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Coordination Dynamics of Learning and Transfer: Collective and Component Levels

P. G. Zanone and J. A. S. Kelso
Florida Atlantic University

The dynamics of learning a new coordinated behavior was examined by requiring participants to perform a visually specified phase relationship between the hands. Results showed that learning may involve qualitative or quantitative alterations in the layout of the coordination dynamics depending on whether such dynamics are bistable or multistable before exposure to the learning task. In both cases, the process stabilized the to-be-learned behavior *and* its symmetry partner, even though the latter had not actually been practiced. Kinematic analyses of hand motion showed that previously existing coordination tendencies were exploited during learning in order to match visual requirements. These findings and the concepts presented here provide a framework for understanding how learning occurs in the context of previous experience and allow individual differences in learning to be tackled explicitly.

Biological constraints (e.g., Bolles, 1970; Garcia & Garcia, 1985), or behavior systems (Germana, 1989; Timberlake, 1993), approaches, consistent with general precepts of ethology (e.g., Lorenz, 1970; von Frisch, 1967), emphasize that all learning occurs as a modification of existing structures and processes. Lawful accounts of what is learned and how learning occurs must then address two chief issues: First, the initial state of the learner before learning needs to be evaluated. Second, it is necessary to determine how this state is modified during the learning process itself. Although the idea that learning (and development, cf. Sporns & Edelman, 1993) somehow involves a modification of the current behavioral repertoire of an individual appears intuitive, the actual operationalization of this notion within a self-contained description is extremely difficult. In this article, we approach these problems using the conceptual framework of self-organization in nonlinear dynamical systems (e.g., Beek & van Wieringen, 1994; Haken, Kelso, & Bunz, 1985; Kelso, 1984; Kelso & Schöner, 1987; Schöner & Kelso, 1988a, 1988b; Thelen, Kelso, & Fogel, 1987; Turvey, 1990).

In recent years, several researchers have examined the issue of perceptuomotor learning from a dynamical perspective (e.g., Beek & van Santvoord, 1992; Saltzman & Munhall, 1992; Schmidt, Treffner, Shaw, & Turvey, 1992; Swinnen, Walter, Lee, & Serrien, 1993; Vereijken, Whiting, & Beek, 1992) without, however, providing any operational or formal treatment of individual spontaneous coordination tendencies that may exist before, during, and after learning. Such tendencies likely influence the learner's ability to perform the required task at any moment during practice. In particular, they determine how well environmental task requirements are matched when the learner is first exposed to the learning situation.

Knowledge of coordination tendencies that exist before learning is important in several respects. First, to understand learning as a process (as dynamics, we would say), it is mandatory that subjects practice a behavioral pattern that they have not mastered already. Otherwise, the task would involve recognition and recall, but not learning per se. Second, individual differences in learning a task are likely related in some fashion to an individual's history and past experiences. A usual provision taken to avoid putative effects attributable to individual differences is to simply cancel them out by setting as arbitrary a learning task as possible. Despite this procedure, one may still question the validity of the resulting learning curve obtained in terms of its shape and time scale after data have been pooled across subjects. Third, knowledge of what participants are not able to perform before practice is crucial to the issue of transfer of learning. Again, transfer tasks, like the learning task itself, are commonly set in a rather arbitrary fashion, with transfer being assessed in terms of the amount or percentage of transfer across tasks. In contrast, when the task space is known for each individual before exposure to the learning task, insight may be gained into why some tasks are transferable and others are not.

A strength of our approach to learning (Kelso, 1990), which blends experimental (Zanone & Kelso, 1992a, 1992b) and theoretical work (Schöner, 1989; Schöner & Kelso, 1988a, 1988b; Schöner, Zanone, & Kelso, 1992; Zanone & Kelso, 1994), is that it provides concepts and methods that

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P. G. Zanone and J. A. S. Kelso, Program in Complex Systems and Brain Sciences, Center for Complex Systems, Florida Atlantic University. P. G. Zanone is now at Laboratoire de Recherche en Activités Physiques et Sportives, Université Paul Sabatier, Toulouse, France.

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Correspondence concerning this article should be addressed to J. A. S. Kelso, Center for Complex Systems, Florida Atlantic University, 777 Glades Road, P.O. Box 3091, Boca Raton, Florida 33431. Electronic mail may be sent via Internet to kelso@walt.ccs.fau.edu.

explicitly treat existing coordination tendencies[1] and their evolution before, during, and after learning. Thus, not only can learning be identified in terms of improvement in performance toward some criterion level, which is the usual case in learning experiments, but learning can also be assessed directly as alterations of extant coordination tendencies in the direction of the task to be learned. Coordination tendencies are thus treated in terms of dynamics (i.e., as equations of motion of a relevant collective variable that changes during the learning process). Because this collective variable expresses the ongoing interaction between the numerous neural, muscular, and metabolic elements involved in perception and action, we refer to its time-dependent behavior as *coordination dynamics* (Kelso, 1994a; Zanone & Kelso, 1994). Environmental requirements, such as the learning task, are expressed as specific parameters on these dynamics. Thus, the learning requirement and what the learner brings into the learning situation (viz. individual coordination tendencies) are captured within the same description. Finally, although the unit of analysis is the individual, each with his or her own signature (i.e., initial coordination tendencies), laws of learning are expressed in terms of generic mechanisms (e.g., stability, instability, competition, cooperation, etc.) that are deemed to underlie learning in all individuals.

The backbone of our approach is a systematic probe of the individual's spontaneous coordination tendencies while the to-be-learned task is practiced. The foundation for such probes lies in the interplay of the task requirement and the individual preferred coordination modes (Schöner & Kelso, 1988a, 1988b). Theoretically, when the task requirement corresponds to an existing coordination tendency, a cooperative mechanism stabilizes the performed pattern at the required value. Alternatively, when the task requirement differs from spontaneous tendencies, a competitive mechanism may induce loss of stability (seen as enhanced variability of the collective variable) and/or attraction of the performed pattern to an underlying coordination tendency (seen as a systematic bias of the collective variable toward a specific value). Importantly, the relative roles of competition and cooperation can be assessed in terms of subjects' responses to experimental procedures that probe a large range of task requirements, thereby scanning the space of the collective variable.

Our window into the topic of learning is bimanual coordination. Extensive experimental (e.g., Byblow, Carson, & Goodman, 1994; Kelso, 1984; Kelso, Scholz, & Schöner, 1986; Scholz & Kelso, 1989; Scholz, Kelso, & Schöner, 1987; Walter & Swinnen, 1992) and theoretical work (Haken et al., 1985; Schöner, Haken, & Kelso, 1986) has shown that spontaneous coordination tendencies of the bimanual system are captured by the dynamics of the relative phase (ϕ) between the relevant components at this level of description, the fingers. These coordination dynamics are bistable at $\phi = 0°$ and $\phi = 180°$, giving rise to stable in-phase or anti-phase motion of the components. Thus, to study learning a logical first step is to impose a learning task that differs from these already-existing attractive states of the coordination dynamics.

Recently, we carried out such an experiment (Zanone & Kelso, 1992a) in which the learning task was a 90° relative phase specified by a visual model. This task was set halfway between the initially assessed in-phase and anti-phase stable coordination modes. By systematically evaluating coordination tendencies during the entire practice period and in a recall session, we found that learning a specific bimanual pattern involved not only improved performance in the learning task itself (the usual outcome) but also long-lasting alterations of the underlying coordination dynamics. In particular, the learned pattern was stabilized, becoming an attractive state of the coordination dynamics "in between" the already existing stable states at 0° and 180°. Such modifications represent qualitative changes in the attractor layout defined by the coordination dynamics, so-called *bifurcations* or *phase transitions*,[2] in which attractive states are formed anew or previously attractive states vanish. When the to-be-learned pattern is incorporated into the coordination dynamics, any competition between the task and initial tendencies is resolved.

In the present study we address three issues regarding the dynamics of learning, motivated in part by our previous work (Zanone & Kelso, 1992a): task novelty, transfer of learning, and component dynamics.

Task Novelty

As noted earlier, the task to be learned in our previous study (90°) was set midway between the bistable coordination states of in-phase and anti-phase. Strictly speaking, this pattern might not have been entirely new for all subjects. To understand how competition between the learning task and existing coordination tendencies eventually leads to changes in the underlying coordination dynamics (viz. learning), it is necessary that the pattern to be learned constitute a novel task for the learner. A feature of the current experiment was that the learning task was set on an individual basis such that it did not conform to any already-existing coordination tendency. As we show, this procedure reveals new processes and paths to learning.

Transfer of Learning

In our previous study (Zanone & Kelso, 1992a), only the 0–180° interval was probed before learning, spanning

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[1] Spontaneous coordination tendencies have been called *intrinsic dynamics* (Kelso, Scholz, & Schöner, 1988; Schöner & Kelso, 1988a, 1988b) to conceptually differentiate those tendencies from "extrinsic" influences that may be specified by memory, by intention, or by the environment, which were captured as "behavioral information." In this article, we do not use the term *intrinsic dynamics* in order to avoid unfortunate connotations with constraints that are innate, hardwired, permanent, and rigid and to emphasize the informational nature of coordination dynamics (for further discussion and analysis, see Kelso, 1994b).

[2] Mathematicians typically call such phenomena *bifurcations*, whereas physicists tend to retain the term *phase transitions* because critical phenomena accompanying transitions, such as fluctuations, are treated explicitly. Here, we use these expressions interchangeably.

the 90° relative phase to be learned. To rigorously test the hypothesis that learning influences the entire layout of the coordination dynamics, we carried out probes between 0° and 360°, that is, over the entire range of possible lead–lag relationships between the components. By so probing the entire task or workspace (e.g., Fowler & Turvey, 1978; Newell & McDonald, 1992; Saltzman & Kelso, 1987), it should be possible for us to detect whether phasing patterns other than that actually practiced stabilize spontaneously with learning. From a theoretical point of view, the question may be rephrased as to whether the initial symmetry of the coordination dynamics, in which in-phase and anti-phase are sole attractive states, is preserved when another, new phasing pattern is learned, stipulating a given lead–lag relationship between the components. At an epistemological level, the occurrence of transfer of learning poses the question of what is actually learned, that is, how abstract or effector-independent the learned phasing pattern is. As we shall show, our results suggest that learning may occur independent of the temporal ordering (i.e., the lead–lag relationship) between the components.

Component Dynamics

According to the theory of coordination dynamics, a complete understanding of a given phenomenon requires at least three levels of description: the task or goal level; the coordinative, collective variable level; and the component level (Kelso, 1994a; Zanone & Kelso, 1991). One of us (Kelso, 1995) has referred to this as the "tripartite scheme" for understanding complex biological systems. For example, in the case of interlimb coordination, the task may be to move the limbs rhythmically out of phase with each other, the collective variable is the relative phase that characterizes emerging patterns, and the components are conceived of as nonlinear oscillators. This is not, of course, a rigid picture. Mutability exists among levels. Thus, a component level defined in terms of nonlinear oscillators may be viewed as a collective variable for finer grained distinctions such as agonist–antagonist muscle activity.

Nevertheless, in our work so far, the learning process has been clarified only in terms of the dynamics of the collective variable relative phase. It is therefore relevant to inquire how the individual coordinating components adjust to satisfy learning task requirements. Thus, we describe how the initial competition between task demands and individual component dynamics is overcome through observed changes in the component kinematics. Briefly, we identify different "strategies" that incorporate preexisting coordination tendencies into new, learned kinematic assemblages between the components and show that such strategies defined at the component level pertain to the relative strength that these tendencies exhibit at the level of the collective variable dynamics before exposure to the task.

Method

The method was identical to that used in the previous study by Zanone and Kelso (1992a) unless stated otherwise. The experiment was carried out on 2 consecutive days. On the first day, after informal familiarization with the task and the experimental setup, initial coordination tendencies were probed for each subject between 0° and 360°. No knowledge of results (KR) was provided to subjects during these probes. The to-be-learned pattern was then set on an individual basis such that it did not correspond to a spontaneously stable pattern. This new pattern was then practiced for 20 trials, with KR given at the end of each trial. On the second day, the coordination tendencies were first evaluated within 0° to 180° or 0° to −180°, whichever encompassed the practiced phasing pattern. This allowed us to assess any early changes in the coordination dynamics with learning while avoiding any experience of the symmetry partner of the relative phase that was practiced. Thirty additional practice trials of the to-be-learned phasing pattern were then administered. At the end of the training period, a full probe (i.e., 0–360°) of the coordination dynamics was again carried out.

