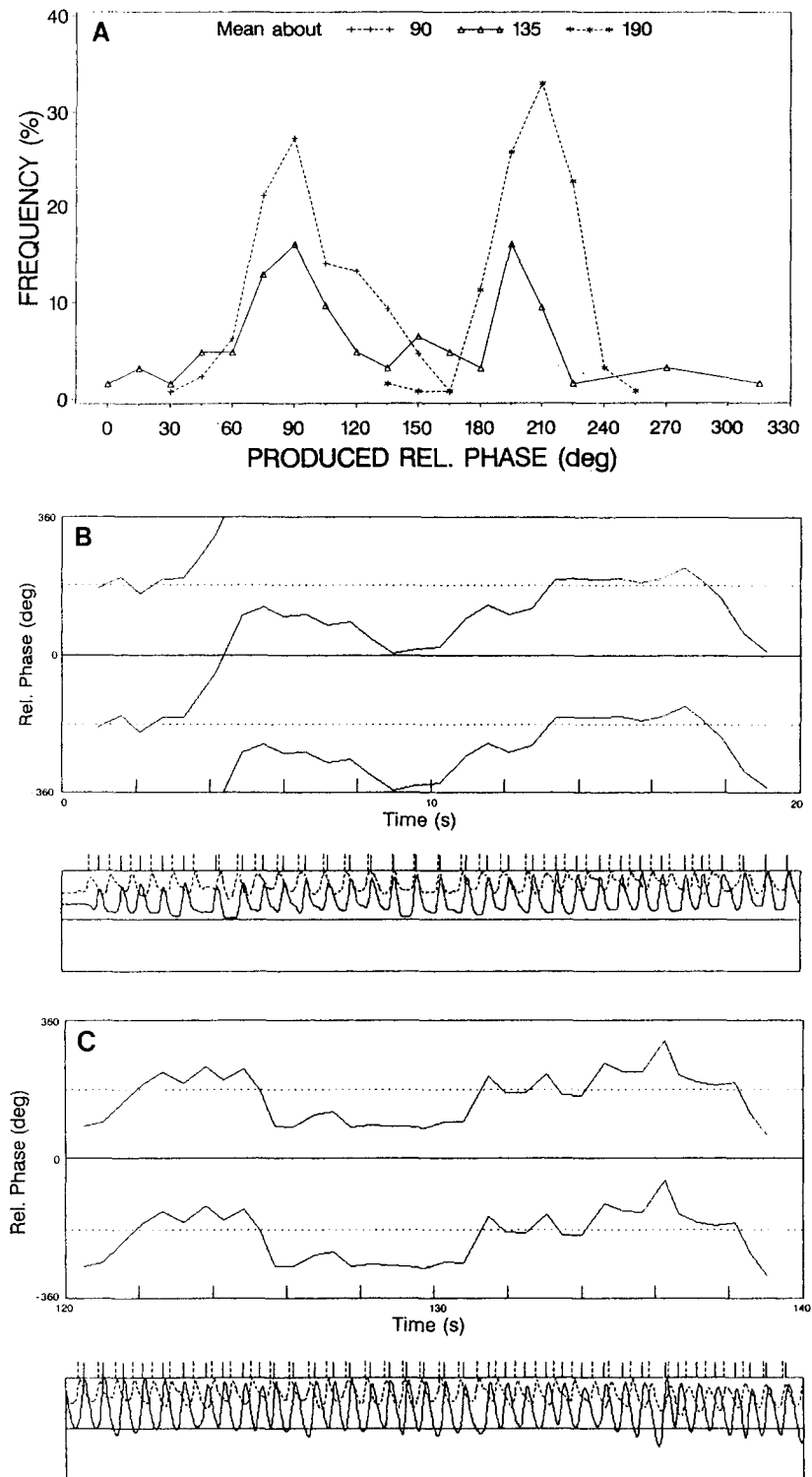


Figure 8. Switching behavior in Subject J.T. (In Panel A, the overall frequency distribution of the cycle-by-cycle relative phase in the trials of Day 1 is pooled as a function of their mean [see text for details]. In Panel B, the upper window displays the time series of relative phase in a selected learning trial. The lower window plots the corresponding finger movements [see text for details]. Panel C does the same as Panel B but for the 90° required relative phase plateau in a selected scanning probe.)

to 0°. An interpretation of this consistent behavior is that the equilibration time of the system (τ_{equ})—the time it takes a stochastic system to reach a stationary probability distribution (e.g., Schöner et al., 1986)—is close to the duration of a scanning plateau or a learning trial. Thus, the system may be in the global stability regime where it visits its various attractors, so that spontaneous switches among stable patterns may occur within this time interval.