Subjects

Fourteen subjects (mean age = 26.8 years) were paid to participate in the experiment. The only prerequisite was that no visual or physical impairment impeded perceiving or producing the required phasing pattern. Four subjects were self-professed left-handers.

Apparatus

Subjects were seated in front of a "visual metronome" composed of two LEDs that displayed the required relative phase at a constant frequency of 1.25 Hz. Subjects' hands were slipped into a bimanual apparatus that allowed monitoring of flexion–extension movements of the index fingers in the horizontal plane, so that flexion corresponded to motion toward the body midline. Signals from the visual metronome and the bimanual apparatus were digitized in real time at a sampling rate of 200 Hz per channel. KR,[3] when appropriate, was given to the subject on a computer screen located beside the visual metronome (for details, see Zanone & Kelso, 1992a).

Task

Subjects were instructed to produce the required phasing pattern specified by the metronome as precisely as possible using appropriate finger movements. Specifically, subjects were required to attain exact synchronization of maximal finger flexion with the onset of the ipsilateral LED. Otherwise, individual movement kinematics were free to vary. Thus, the goal was to induce 1:1 frequency and phase entrainment.

Procedure

Full (i.e., 0–360°) probes of the coordination dynamics were carried out in two runs, each of which investigated the set of right-lead or left-lead phasing patterns. In each run, the required relative phase was systematically scanned from the starting value of 0–360° to the final value of ±180°. Practically, the metronome LEDs were first blinking simultaneously; then, by increasing the

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[3] Knowledge of results was given on a screen displaying the time series of the actual finger excursions and that of the relative phase produced during a practice trial, along with various descriptive statistics about phasing and synchronization performance over a trial (for details, see Figure 3 in Zanone & Kelso, 1992a).

time delay between them, the LEDs were eventually blinking alternately. Accordingly, the fingers had initially to move similarly, both flexing and extending synchronously, whereas they had finally to move in opposite directions, one finger flexing while the other was extending. During such scanning runs, the required relative phase was varied every 15 s in 12 discrete steps of 15° or −15°, respectively. In other words, a scanning run was composed of 13 successive plateaus during which the required phasing was held constant at a different value. For each subject, the first run of the full probe always scanned the set of relative phases with the same lead–lag relationship as the task to be learned. No KR was provided during or after scanning runs.

A typical practice trial lasted 20 s and was followed immediately by KR. Practice was administered in consecutive blocks of 10 trials, with an average intertrial interval of about 15 s and an interblock interval of about 1 min. Note that 10 trials here actually corresponded to 250 attempts to produce the required phasing pattern. The relative phase pattern to be learned was chosen according to the results of the initial full probe under the caveat that to be novel, such a pattern should not coincide with an already-existing coordination tendency (see Figure 1 for an operational description of how to determine attractive states from the results of the probes).

Two Measures of Relative Phase

As a matter of convention, we always defined relative phase with reference to right-hand events. Thus, metronome and finger patterns in which the right event led with respect to the left were attributed a positive relative phase (i.e., ranging from 0° to 180°). Conversely, left-lead phasing patterns had negative values varying between 0° and −180° or, equivalently, positive values between 360° and 180°. Two measures of relative phase were used depending on the collective versus component level of description (see the middle panels of Figures 5–7 for an illustration). Consonant with the discrete task requirement, a first measure of the produced pattern, ϕ, was a *point estimate* of the relative phase between finger movements. The time difference between the occurrence of maximal flexion of the left finger and that of the right finger closest in time was expressed (in degrees) relative to the period of the corresponding right finger cycle (for details, see Zanone & Kelso, 1992a). Typically, maximal flexion was determined with software for every movement cycle as the movement at which the point of peak flexion was first reached within a given noise criterion level. Thus, if some rest period existed at such a point (e.g., see the bottom panels of Figures 6 or 7, presented later), the left edge of the flat trajectory segment was picked. This point-estimate measure was used to characterize behavior at the collective level of the coordination dynamics. For the component level, that of the kinematics of the individual finger motion, we used a second measure, the *continuous relative phase.* Its computation used the foregoing points of maximal flexion to normalize performed trajectories in amplitude and time to unity for each cycle. Thus, a phase angle (i.e., the angle formed by velocity and position on a phase plane) was calculated for each sample in both time series, the difference of which yielded the relative phase (see Kelso et al., 1986, for details). It must be emphasized from the outset that although the point-estimate and continuous relative phases suggest different behaviors is terms of stability, both measures are perfectly equivalent for capturing the system's underlying coordination dynamics (for an experimental, methodological, and theoretical discussion, see the Results and Discussion section and the Appendix).

Results and Discussion

The results are presented in five sections. In the first three sections we deal with our main hypotheses that learning and transfer lead to changes in the entire layout of the coordination dynamics and address the nature of these changes. In the fourth section we provide a closer look at the individual finger movement kinematics to see how these are modified with learning and how coordination requirements imposed by the task are actually achieved at both the collective and component levels. This provides a coherent and finer grained picture using the continuous measure of relative phase to evaluate how new coordination patterns are learned and realized (see also the Appendix for a theoretical treatment). In the final section we establish the linkage between the collective and component levels as they relate to the learning process.

The cornerstone of our approach to learning is to set the learning task on an individual basis according to each subject's coordination capabilities that exist before exposure to the task. In probes of the individual coordination dynamics carried out before practice, 10 subjects exhibited stable behavior at 0° and 180°. These subjects were then assigned to two groups of five who practiced either 90° or 270° (−90°), respectively. Two subjects with multistable coordination dynamics at 0°, 180°, and ±90° practiced either 135° or −135° (225°). A third subject exhibited initial multistability at 0°, 180°, and ±60°. For her, the to-be-learned relative phase was arbitrarily set at 90° of relative phase. Finally, the last subject exhibited initial stability at 0°, 180°, and ±135°. The learning task was then set at −90° (or 270°) relative phase.[4]

Probes of the Collective Variable Dynamics

Figures 1A and 1B show the results of the three probes carried out during the learning procedure for initially bistable coordination dynamics, that is, for subjects who practiced 90° or 270°, respectively. In each panel, top curves display the mean error of the produced relative phase[5] as a function of the relative phase required in each plateau, and the bottom curves plot the corresponding within-plateau standard deviation. For the first (leftmost) and last (rightmost) probes, which spanned the full range between 0° and 360°, the two runs scanning the right-lead and left-lead patterns separately are juxtaposed graphically. Thus, the scores for ±180° (actually the same phasing value) are drawn slightly apart, whereas 0° and 360° constitute both "ends" of the curves, although they represent the same requirement and should be glued together mentally. Note that the first probe on the second day scanned only the set of relative phases having the same lead–lag relationship as that

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[4] The skewed population exhibiting multistable dynamics stemmed from our prerequisite of obtaining an equal number of individuals with *bistable* dynamics to test our main hypotheses. Intervening cases of multistable dynamics were analyzed as they occurred without reaching an equal population. The general picture, however, was remarkably coherent across all multistable cases in spite of such individual differences.

[5] Remember that in all of the sections on the collective variable dynamics, we used a point estimate of relative phase.

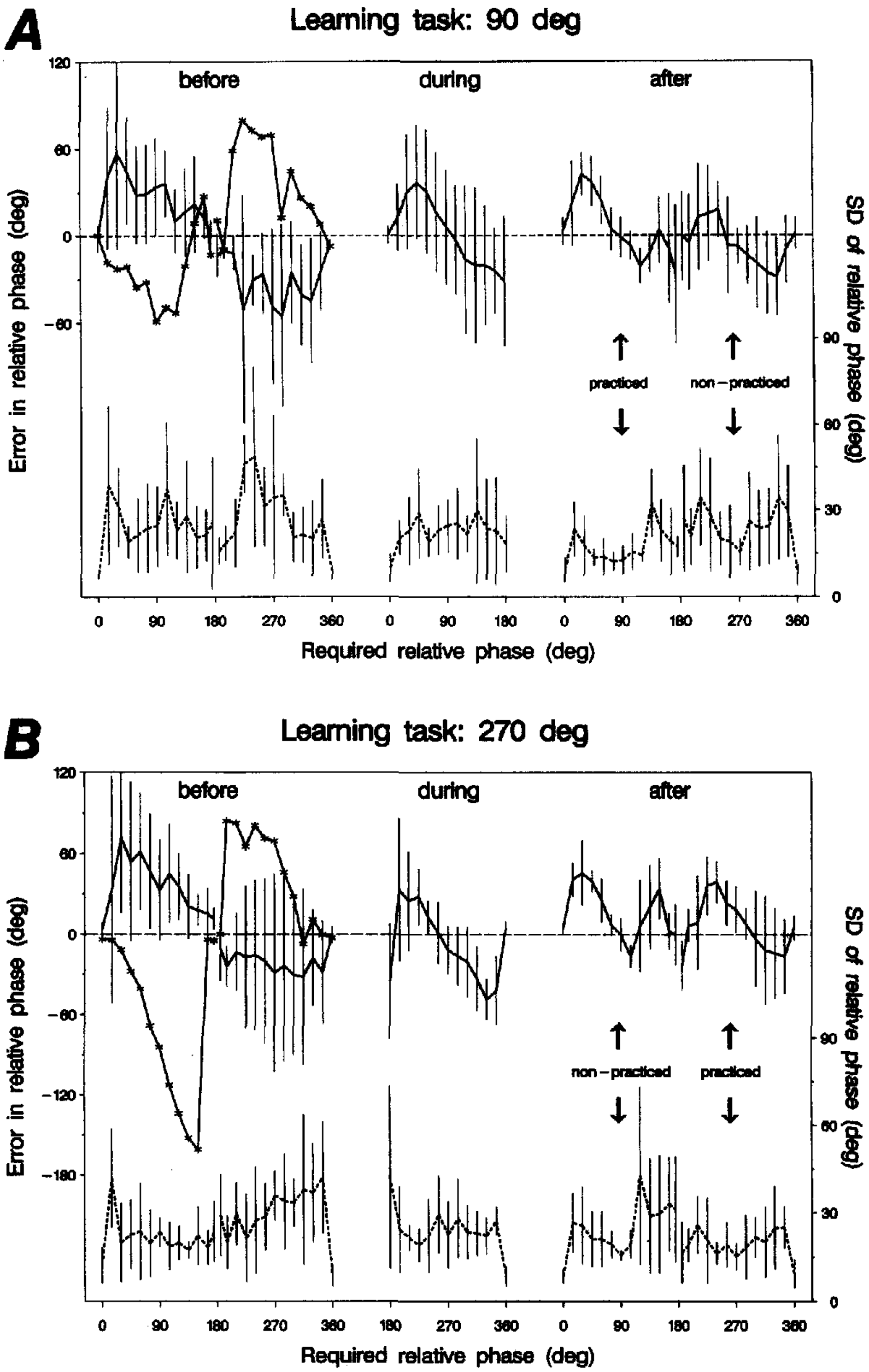

Figure 1. Probes of the collective dynamics before, during, and after learning for initially bistable dynamics. A: The results for the 5 subjects who practiced 90°. In the prelearning probe, the data for 4 subjects are pooled together, and 1 is singled out (denoted by asterisks). The top, solid curves display the average error in performed relative phase as a function of the required relative phase. The bottom, dashed curves represent the corresponding within-plateau standard deviations. Vertical bars denote between-subjects standard deviations if applicable. B: The results for the 5 subjects who practiced 270°. The legend is the same as for A, except for a change in the left ordinate. Zero crossing of the error curve with a negative slope and low standard deviation are indicative of an attractive state of the underlying coordination dynamics. Comparison of A and B shows that learning and transfer of learning lead to a bifurcation establishing new attractive states (denoted by arrows) at the practiced pattern and its nonpracticed symmetry partner.

of the practiced pattern. Because two types of behavior were observed in both learning groups before learning, the error scores (top left graph) of 4 subjects exhibiting comparable performance were collapsed together, with the mean value being displayed along with the ±1 between-subjects standard deviation (vertical bars). Individual error scores for the one remaining subject in each group are represented by the asterisk curve for the sake of demonstration. The corresponding within-plateau standard deviation (bottom left graph) is not singled out, however, in order to avoid unnecessary clutter in the figure.