General Discussion

The coordinated patterns produced by animals and people may be understood in the language of nonlinear, dissipative dynamical systems.⁴ In dynamic pattern theory (e.g., Kelso & Schöner, 1987; Schöner & Kelso, 1988e), following synergetics (Haken, 1977/1983b), patterns of coordination on a chosen level of description are characterized by collective variables or order parameters. These collective variables capture the ordering relations between interacting components and thus reflect the underlying neural organization. The pattern dynamics can be determined as equations of motion of the collective variables (cf. Equations 1 and 2). In particular, observable (i.e., reproducible, stationary over a certain time scale) behavioral patterns are mapped onto attractors of the order parameter dynamics whose stability can be measured. Boundary conditions (environmental, task, or energetic constraints) act as parameters on the collective dynamics. Such parameters may be nonspecific, simply moving the system through a sequence of patterns, or specific, requiring a particular pattern. Pattern change, continuous or abrupt, is tied to the essential nonlinearity of the system and may take the form of bifurcations (qualitative changes in the phase diagram or attractor layout). Typical predictions about change, such as enhancement of fluctuations, critical slowing down, and the distribution of switching times, can be detected experimentally if careful attention is paid to time scales. Depending on the nature of the dynamics (stable or unstable fixed points of the collective variable, saddles, limit cycles, etc.), jumping among basins of attraction may occur.

Building on previous work on an experimental model system in which multistability and pattern transitions were observed, we identified the relative phase, ϕ , as a relevant collective variable characterizing the coordination patterns between two components moving rhythmically. In the present experiment we studied how the relative phase dynamics evolved according to the specific behavioral requirement of learning a relative phase that did not, at first blush, correspond to the intrinsic dynamics. In particular, we tested the prediction that phase transitions in learning may occur, seen as qualitative changes in the phase diagram or attractor layout. Analysis of performance changes over time in conjunction with periodic probes of the phase diagram provided strong support for this prediction. Depending on the initial intrinsic dynamics for a given subject, multiple attractors of the behavioral pattern dynamics were seen to evolve, sometimes accompanied by loss of stability of one of the intrinsic patterns (see Panel C of Figures 5, 6, and 7). As evident in recall performance (see Figure 4), such modification of the dynamics persisted beyond local within-day and across-day time scales. The

fact that learned patterns persisted over time attests to the crucial concept of stability of the underlying collective variable dynamics.

The present approach includes an entire layer of dynamics (the intrinsic pattern dynamics) often omitted from formal learning theories. Not only does the theory predict nonequilibrium phase transitions in learning, but there are also methodological implications for the study of learning. First, a central emphasis is placed on identifying any existing spatiotemporal pattern dynamics before the introduction of a learning task. In essence, we assume that subjects' performance on the initial scan reflects the collection of past experiences, natural tendencies, and so forth that might contribute to his or her ability to produce rhythmic behavioral patterns. Depending on these intrinsic dynamics, an individual subject's consequent behavior may be predicted. For example, if the 90° pattern is not stable initially relative to in-phase and anti-phase patterns, a phase transition is predicted. *Competition* between external behavioral requirements and the intrinsic dynamics is at the heart of this pattern change (Kelso & DeGuzman, 1988; Schöner, 1989; Schöner & Kelso, 1988c, 1988d). However, if for some reason, the 90° pattern is part of the phase diagram, no phase transition is expected initially. Instead, as practice proceeds, consolidation of the 90° pattern occurs. The mesh between behavioral information and the intrinsic dynamics is thereby strengthened because of their *cooperation*. Further practice may lead to phase transitions, following the destabilization of the anti-phase pattern (shown experimentally here) and eventually, even of the in-phase pattern (predicted by the theory). A putative sign of the latter bifurcation may be the marked shift in RP between the first and last probes for the 0° requirement (see Figure 4, Panel B).

In our final remarks we address some of the typical questions raised about the present approach.⁵ We use this format as a way to locate the present approach with reference to others and to briefly enlarge upon its implications.

1. *Does learning always involve a phase transition?* As theory predicts and as we have shown, whether qualitative change in the behavioral pattern occurs or not depends on the relation between the initial intrinsic dynamics and behavioral information. A general problem with determining whether phase transitions constitute an important mechanism of learning surrounds the issue of how, in the first place, one defines relevant variables (characteristic of the "state") of a complex system on a chosen level of description. On the relatively rapid time scale of behavioral performance in rhythmic tasks, we have used qualitative change induced by nonspecific parameter changes as a means of clearly distinguishing one behavior from another. Relative phase proves to

⁴ Mathematically, dissipative systems are non-Hamiltonian systems, that is, characterized by a reduction of their volume in phase space. Phenomenologically, dissipative systems, unlike conservative systems, eventually relax into a stable state from different initial states. Dissipation is then equivalent to attraction, which can take several forms, for instance, attraction to a point, to a periodic orbit, or to chaos.