Consider first the results of the initial probe for most subjects who practiced 90° of relative phase (curves with a vertical bar in Figure 1A). The mean error (top curve) was minimal for phasing requirements of 0° and 180°, whereas it was substantially larger for other required relative phases. More precisely, when a pattern different from 0° (or 360°) was required, the error was roughly proportional to the difference between the actual requirement and 180°, exhibiting a negative slope near 180° where it crosses the abscissa. This means that over a large span of phasing requirements different from 0°, the performed pattern was systematically biased toward 180°. Concerning performance variability, the lower curves show that the within-plateau standard deviation was smallest for phasing requirements of 0° and 180°, more so for the former than the latter. Such stability of the 0° and 180° patterns relative to intermediate values is also reflected by the lowest between-subject variability in both scores (vertical bars). This initial picture suggests bistable coordination dynamics characterized by attraction to in-phase and anti-phase. Notwithstanding an altogether different behavior during the probe, this conclusion also held true for the remaining individual (the asterisk curves in Figure 1A). The negative slopes about 0° and 360° reflect strong attraction to the in-phase pattern, until performance eventually switches to 180° at about ±150° of required relative phase, indicating attraction to the anti-phase pattern.

A comparable pattern of results was observed for subjects who practiced 270° of relative phase (the leftmost curves of Figure 1B). For the 4 subjects pooled together, the top curve is closer to zero at 0° and 180° and exhibits a typical negative slope around 180°, while the bottom graph shows that performance variability is smallest for both phasing requirements. Thus, as soon as the task no longer required the 0° phase relationship, the produced pattern appeared to be pulled toward 180° of relative phase to a large degree regardless of the actual requirement. A similar disregard for the task requirement in the intermediate range was also observed for the individual represented by the asterisk curves. Performed relative phase was strongly attracted to in-phase, before switching to anti-phase for the last two phasing requirements. Thus, both behaviors illustrated in Figure 1B suggest underlying coordination dynamics that are basically stable at in-phase and anti-phase, with the only difference being the plateau at which switching from in-phase to anti-phase actually occurred.

Note that when there is strong attraction to an underlying coordination tendency in spite of the task requirement, variability may well be low because what is actually performed is a stable, preferred phasing pattern. Meanwhile, however, the actual performance error may be large. An example is provided in Figure 1B, where the standard deviation curve (bottom) for the first probe between 30° and 180° is fairly low because all subjects consistently performed either 0° or 180°, one of the stable patterns of the underlying coordination dynamics. This large mismatch gives rise to the negative slope in the error curves (top). Conversely, the mean error may be close to zero because of averaging across a range of phasing scores that reflect the subject's unsuccessful attempts to perform the task. However, variability, both within and across subjects, is then large. Thus, when competition arose between task requirements and preferred coordination patterns, there was a trade-off between the mismatch error and the variability of performance. Both measures must therefore be considered simultaneously to assess the situation correctly.

In summary, the similarity between the left graphs of Figure 1A and 1B leads to a common conclusion: Initial probes for all subjects indicated that the underlying coordination dynamics were bistable at 0° and 180° before exposure to the learning task. This, of course, is the reason why these subjects practiced either the 90° or 270° phasing pattern. Theoretically, the latter relative phases constitute unstable fixed points or repellers of the underlying coordination dynamics. As seen in Figure 1, it is around these unstable states that the error and the variability culminate, giving rise to the characteristic tilde-like curve for the error and double-humped curve for the standard deviation. Thus, both shapes, because of the nature of the variables, reflect a certain symmetry in the bistable coordination dynamics exhibited before practice.

How, then, was the putative coordination dynamics affected by 2 days of practice? Consider the rightmost graphs of Figure 1A, which show the results of the final probe for all 5 subjects who practiced the 90° pattern. For the error in relative phase (top graph), the scores are near zero at 0° and 180° and there is a negative slope around the 180° pattern, which is similar to the situation before learning (cf. leftmost curves). Stability measures (lower graphs) indicate that the 0° pattern was less variable than the 180° pattern, although both were more stable than most intermediate values. The main novelty of the final probe was that the error curve showed a negative slope and the standard deviation was low around the practiced pattern of 90° as well as 270°, suggesting that these patterns had become attractive states of the coordination dynamics. Such a tendency also was confirmed by the low between-subject variability for these phasing requirements. Thus, the coordination dynamics after learning is multistable at 0°, 90°, 180°, and 270° and is again quite symmetrical in nature. For the subjects who practiced 270°, the rightmost graphs of Figure 1B reveal a similar pattern of results. Negative slopes and low standard deviations around 0°, 90°, 180°, and 270° suggest that these patterns constituted attractive states of the coordination dynamics after learning. Moreover, the curves in both figures were reasonably symmetrical.

Comparison of initial and final probes (cf. left- and rightmost graphs of Figures 1A and 1B, respectively) for subjects with bistable coordination tendencies before learning yielded consistent findings. Whatever its actual value, the to-be-learned pattern became an attractive state of the coordination dynamics with practice. Concomitantly, the symmetry partner of the to-be-learned pattern became an attractive state as well, although such a pattern was not practiced at all. Such automatic stabilization of a nonpracticed pattern is unmistakable evidence of *transfer of learning*. Thus, for subjects who practiced ±90°, the entire process of learning and transfer led to a qualitative alteration of the coordination dynamics from an initially bistable to multistable regime. A fascinating outcome of this bifurcation or phase transition is that it appears to preserve the original symmetry of the coordination dynamics.

We confirmed the foregoing pattern of results statistically by comparing the 0°, ±90°, and 180° patterns in each individual scanning run (i.e., half of a complete probe covering the right- vs. left-lead patterns) across practice days and learning tasks (i.e., 90° vs. −90°). In the subsequent analyses, we used the absolute mean error in relative phase as a measure of accuracy. One reason for choosing this measure was to cancel out behavioral differences among subjects regarding when they switched from 0° to 180° during a scanning run. A second reason was to eliminate the differences attributable to the signed error associated with attraction to a given phasing pattern. Two 2 × 2 × 2 × 3 analyses of variance (ANOVAs; Task × Day × Run × Pattern) with repeated measures on the last three factors were carried out for both dependent variables, namely, the mean and standard deviation of the absolute error in relative phase. For the mean error, the main effects of day, $F(1, 8) = 6.35, p < .04$, and pattern, $F(2, 16) = 10.88, p < .01$, were significant, as was their interaction, $F(2, 16) = 10.57, p < .01$. This analysis led to three conclusions: First, the interaction confirmed that, beyond the overall and trivial differences between patterns and days, learning did not affect all phasing patterns equally. Second, the lack of significance of the run effect or any of its interactions reflected the persistence of the symmetry between left-lead and right-lead scanning runs. Finally, because the effects of the learning task and its interactions were not significant, these conclusions are true regardless of which relative phase was practiced. An a priori contrast analysis of the day effect distinguished the 0° and the 180° patterns from the 90° and 270° patterns, $Fs(1, 8) = 11.36–33.13, ps < 01$, but did not differentiate the 0° and 180° patterns or ±90° from each other. In summary, statistical treatment of phasing error confirmed quantitatively the observations illustrated in Figures 1A and 1B (top graphs), that is, the emergence of a zero crossing at 90° and 270° with learning, thereby reflecting qualitative change (from a bistable to multistable regime) in the evolving coordination dynamics.

The same analyses were conducted on the mean within-plateau standard deviation. A Task × Day × Run × Pattern ANOVA revealed that the main effects of day, $F(1, 9) = 13.33, p < .01$, and pattern, $F(2, 16) = 16.38, p < .01$, and their interaction, $F(2, 16) = 4.32, p < .03$, were significant. In addition, the Day × Run interaction was significant, $F(1, 8) = 7.32, p < .03$, as well as the Day × Pattern × Run interaction, $F(2, 16) = 4.69, p < .03$. The Day × Pattern interaction indicated that the 90° and 270° patterns underwent a substantial decrease in variability with learning, whereas the 0° and 180° patterns remained essentially the same. However, the three-way interaction indicated that the 180° pattern was not as stable in both runs. In fact, the standard deviation in the second run of the probe (i.e., with a lead–lag relationship other than the practiced pattern) appeared to be generally larger than in the first run, a fact that was at the origin of the Day × Run interaction. In brief, like the foregoing error data, these statistical analyses of the standard deviation of relative phase strongly suggest that the practiced pattern and its symmetry partner become more stable with learning. Overall, the analyses on the error and variability of performance as a function of the required relative phase indicate that the to-be-learned pattern stabilizes with learning and that learning a specific phasing is automatically transferred to its symmetrical partner.

The take-home message concerning the evolution of bistable attractor layouts with learning a new phasing pattern is that the practiced pattern and its symmetry partner do indeed stabilize and become attractive states of the underlying coordination dynamics. These findings unequivocally support our hypothesis that learning involves a phase transition. Moreover, they indicate that the symmetry of the underlying coordination dynamics is preserved by the automatic transfer of learning.

Practice Trials

A general picture of the evolution of task performance with practice is provided in Figure 2. Figures 2A and 2B show data for subjects who learned the 90° or 270° patterns, respectively. The scores connected by a line represent the practice trials, and the scores drawn slightly apart with horizontal tickmarks represent the plateau of the three probes in which the to-be-learned relative phase was actually required. The upper curves represent the absolute mean error in relative phase for a trial (or a plateau) collapsed across subjects. The lower curves show the corresponding within-trial (or within-plateau) standard deviation. For all curves, vertical bars indicate the variability across subjects, encompassing ±1 *SD*. The 50 scores are graphically separated according to the day of training, although the trial numbering is continuous for graphical purposes.

First, we focus on the practice trials (connected scores). The graphs displayed in Figures 2A and 2B present several characteristic features of classical "learning curves." As the practice of the 90° or 270° phasing pattern proceeded, the absolute error (upper solid curves) diminished substantially from an initial value of 54.90° to that of 8.42°, on average.[6] Likewise, performance variability decreased from an average value of 29.95° to 13.00°. For both scores, between-trial fluctuations and between-subject variability (denoted by the

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[6] An individual breakdown of the scores on the first trial showed undershoot and overshoot of the required phasing pattern by at least ±30°. This also reflected an overall attraction to in-phase or anti-phase before learning.

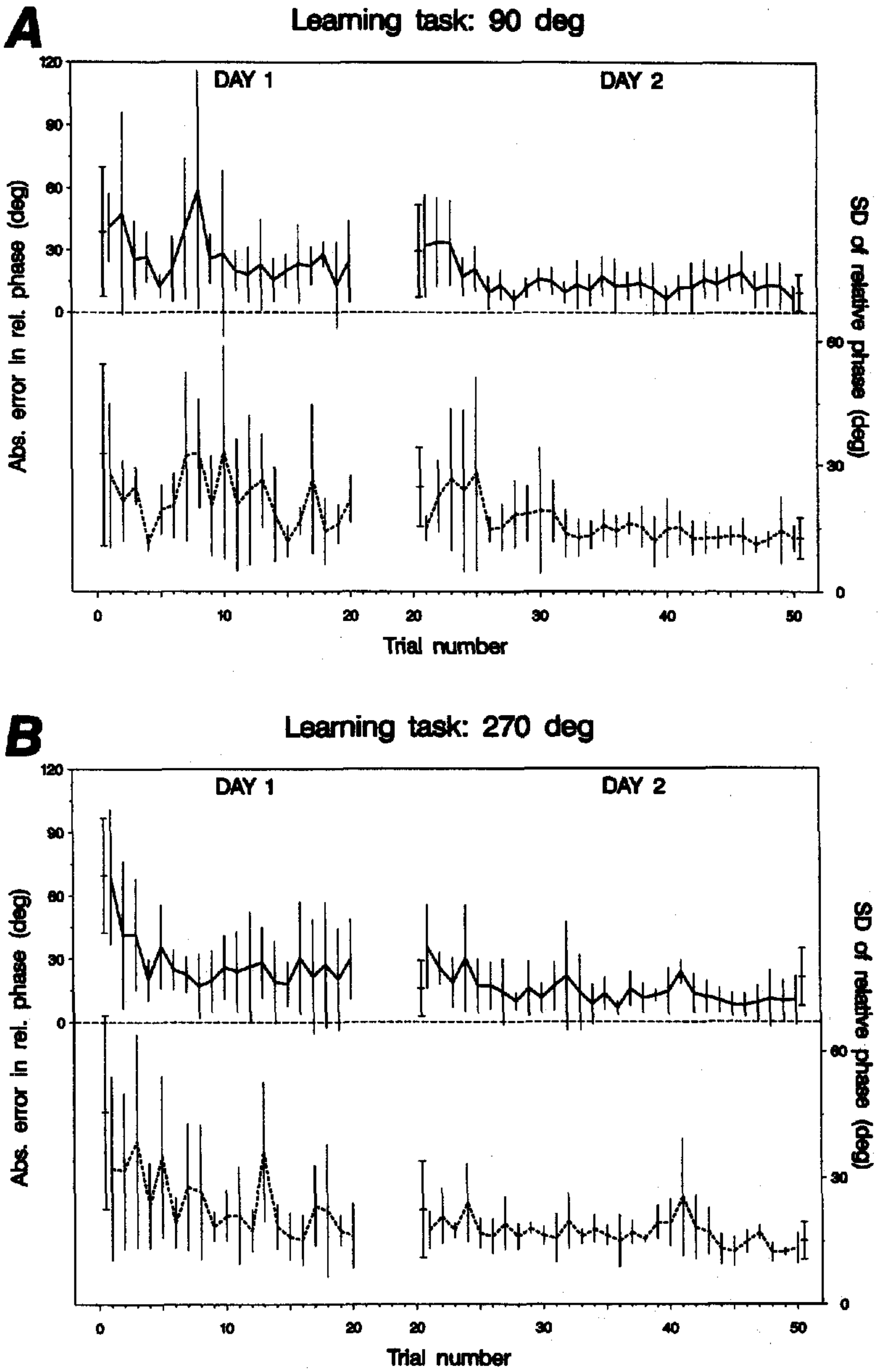

Figure 2. Evolution of performance in the practice trials for subjects who practiced 90° (A) or 270° (B). The top, solid curves show the average absolute (Abs.) mean error in performed relative (rel.) phase as a function of the trial number. The bottom, dashed curves plot the corresponding within-trial standard deviations. For the sake of comparison, performance on the plateaus in which the to-be-learned phasing pattern was required during the three probes is plotted slightly apart. Vertical bars denote between-subjects standard deviations. Both panels represent "typical learning curves."

vertical bars) also declined markedly. Thus, consistent with a minimal definition of learning, practice substantially improved performance toward the criterion level.

Regarding the plateaus of each probe in which the to-be-learned pattern was required (disconnected scores), the decrease in the absolute error and variability of the produced relative phase, including between-subject variability, was noticeable and appeared to be quantitatively similar to that observed in the practice trials. Moreover, the evolution of performance in the learning task and the evolution of the underlying coordination dynamics assessed using the scanning probes were compatible timewise. From the data of Figure 1, it appears that the intermediate probe carried out during learning revealed a substantial stabilization of the to-be-learned pattern. Accordingly, a steep performance improvement was observed during the first trials of the second day (i.e., between Trials 20 and 25), such that the final level of performance was almost achieved (see Figure 2). Together, these findings provide evidence that both the learning and scanning tasks were tapping into the same basic coordination dynamics.

An essential finding of this study is that not only did the trained pattern stabilize with learning but, simultaneously, its symmetry partner did as well. Among the total number of 500 practice trials performed by the subjects, 11 exhibited spontaneous switching between a given relative phase and its inverse (e.g., from 90° to 270°). Two examples are provided in Figure 3. The top window in Figures 3A and 3B plots the cycle-by-cycle point estimate of relative phase as a function of time. Note that the ordinate covers the range from $-360°$ to $360°$, so that each data point is plotted twice for ease of visualization. The bottom window displays the time series of the finger motion, with the solid line representing angular displacement of the right finger and the dashed line the left finger. Upward movement of the lines corresponds to finger flexion, so that tick marks denote the moment of peak flexion of both fingers.

Figures 3A and 3B show examples of practice trials for 2 subjects who practiced 90° or 270°, respectively. Both show steep and successive jumps, back and forth, between relative phase values centered about 90° and about 270° (denoted by the arrows), regardless of the actual requirement. Such switching was sudden relative to the intervening epochs of stable behavior and could not be attributed to a gradual change or shift in relative phase. These data suggest that at this point in their evolution, the underlying coordination dynamics are actually multistable, with both the to-be-learned and the symmetrical patterns qualifying as attractive states of roughly equal strength. This hypothesis appears reasonable because all trials exhibiting spontaneous switches occurred after 10, but before 25, practice trials were completed, that is, after enough practice had been provided to stabilize both patterns. Indeed, the scanning probe closest in time (i.e., at the beginning of the 2nd day; see the half scans carried out during practice in Figure 1) already revealed the presence of attractive states at 90° or 270°.

Other Routes to Learning

We now discuss the 4 subjects who, by virtue of the initial scanning probes, exhibited coordination dynamics in which patterns other than 0° and 180° were attractive states before exposure to the learning task. Figure 4 shows the evolution of these initially multistable dynamics with learning on an individual basis. For each subject, the general layout of Figures 4A–4D is the same as that of Figure 1. The top graphs plot the average error in relative phase for each plateau, and the bottom graphs display the corresponding variability. Left- and rightmost curves represent the complete probes carried out before and after practice; the middle curves represent the half probe conducted at the beginning of the second day of practice. A difference is, of course, the absence of vertical bars denoting between-subject variability. A second difference is the addition of the linear regression (dashed line) computed over the entire span[7] of each negative slope of the error. Such linear trends help quantify the attraction of the underlying stable states of the coordination dynamics, in that it affords a better, statistically grounded estimation of the point zero crossing. For all negative slopes, the linear regressions were significant ($R > -.85$).

Figures 4A and 4B show the data of 2 subjects whose coordination dynamics were initially stable about the ±90° relative phases. The leftmost pair of curves exhibit negative slopes and zero crossings of the error (top curve) close to these values, as denoted by the linear regressions (dashed lines) that cross the abscissa within a ±15° interval around 90° or 270°. Moreover, there is reduced variability (bottom curve) around these values.[8] Recall that negative slope and low variability are signature features of attractive states.

The final coordination dynamics (rightmost curves) show signs of attraction to ±135°, as reflected by the clear shift of the regression (dashed) lines toward these values. Actually, the zero crossings of the error curves occur, in both cases, at 150° and 135°. At the same time, the variability is relatively low. This pattern of results again suggests that both the to-be-learned pattern and its symmetry partner stabilized, even though only the former was practiced. Thus, in keeping with results concerning bistable initial dynamics (cf. the section on probes of the collective variable dynamics), learning a novel relative phase transfers automatically, in such a way that the symmetry of the coordination dynamics is preserved.

It is important to note that the initially stable states at

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[7] The span of the negative slope was defined as the interval, on each side of a zero crossing, within the phasing values associated with the largest or smallest errors or those preceding another crossing of the abscissa, whichever came first.

[8] Because these are individual data, the pattern of results regarding variability is less clear than the data collapsed across subjects (cf. Figure 1). Nevertheless, the data indicate that the closer to 90° the relative phase actually performed was (i.e., the sum of the required phasing and the mismatch), the smaller the standard deviation became. Such a relationship still reflects the differential effects expected from competitive or cooperative mechanisms between preferred and required patterns.

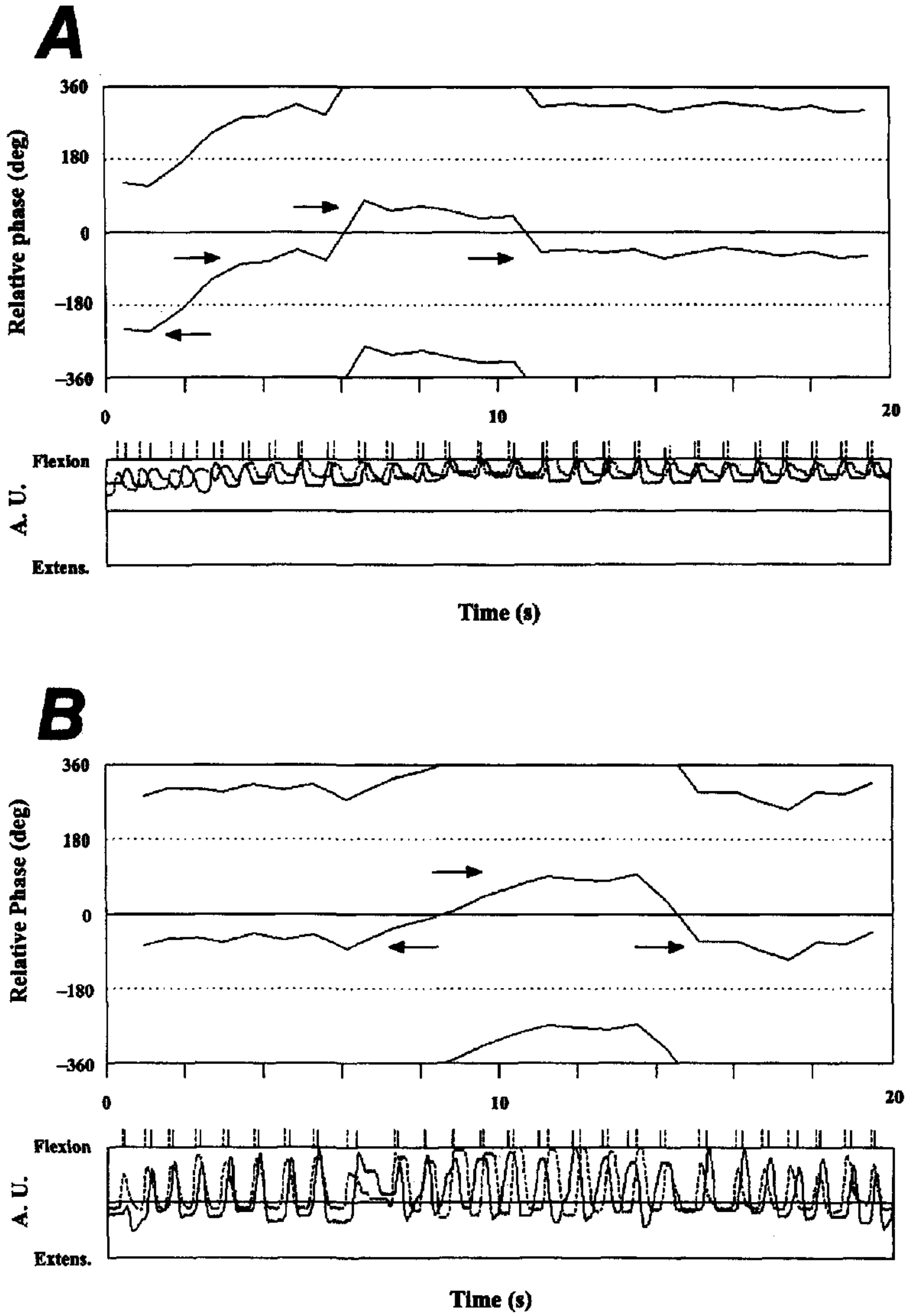
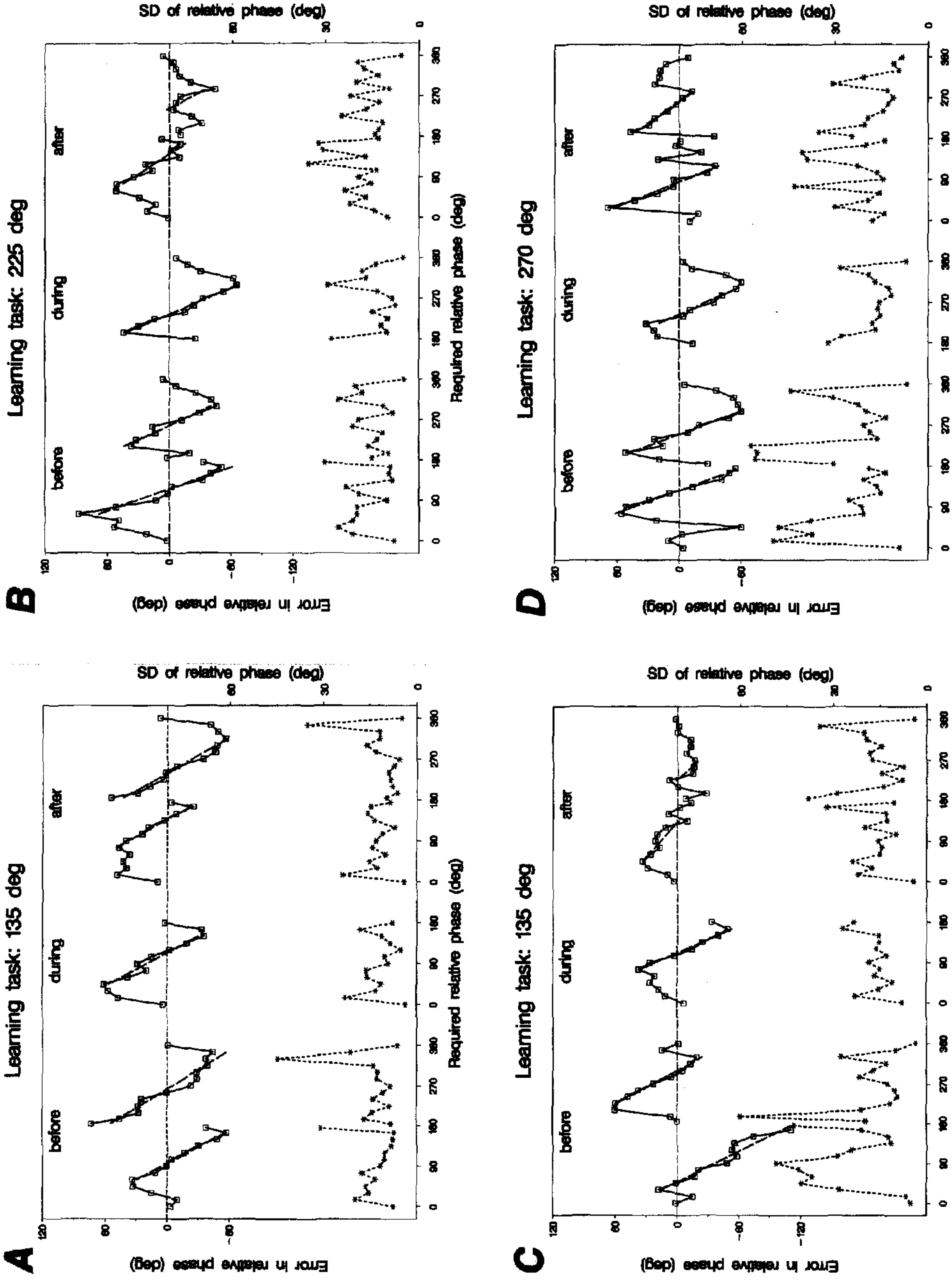


Figure 3. Examples of switching behavior in practice trials for 2 subjects who practiced 90° (A) and 270° (B). In each panel, the top window plots a point estimate of the relative phase between fingers, and the bottom window displays the actual excursions of the right (solid line) and left (dashed line) fingers in the indicated directions. In both cases, successive bouts of stable performance (denoted by arrows) correspond to executing almost exclusively the learned pattern and its symmetry partner. Extens. = extension; A.U. = Arbitrary Units.