⁵ We are indebted to an anonymous reviewer for formulating these questions.

be a relevant collective variable in our experimental model system, which can then be tracked during the longer time scale of learning. Thus, phase transitions on the short time scale of behavior are instrumental in discovering whether phase transitions occur on the longer time scale of learning. The former are used as a methodological strategy for identifying collective variables, that is, the "what" in the question of "what changes" when learning requirements are imposed. A similar approach may be taken for other learning tasks on other levels of description, in which, of course, relative phase may be quite irrelevant as an essential variable. Our point is that the observables may differ for different functional tasks, but the principles, we hope, will be the same.

Although the identification of a phase transition mechanism is what sets the present approach off from others, as we have stressed, not all learning need involve a phase transition. For example, in preliminary work (Zanone & Kelso, in press), we have studied the ability to learn a pattern at $\psi = 135^\circ$. The reason for this choice with a given subject was because an initial probe of the phase diagram showed evidence of tristable dynamics (i.e., 0° , 90° , and 180°). We found that the initially stable pattern at 90° was gradually shifted toward the required phasing pattern of 135° . Thus, it may be that when $\phi = 90^\circ$ is already a stable pattern, the resulting changes due to learning are continuous, not abrupt. The distance in collective variable space between behavioral requirements and intrinsically preferred patterns appears to determine the nature of change. However, simply because learning may take a continuous and gradual form does not invalidate a dynamical description. Indeed, it is the existence of qualitative change in the dynamics that renders gradual change more easily interpretable.

2. *Is it possible that by looking at the intrinsic dynamics one can make predictions about what is learnable and what is not?* Depending on the nature of the intrinsic dynamics, some tasks may be more easily learned than others. If by chance or design, a task requirement happens to match the intrinsic dynamics, or vice versa, learning is likely to be rapid because of cooperation. Our choice of $\psi = 90^\circ$ was theoretically motivated by the fact that 90° is an unstable fixed point of the collective variable dynamics, separating the two basins of attraction for $\phi = 0^\circ$ and $\phi = 180^\circ$ (see Figure 1, Panel A). Thus, the task as originally conceived was to make an unstable fixed point stable through learning, thereby promoting qualitative changes in the phase diagram, theoretically through the mechanism of competition.

The general class of tasks investigated here involves 1:1 frequency- and phase-locking. An extended version of the theory considers empirically observed frequency relations that are not 1:1 (DeGuzman & Kelso, 1991; Kelso & DeGuzman, 1988). In both cases, whether a pattern is easily produced or not depends on its stability. Some stability regions (e.g., 1:1 or 2:1) are large and easy to access; others are extremely small and difficult to access (e.g., 3:5 or 8:13). One reason why musicians must practice so-called difficult rhythms stems from this differential stability. "Errors" can occur, seen as jumps from less stable (e.g., 5:2 or 4:3) to more stable (e.g., 2:1 or 1:1) frequency relations. In theory, differential stability may also explain why, in practice, only a few rhythmic

patterns are typically observed, although all patterns are theoretically learnable (see Deutsch, 1983; Jagacinski, Marshburn, Klapp, & Jones, 1988; Povel, 1981). We believe that such results may be enormously informative about the design of complex nervous systems.

3. *What does a "phase transition in learning" mean as opposed to simply "learning will occur"?* As we have emphasized, a phase transition, or bifurcation, refers to qualitative change in the dynamics. By establishing the phase diagram of the pattern dynamics, our approach affords a novel picture of transfer or generalization. Thus, we look not only at one trained phasing pattern ("simple" learning) but also at the effects of one trained relative phase on all phases. And, we would add, the approach allows one to see if and how preexisting preferred relative phasing patterns (so-called intrinsic dynamics) are modified in the process of learning a new phase. From the resulting pattern we infer the nature of change (abrupt vs. continuous) and the underlying processes (cooperation and competition). Moreover, it is possible that creating a novel attractor at a to-be-learned pattern will generalize to other patterns that have not been practiced at all. First examples of such transfer (Zanone & Kelso, in press) suggest that the relative phase symmetric (e.g., $\phi = 270^\circ$) to the one learned (e.g., $\phi = 90^\circ$) can become an attractor of the pattern dynamics. Such results indicate that dynamical principles, such as preservation of symmetry, may be relevant to the transferability to other tasks and set the present approach apart from others.