±90° are no longer present in the final probes. They have, as it were, been "replaced" by the new ones corresponding to the learning requirement and its symmetry partner. However, this does not mean that the underlying coordination dynamics were altered qualitatively with learning because such dynamics was and remained multistable (i.e., with four attractive states) before and after practice. Rather, these findings hint strongly at an alternative route to learning, the


A
Learning task: 135 deg
B
Learning task: 225 deg
C
Learning task: 135 deg
D
Learning task: 270 deg
before
during
after
Error in relative phase (deg)
SD of relative phase (deg)
Required relative phase (deg)
120
60
0
-60
-120
30
0
90
180
270
360

nature of change corresponding to the shift of an already-existing attractor in the direction of the to-be-learned pattern. Such a gradual shift was nicely captured "in flight" by the intermediate, incomplete probe carried out during learning at the beginning of the second day of practice. The middle graphs of Figure 4A show that the zero crossing in the mean and the minimum in the standard deviation have already moved from the original relative phase of 90° to an intermediate value of about 120°. Similarly, Figure 4B indicates an equivalent shift in the direction to the task requirement from 270° to about 240°. Regarding the other half of parameter space not evaluated by the intermediate probe, one has to assume that a similar process occurs for the symmetry partners of these shifted attractive states because they eventually drift to the symmetry partner of the required patterns. Thus, a complete picture of the process presented in Figures 4A and 4B is that both learning and transfer gradually pull an existing pair of symmetrical attractive states from their initial values toward the task requirement and its symmetry partner.

Support for the foregoing scenario is boosted by the results presented in Figures 4C and 4D. In Figure 4C, the initial probe (leftmost curves) shows zero crossings of the regression line at 60° and 285° in addition to the more usual attraction to 0° and 180°. Roughly speaking, the underlying coordination dynamics exhibited signs of attraction to a symmetrical pair at ±60°. The to-be-learned pattern was thus set at 135°, in the middle of the interval between existing stable patterns. With practice, the 60° pattern progressively moved toward the task requirement, with the intermediate probe (middle curves) showing attraction to 105°. Finally (cf. rightmost curves), stable states are shown at 135° and 210°, close to the learning requirement and its symmetrical value (225°). The same dual process is illustrated in Figure 4D. Initially, attractive states appear near 135° and 205° (about ±135°). With increasing practice of an intermediate 270° pattern, a shift of the 205° attractor to the to-be-learned phasing is observed, mirrored by a move of its symmetry partner toward 90°.

General features of learning curves (i.e., decrease of the performance error and variability with practice; see Figure 2 for an illustration) were again observed in these 4 subjects (data not shown here). Note that the scores in the plateau of the probes requiring the same phasing pattern as the learning criterion are in keeping with these trends. Moreover, the error score in the first practice trial was biased in the direction of the nearby attractive state (i.e., 60° or 90°) for all subjects. Again, this suggests that the practice task and the probes are indeed tapping into the same underlying coordination dynamics.

Component Dynamics

After analyzing the effects of learning this discrete timing task at the coordinative level, expressed through a point estimate of the collective variable, relative phase (ϕ), we now consider events at the component level of description. Basically, we scrutinize the actual motion of each finger while the subject is involved in the task of learning a novel relative timing pattern. Specifically, through kinematic analysis, we investigate how individual finger motion is modified by virtue of learning a novel coordinative task.

In the first practice trials, component kinematics appeared to be characterized by a variety of behaviors across subjects and task requirements. By and large, finger motion was jerky (e.g., see Figure 3B) and the performed relative phase was variable, reflecting more or less successful attempts to produce a new phasing pattern. In contrast, the last practice trials for subjects who practiced 90° or 270° revealed three types of behavior in realizing the required relative phase. Certainly at that time, the required pattern was learned, given the stable and accurate performance in the practice trials (see Figure 2) and the accompanying changes in the collective variable dynamics (see Figure 1). Figures 5, 6, and 7 show typical examples of successful performance during one entire practice trial for 3 subjects who practiced 270°. Later on, we show that these behaviors are representative of the group as a whole (cf. Figures 9–11). Each figure is composed of three windows. The bottom window plots the time series of angular displacement of both fingers (in arbitrary units). The middle window displays the relative phase between them, both in terms of continuous (solid line) and point-estimate measures (denoted by solid circles). The top window shows the angular velocity time series of both fingers. Solid and dashed lines represent the right and left components, respectively. In the upper part of all windows, the onset of the pacing signals is represented by tick marks. Long and short tick marks refer to the left, leading, and right lagging metronome signals, respectively.

The bottom window of Figure 5 shows two displacement curves that are roughly similar to sinewaves of constant amplitude, except that some flattening is observed about

Figure 4 (opposite). Probes of the collective dynamics before, during, and after learning for initially multistable dynamics. Presented are individual data for participants who practiced 135° (A and C), for 1 subject who practiced 225° (B), and 1 subject who practiced 270° (D). The top, solid curves show the average error in performed relative phase as a function of the required relative phase. The bottom, dashed curves represent the corresponding within-plateau standard deviations. Zero crossing of the error curve with a negative slope (graphically enhanced by a linear regression carried out over its span) and low standard deviation are indicative of an attractive state of the underlying coordination dynamics. The data in the four panels suggest that learning induces a shift of a preexisting attractive state to the to-be-learned relative phase. Concomitantly, the transfer of learning induces a mirroring shift of another preexisting attractive state to the nonpracticed, symmetry partner of the learned pattern.

extrema, especially extension. Accordingly, the velocity curves (top window) are fairly regular and sinewave-like too, albeit with noticeable plateaus about zero velocity. We call such behavior the *sinelike strategy.* Were all these time series almost pure sinewaves, continuous relative phase would be close to 270° over the entire trial. In reality, its time series (solid line in the middle window) appears rather rough. In spite of this, two main features can be detected. First, continuous relative phase evolves in an orderly fashion over one cycle of finger motion with periodic spikes toward 0° (or 360°). These spikes correspond to the zero-velocity plateau at peak extension (viz. valleys of the displacement curves shown in bottom window). Second, between two such spikes, continuous relative phase hovers around the required value of 270° (dashed horizontal line), albeit with some fluctuations caused by specific anharmonicities in the kinematics of each finger. These epochs occur when the fingers are both flexing toward or extending away from the point of maximal flexion (peaks of the displacement curves in the bottom window). Note that this is a direct consequence of the discrete task requirement, which was to synchronize maximal finger flexion with the onset of the metronome signal. Indeed, peak flexion of the fingers coincides fairly well with its respective metronome (cf. long tick marks with dashed peaks and short tick marks with solid peaks). Accordingly, the pointwise relative phase (see the solid circle) remains close to the required value over the entire trial ($M = 275.2°$, $SD = 10.5$). Thus, Figure 5 nicely captures the link between the individual component motions and the relative phase, for both the continuous and point-estimate measurements, showing how coordination emerges from the interaction between the specific task requirement and the individual components. In strict compliance with the task demand, the components are tightly coordinated at specific points in time (i.e., they are locked at the correct relative phase), whereas they appear to be slightly less coupled elsewhere during the cycle. This provides an a posteriori confirmation of the pertinence of our point-estimate measure at peak flexion for capturing the coordinated behavior of the fingers in this task (and others). In other words, such a point estimate is indeed a relevant collective variable characterizing the underlying dynamics (see also the Appendix).

Another interesting feature of Figure 5 is that fluctuations of continuous relative phase as well as within-cycle patterning tend to diminish with time. Such smoothing of finger motion is reflected, for instance, by increased regularity of the velocity curves in the last cycles and decreasing length of the zero-velocity plateaus (see the top window). This may indicate the existence of a time scale along which both individual components gradually recover from the perturbation imposed by the task on their natural tendency to exhibit stable relative phase relationships at in-phase and anti-phase.

Another typical behavior is presented in Figure 6, in which the two fingers also exhibit roughly comparable kinematics. Displacement curves (bottom windows) are no longer near-sinusoidal but instead exhibit sharp peaks (viz., rapid flexion–extension movements) and flat plateaus (viz., standby at extension). It follows that continuous relative phase (solid line in the middle window) is not constant over a cycle but that it periodically oscillates between approximately 90° and 0° (or 360°). The 0° (or 360°) value corresponds to moments when both fingers are immobile at maximal extension, hence remaining together in-phase. We call the behavior shown in Figure 6 the *in-phase strategy.* Notice that the continuous relative phase actually reaches the required value of 270° (horizontal dotted line) twice per cycle. This happens close to the occurrence of peak flexions, that is, when both fingers must be synchronized with their respective pacing signals to accomplish the task. In particular, the point-estimate relative phase calculated at peak flexion (see the solid circles) reveals good performance ($M = 260.6°$, $SD = 13.1°$). Here again, task constraints at the collective level manifest themselves at the level of the component dynamics. Consonant with the task requirement, component motions come together appropriately at specific points in their excursions, while tending to assume a more basic coordinative pattern (i.e., in-phase) elsewhere. Essentially, a mechanism comparable to the sinelike strategy illustrated in Figure 5 also seems to operate here, except for the reduced time and strength with which the phase coupling to the required value operates. From another (but not contradictory) perspective, Figure 6 suggests that with learning, a preexisting coordination pattern (i.e., in-phase) is locally altered to meet a competing task requirement, leading to a composite, in-phase strategy.

Further notable feature of the coordination between components is apparent in the velocity curves of Figure 6. These show a tight time coincidence between peak positive velocity of the lagging component (right finger) and peak negative velocity of the leading component (left finger; cf. peaks of solid line and valleys of dashed line, respectively). This means that the right finger tended to flex to synchronize with its visual prompt precisely when the left finger returned from its own point of synchronization (cf. tick marks representing metronome onsets). Accordingly, displacement curves (lower window) show that flexion of the right lagging component (viz. upward movement of the solid line) was accompanied by extension of the left leading finger (downward movement of the dashed line). These epochs of opposite motion of the components resulted in successive drops of continuous relative phase (middle window) toward 180°. Such a drop may lead to values lower than 180° because of cycle-by-cycle idiosyncrasies in each finger's kinematics, as can be seen, for example, at about the sixth cycle, when the left finger did not stay extended as long as usual but immediately shifted a bit toward flexion.

Coordination epochs in which components moved anti-phase with each other are even more apparent in the behavior presented in Figure 7. The bottom window shows that fingers tended to move in opposite directions for the entire trial, so that the displacement of one finger seemed to precisely mirror that of the other. We call this behavior the *anti-phase strategy.* Accordingly, the top window illustrates that peak negative velocity of one component coincided with peak positive velocity of the other component while both fingers paused (zero velocity) for about the same amount of time. Thus, the continuous relative phase between the two

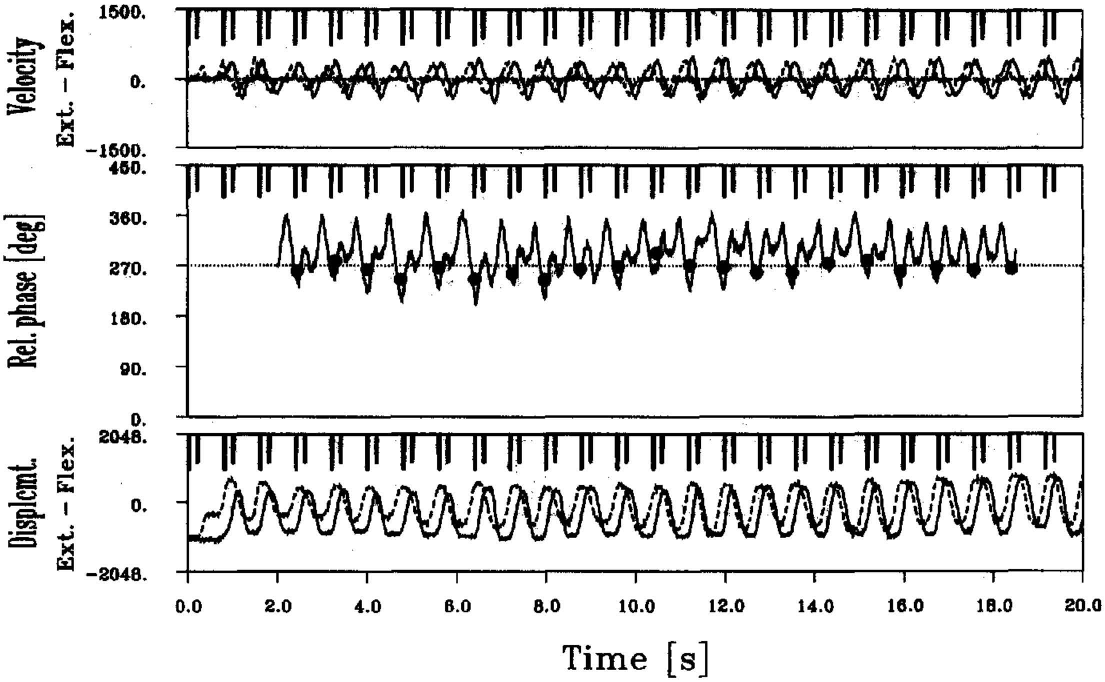


Figure 5. Kinematic exemplar of the sinelike strategy. The top and bottom windows plot angular velocity and displacement (Displcmt.) of the right and left fingers (solid and dashed lines, respectively) in the indicated directions. The middle window displays the continuous relative (Rel.) phase (solid line) between fingers and its point estimate (denoted by solid circles) calculated at peak flexion. In all windows, long and short tick marks represent the occurrence of the leading (left) and lagging (right) metronome signals, respectively. Coordinated sinewave-like motion leads to a continuous relative phase that hovers around the 270° value, particularly at peak flexion, the designated task requirement for the fingers to be synchronized with their respective metronomes. Ext.–Flex. = extension–flexion.

components (solid line in middle window) tended to stay around 180° for much of the cycle. A closer look at the displacement curves (bottom window) reveals that, for both fingers, the rest period lasted roughly as long as the movement itself. More precisely, during half a cycle, the finger was immobile in a given position (flexion or extension), moved away (to extension or flexion, respectively) for the next quarter of the cycle, and finally returned to its initial position in the last quarter of the cycle (flexion or extension). A consequence of this inverted kinematic pattern is that the fingers tend to momentarily realize the required relative phase at the point in time defined by the metronomes, as shown by the synchronization of the peak continuous relative phase near 270° (see the solid line in the middle window) with the pacing signals, whereas they basically remain anti-phase for the remainder of a cycle. Accordingly, the point-estimate values of relative phase (see the solid circles) fall right on top of these peaks of the continuous measure toward 270°, exhibiting an average of 244.2° with a standard deviation of 10.6°. Here again, another composite strategy is observed in which the existing anti-phase pattern is locally tuned to meet a competing task requirement.

One advantage of both the in-phase and anti-phase strategies (see Figures 6 and 7, respectively) may be that, instead of maintaining the required phase relationship constant throughout a cycle or a trial, the subject may achieve the task by resorting to a stable coordination pattern (viz. anti-phase) around the points of synchronization with the discrete metronomes. Of course, this is possible only if the finger displacement is not of the near-sinusoidal type illustrated in Figure 5 but instead exhibits resting epochs within a motion cycle in which the components stay either in-phase or anti-phase with each other.

This point is substantiated in Figure 8, which shows data from 6 subjects who exhibited a strategy somewhat consistently across trials.[9] In Figure 8A, the top solid curve plots the average absolute lag between peak positive velocity of the lagging finger and peak negative velocity of the leading finger for the first five and last five practice trials. The bottom curve displays the corresponding standard deviation, and vertical bars represent between-subject standard deviations. Absolute lag dropped by more than 50% within the first trials of practice and eventually hovered around 28° in the last trials, corresponding to about a 70-ms time differ-

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[9] The 2 subjects whose data are shown in Figures 6 and 7 and 4 other subjects who practiced ±90° composed the group of 6 subjects who exhibited either the in-phase or the anti-phase strategy shown here. The data for these subjects also are presented individually in Figures 9 and 10, respectively.

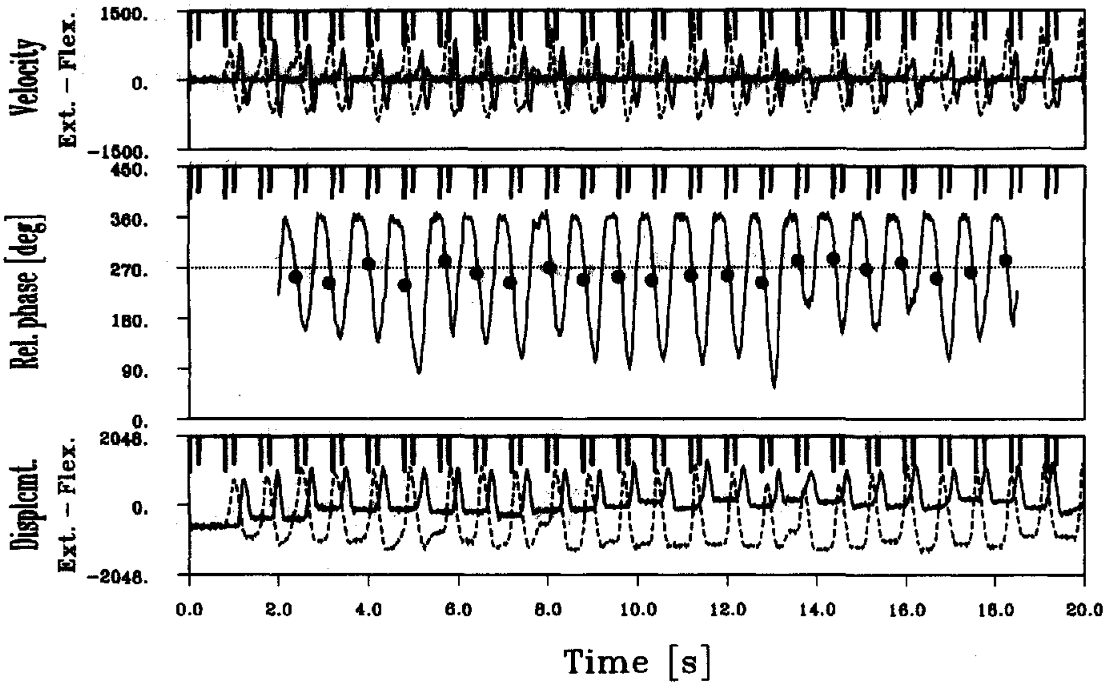

Figure 6. Kinematic exemplar of the in-phase strategy. The top and bottom windows plot angular velocity and displacement (Displcmt.) of the right and left fingers (solid and dashed lines, respectively) in the indicated directions. The middle window displays the continuous relative (Rel.) phase (solid line) between fingers and its point estimate (denoted by solid circles) calculated at peak flexion. In all windows, long and short tick marks represent the occurrence of the leading (left) and lagging (right) metronome signals, respectively. Coordination of spikelike finger motion results in a continuous relative phase that remains about 0° for most of the time but reaches the 270° required value twice per cycle, particularly when the leading finger attains peak flexion and is synchronized with its metronome. Ext.–Flex. = extension–flexion.

ence between the fingers. Note that such a score reflects the absolute error in synchronization, whereas the constant error (not shown here) is about zero on the average. This decrease in absolute lag was accompanied by a decrement in within-trial and between-subject variability. Thus, Figure 8A suggests that subjects performed the required task more stably by synchronizing velocity peaks of both fingers with increasing practice. In other words, this finding supports the idea that subjects resorted to a composite strategy for performing the required relative phase, in which the anti-phase coordination pattern was periodically involved. The top curves in Figure 8B plot the average lag between peak flexion displacement (solid lines) and peak flexion velocity (dashed line) of the leading finger with respect to its metronome signal for the first five and last five practice trials. The bottom curves show the within-trial standard deviations, and vertical bars denote between-subject standard deviations. At the beginning of practice, peak velocity appeared to be well synchronized with the metronome, whereas peak flexion lagged behind by about 30°. At the end of practice, peak flexion was better synchronized, with peak velocity slightly ahead of the metronome by a comparable amount. Meanwhile, the variability of both variables decreased. Thus, Figure 8B indicates that with learning, peak flexion became synchronized more precisely with the metronome, which was exactly the explicit task requirement. Taken together, the findings shown in Figure 8 suggest that for the 6 subjects who adopted a composite strategy, coherence between components was increased by temporally coupling velocity peaks, thereby momentarily performing a predominantly anti-phase pattern. Moreover, such moments of increased coordinative coherence appeared to occur in tight synchrony with the discrete temporal requirement imposed by the task, at least early in practice. With further learning, between-peaks synchronization shifted in time, such that maximal flexion of each component coincided with the metronomes. In summary, the temporary implementation of an anti-phase pattern at the moment of synchronization, shown in both the in-phase and anti-phase strategies, may provide convenient "anchor points" to coordinate the two components with each other and to coordinate them with the task requirement (see the General Discussion section).

Link Between Component and Collective Levels

The possibility of implementing different strategies for realizing the same task raises a series of questions. Why are there three strategies? Do such strategies reflect idiosyncrasies in coping with the task? Do they characterize a given level of learning? Are they specific to the actual phasing to

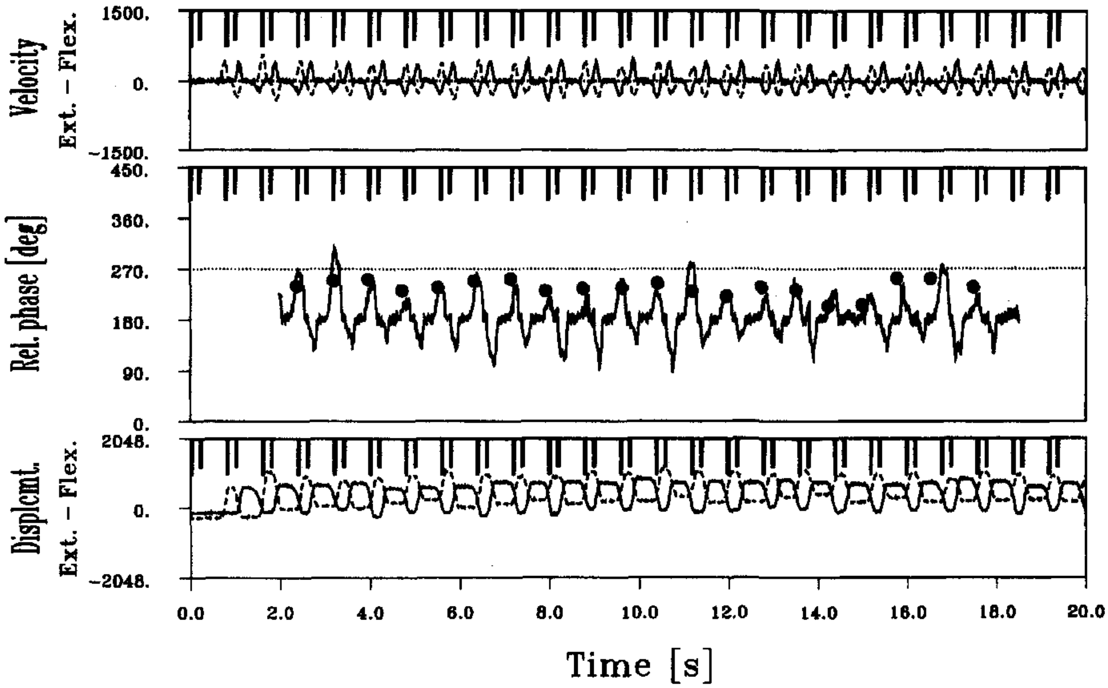

Figure 7. Kinematic exemplar of the anti-phase strategy. The top and bottom windows plot angular velocity and displacement (Displcmt.) of the right and left fingers (solid and dashed lines, respectively) in the indicated directions. The middle window displays the continuous relative (Rel.) phase (solid line) between fingers and its point estimate (denoted by solid circles) calculated at peak flexion. In all windows, long and short tick marks represent the occurrence of the leading (left) and lagging (right) metronome signal, respectively. Coordination of mirrorlike finger motion results in a continuous relative phase that remains about 180° for most of the time but tends to reach the 270° required value twice per cycle, particularly when the leading finger attains peak flexion and is synchronized with its metronome. Ext.–Flex. = extension–flexion.

be learned? A critical issue, especially in our approach to learning, is whether these three different strategies pertain to individual characteristics already present before exposure to the learning task.