4. *Are the intrinsic dynamics an accident of experience? Why are 0° and 180° favored?* These questions are pertinent in this context because the intrinsic dynamics persist throughout the learning period except for temporary losses of the anti-phase pattern. Our framework makes no claims about the intrinsic dynamics' being the result of experience or innate factors. On the other hand, the tendency for phase and frequency synchronization is ubiquitous in natural systems and can be found at many levels of observation. For example, remarkable parallels exist between the present work on rhythmic movement tasks in humans and research on central pattern generators in invertebrate and vertebrate neural networks (e.g., Cohen, Rossignol, & Grillner, 1988). Even cells in mammalian visual cortex (e.g., Gray, Konig, Engel, & Singer, 1989) have been found to display phase and frequency synchronization. In-phase and anti-phase patterns constitute stable collective modes of nonlinear coupled oscillators and probably reflect a quite fundamental way to coordinate individual components whose behavior evolves in time (e.g., Kelso, DeGuzman, & Holroyd, in press). Just as stability of the resonances explains the 3:2 relationship between the planet Mercury's orbital and rotational periods (Stewart, 1989), limited forms of stability may underlie the pervasiveness of simple mode-locking in behavioral and neural systems (von Holst, 1939/1973).

5. *What would the intrinsic dynamics look like for a learning task more standard than bimanual coordination?* Science always chooses specific cases on which to build theoretical understanding, and some concrete cases are bound to be better than others. Bimanual coordination happens to have provided a useful window into the abstract, level-independent princi-

ples of coordination that have proven generalizable to a variety of other experimental systems (including the present case of learning) and levels of description. It may not be considered a "standard" task, but neither, one could argue, was rolling a ball down an inclined plane.

On the other hand, it may not be too adventurous to speculate that learning to read and learning to talk follow along the lines we have described here for perception-action pattern learning. For example, recent studies of speech perception and production have demonstrated, following Stetson (1951, cited in Kelso & Munhall, 1988), that phase transitions occur from syllables such as "ape" to "pay" as speaking rate is systematically increased (e.g., Tuller & Kelso, 1991). The transition is invariably from a vowel-consonant (VC) to a consonant-vowel (CV) form, and not vice versa. It is interesting, once again, that it is the relative timing among glottal and oral articulators that distinguishes VC and CV syllables, both in production and perception. Such CV forms also predominate in infant babbling, constituting a unique set of "favorite sounds" (Ferguson, 1979) or "movement patterns" (Locke, 1983). Work by Vihman and colleagues (see Vihman, 1991, for a review) has established that the phonetic characteristics of early words are highly similar to each individual child's babble. Indeed, the child apparently attempts to produce an adult form only when it matches or is close to one of his or her own babbles. Thus, access to the world of language appears to depend, in part, on these preferred perceptual-motor patterns. Though the mapping must be only tentative, we might say that babbling corresponds to a kind of intrinsic dynamics that can be modified by the sounds of adult words, acting as specific behavioral information on these dynamics. Of course, the dimensions on which the intrinsic dynamics and behavioral information are defined and whether phase transitions occur during the process of phonetic development remain very much open questions.

6. *Would any other existing theory not make the same predictions?* It is possible to intuit that learning might involve "phase transitions" in the vernacular sense, or even "quantum leaps," or "insights," as in the case of Kohler's ape. Such intuitions are undoubtedly useful and important to initiate a line of investigation. But in the sense that the formal mathematical aspects of the dynamic pattern approach to learning have been fleshed out and operational tools developed to test specific predictions of the theory, the answer is probably no.

As a viable alternative framework, we should look perhaps to current research in artificial neural networks, which gives learning and associative memory a high priority. Neural nets that implement dynamical systems are also being used for adaptive control and motor learning (e.g., Bullock & Grossberg, 1991; Jordan, 1990; Kawato, Furukawa, & Suzuki, 1987). The dynamics used are usually simple, such as relaxing to fixed-point solutions, although some attention has been given to temporal order in small neural networks using periodic dynamics (Kleinfeld & Sompolinsky, 1989). Such models are probably powerful enough to model the present results, but they do not predict them. A reason could be that many mathematical network models completely ignore the biological components themselves or the behavioral patterns

that they exhibit (Abbott, 1990). In our language, the level of the intrinsic pattern dynamics is missing. To the extent that these nontrivial dynamics are ultimately responsible for predicted and observed transitions in learning, ignoring them may leave an important gap.⁶ Such dynamics, as we stressed, place constraints on what can be learned, if not in artificial, at least in real, systems. Elsewhere, it has been shown that intentional changes in performance are influenced by the intrinsic pattern dynamics. Our results, along with the concepts and tools used here, provide a framework for understanding skill learning as a modification of the intrinsic dynamics. Indeed, the interpretation of learning processes is greatly enhanced when it is preceded by the identification of collective variables for behavioral patterns and their (nonlinear) dynamics.

⁶ Recently, Eimas and Galaburda (1990) made a similar point. Referring to "molecular" associative conditioning in the gill of *Aplysia*, they pointed out that even these simple effects do not occur in an unbiased "connectionist" arrangement of input, output, and hidden units, but rather presuppose an already complex initial state on which only certain stimuli, and not others, are capable of evoking certain responses.

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