We first consider the 10 subjects who learned 90° or 270°. Because coordination strategies tended to correspond to an advanced stage in mastering the task, we focus on the last five practice trials, over which we averaged the performance of both fingers. Nine of 10 subjects exhibited one of the typical behaviors illustrated in Figures 5–7 (sinelike, in-phase, and anti-phase strategies, respectively). Performance for the last subject was difficult to characterize because of trial-to-trial variability in terms of synchronization with the metronome.

The top three rows of windows in Figure 9 show kinematic data for 3 subjects who practiced 90° or 270° (the subject's data depicted in the middle window are those illustrated in Figure 6). The graphs on the left side show the angular displacement (in arbitrary units) of the right and left fingers (solid and dotted lines, respectively), averaged over the last five practice trials and plotted for the first 10 s. Typically, fingers exhibit spikelike excursions to flexion, with noticeable rest periods in extension. The top three graphs on the right side show the corresponding continuous relative phase calculated over the same time period. The relative phase exhibited large oscillations (covering about 270°). Notably, it stayed around a 0 (or 360°) value for a major part of a movement cycle but still achieved the required phasing (denoted by the dotted horizontal line at 90° or 270°) once per cycle. Such behavior is characteristic of the in-phase strategy shown in Figure 6 (cf. the bottom and middle windows, respectively). The bottom windows display scanning probes carried out before (left) and after (right) practice averaged over the same 3 subjects. Both graphs plot the mean error in relative phase as a function of the required phasing, with vertical bars encompassing ±1 between-subject standard deviation. Note that, unlike Figure 1, Figure 9 does not separate the 180° requirement as a function of the two runs composing the probe. Before learning (left window), a negative slope of the error curve about 0° (or 360°) spans a wide range of phasing requirements. Such a steep and marked slope about 0° denotes that the in-phase pattern strongly attracted neighboring relative phases, more so than the anti-phase pattern. Thus, the initial probe for the 3 subjects illustrated in Figure 9 indicates a prevalent coordination tendency to in-phase behavior before learning. After learning (bottom right window), the main feature of the collective variable dynamics is attraction to the newly learned ±90° patterns. Note that both the learned and transferred patterns contribute to the negative slope

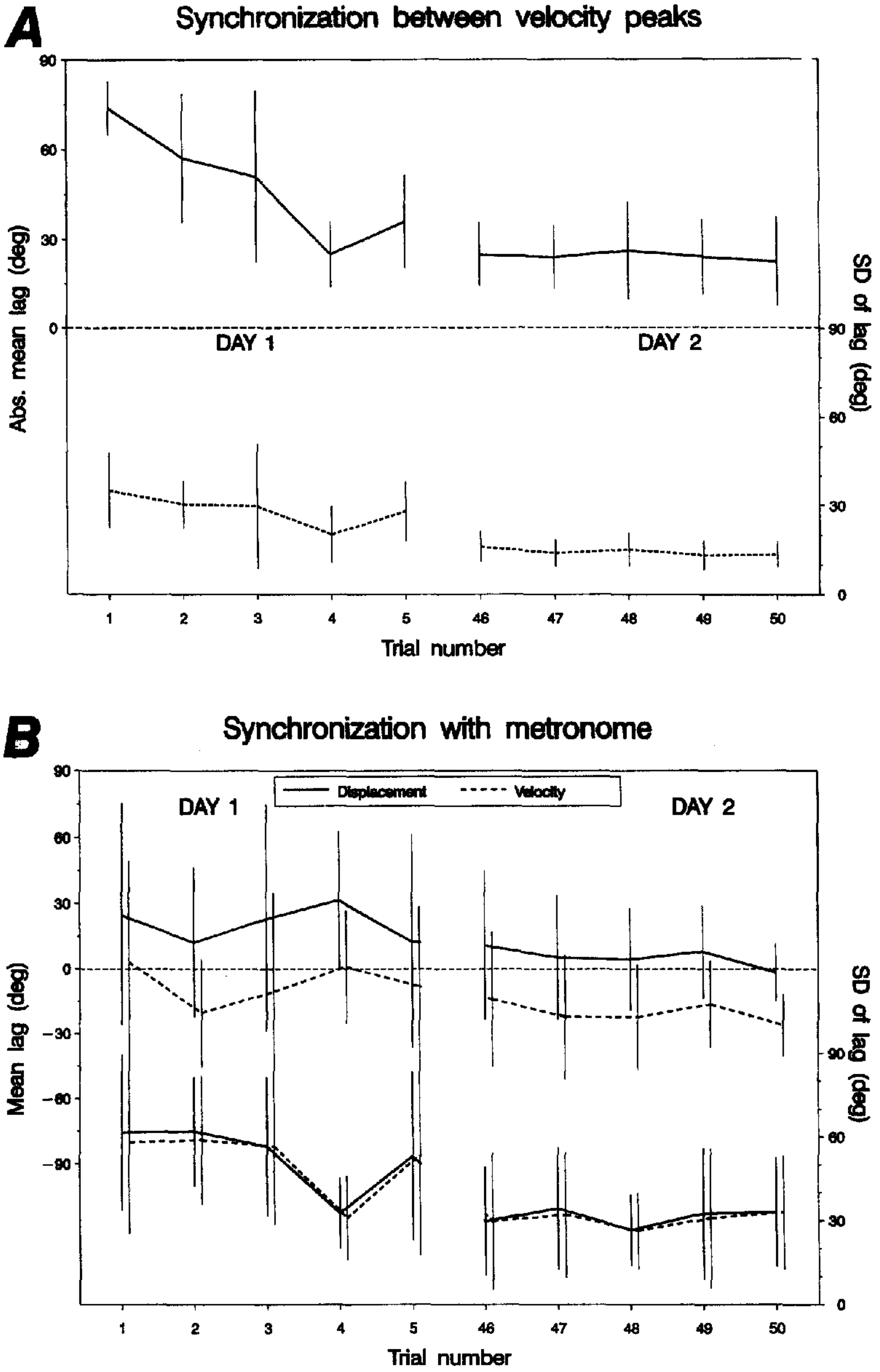

Figure 8. Changes in synchronization with learning. A: The average absolute (Abs.) mean lag between peak positive velocity of the lagging finger and peak negative velocity of the leading finger (top curve) and the associated standard deviation for the first five and last five practice trials. Vertical bars denote between-subjects standard deviations. Learning leads to a tighter synchronization of velocity peaks, suggesting that the task requirement may be met through a composite strategy involving the anti-phase pattern. B: The top curve plots the mean lag between peak flexion (solid lines) and peak flexion velocity (dashed lines) of the leading finger with its pacing signal for the first five and last five practice trials. The bottom curve plots the associated standard deviations, and vertical bars denote between-subjects standard deviations. In compliance with the task requirements, synchronization of peak flexion improves with learning.

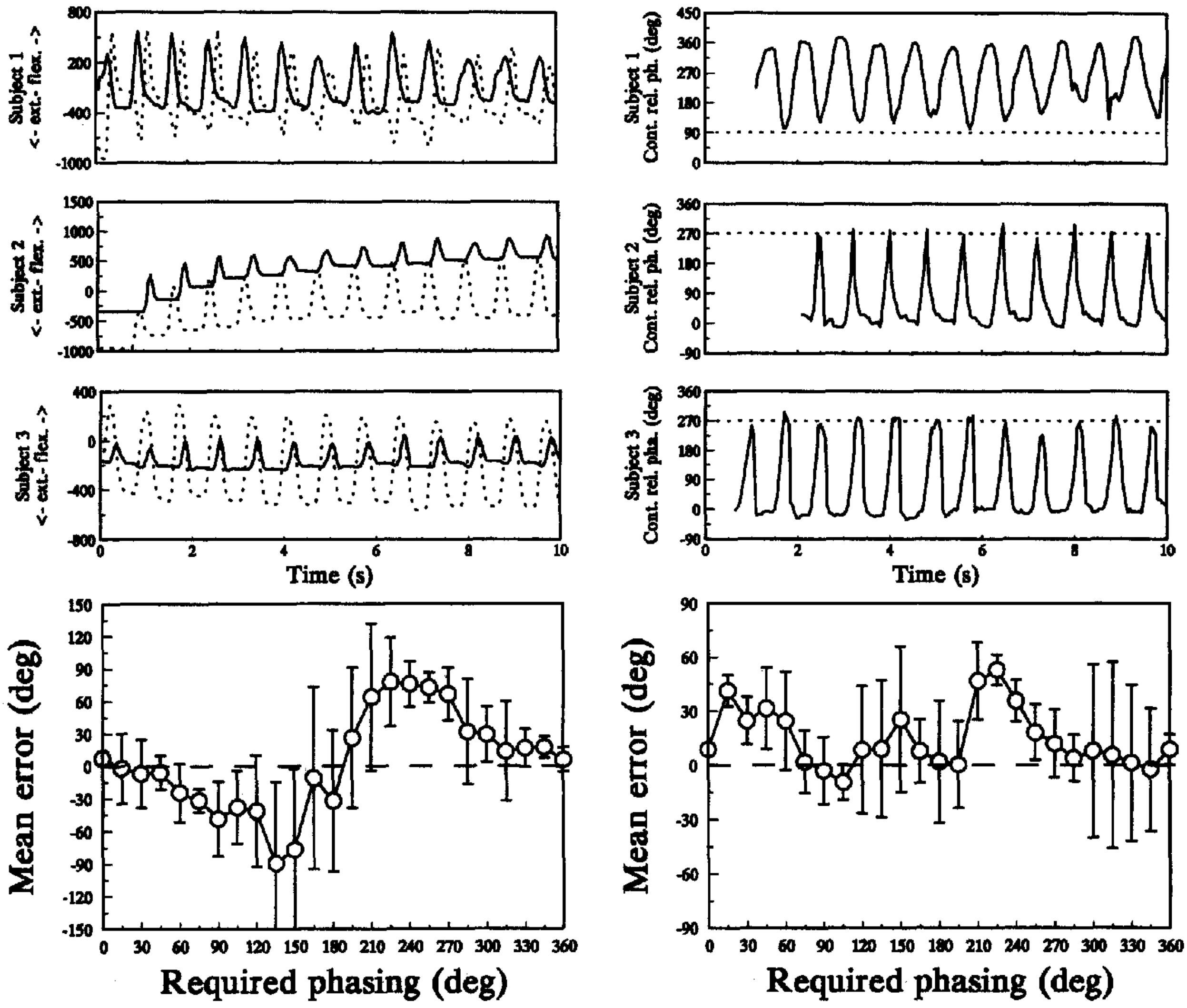

Figure 9. The relationship between component and collective dynamics in the in-phase strategy. The top three pairs of windows show kinematic data for 3 subjects, 1 per row, averaged over the first 10 s of the last five practice trials. The left windows plot the excursions of right and left fingers (solid and dotted lines, respectively) in the indicated directions. All exhibit coordinated spikelike finger motion similar to that described in the bottom window of Figure 6. The three right windows plot the corresponding continuous relative phase (cont.rel.ph.). These display a highly variable phase relationship that meets the task requirement (denoted by the dotted line) periodically while mostly staying around 0°/360° otherwise (cf. the middle window of Figure 6). Such kinematic features are characteristic of the in-phase strategy. The bottom left and right windows display the results of the probes carried out before and after practice, respectively, averaged over the same 3 subjects. The mean error in relative phase is plotted as a function of the required relative phase (vertical bars denote the between-subjects standard deviations). Before learning, the wide and steep negative slope about 0° reflects a strong coordination tendency to in-phase. After learning, performance is attracted instead to ±90°. ext.–flex. = extension–flexion.

because the subjects practiced either 90° or −90°. Coming back to the component level (top windows), it is striking that attraction to in-phase also was noticeable after learning in the kinematics of the components. Although the new phasing pattern was actually performed at peak flexion in synchrony with the metronomes (cf. the solid circles in Figure 6), the components tend to relax to in-phase, whereas, strictly speaking, the periodic "forcing" that actually stipulates the required phasing pattern no longer exists. In other words, behavior at the component level appears to reflect both the remnant effects of an attractive state that existed before practice and the influence of the newly learned pattern.

Figure 10 shows data from 3 other subjects who practiced 90° or 270° (the subject data depicted in the middle window

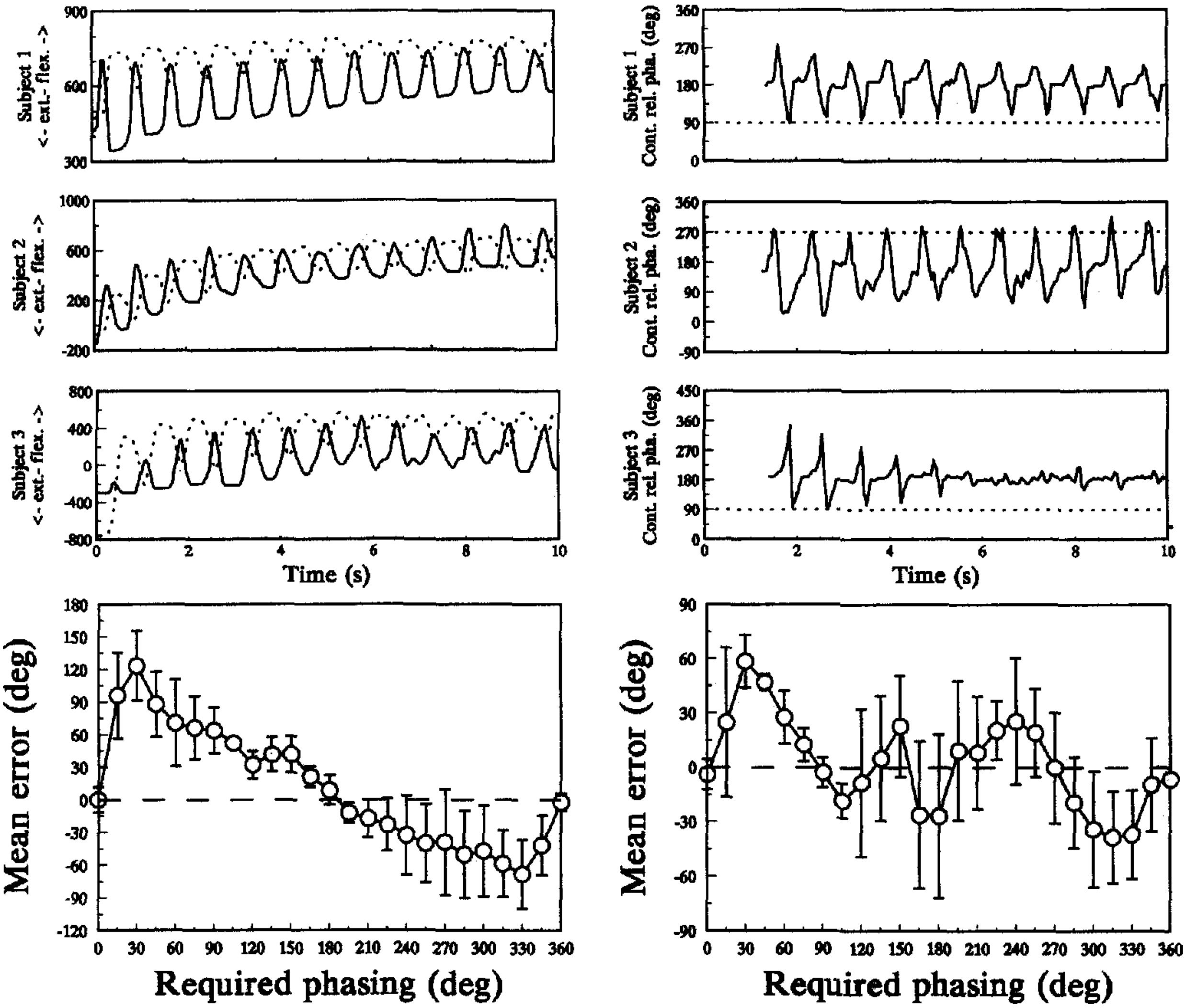

Figure 10. Relationship between component and collective dynamics in the anti-phase strategy. The top three pairs of windows show kinematic data for 3 subjects averaged over the first 10 s of the last five practice trials. The left windows plot the excursions of right and left fingers (solid and dotted lines, respectively) in the indicated directions. All exhibit coordinated mirrorlike finger motion similar to that described in the bottom window of Figure 7. The three right windows plot the corresponding continuous relative phase. These display a highly variable phase relationship that meets the task requirement (denoted by the dotted line) periodically while mostly staying around 180° otherwise (cf. the middle window of Figure 7). Such kinematic features are characteristic of the anti-phase strategy. The bottom left and right windows display the results of the probes carried out before and after practice, respectively, averaged over the same 3 subjects. The mean error in relative phase is plotted as a function of the required relative phase (vertical bars denote the between-subjects standard deviations). Before learning, the wide and steep negative slope about 180° reflects a strong coordination tendency to anti-phase. After learning, performance is attracted instead to ±90°. ext.–flex. = extension–flexion.

are those illustrated in Figure 7). In the three top left windows, finger motion reflects an overall mirrorlike behavior of the components, with marked rest periods in the opposite positions. The continuous relative phase shown in the top right windows is centered about 180°, although it is rather variable (over a 270° span). After learning (bottom right window), the collective variable dynamics clearly exhibits attraction to the newly learned ±90° patterns. The picture is similar to the corresponding one in Figure 9. At the component level, this strong tendency to anti-phase before learning still appears to influence performance after learning because the components tend to relax to a 180° phase relationship after having periodically met the task requirement (cf. the solid circles in Figure 7). Here again, behavior reflects the influence of both initial and learned attractive states.

Figure 11 shows data from 3 other subjects, who practiced 90° or 270° (the subject data depicted in the middle window are those illustrated in Figure 5). The three top left windows exhibit a fairly sinewave-like motion for both fingers, at least without clear rest periods. The corresponding continuous relative phase (top right windows) is less variable and hovers around the required value (dotted line). The initial probe of the coordination dynamics (bottom left window) indicates that the 0° and 180° patterns are the most stable, but their attraction is relatively weak compared with the preceding figures, and their strengths are similar. The lack of marked coordination tendencies before learning suggests that the components might have remained close to the learned phasing over an entire performance cycle because

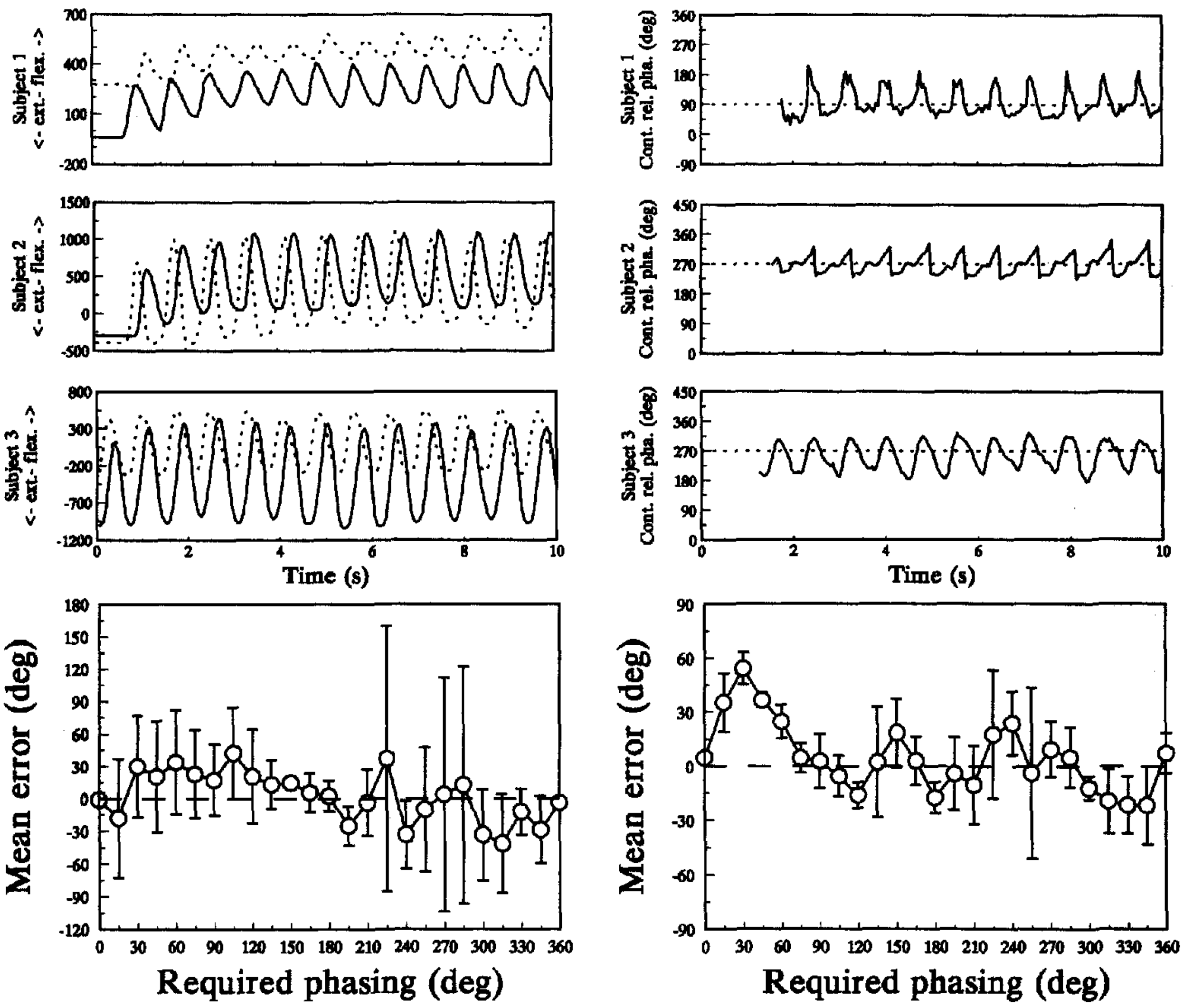

Figure 11. Relationship between component and collective dynamics in the sine strategy. The top three pairs of windows show kinematic data for 3 subjects, averaged over the first 10 s of the last five practice trials. The left windows plot the excursions of right and left fingers (solid and dotted lines, respectively) in the indicated directions. All exhibit coordinated sinelike finger motion similar to that shown in the bottom window of Figure 5. The three right windows plot the corresponding continuous relative phase. These display a less variable phase relationship that hovers around the task requirement (denoted by the dotted line; cf. the middle window of Figure 5). Such kinematic features are characteristic of the sinelike strategy. The bottom left and right windows show the results of the probes carried out before and after practice, respectively, averaged over the same 3 subjects. The mean error in relative phase is plotted as a function of the required relative phase (vertical bars denote the between-subjects standard deviations). Before learning, the narrow and less marked negative slopes about 0° and 180° do not indicate any strong coordination tendency before learning. After learning, performance is attracted to ±90°. ext.–flex. = extension–flexion.

they were not attracted to in-phase or anti-phase as soon as the task stopped specifying the required coordination pattern. After learning (bottom right window), however, the collective dynamics were comparable to those pertaining to the other strategies, showing stabilization of a new attractive state close to the to-be-learned phasing.

In summary, Figures 9–11 suggest that different behaviors described at the level of the components (i.e., in-phase, anti-phase, and sinelike, respectively) may be readily related to an evaluation of the collective variable dynamics conducted before learning: The kinematic behavior of the components after learning a new coordination pattern may be predicted from the relative strength of preexisting attractive states at the collective level, under the caveat that the system will tend to relax to the most prominent attractive state when the (discrete) learning task no longer specifies a given coordination pattern. After learning, however, the collective dynamics are similar regardless of the strategy adopted.

Interestingly, the foregoing description also holds for the 4 subjects who already exhibited the ±90° attractive states in the initial probe and therefore had to learn another phasing pattern (see Figure 4). In Figure 4A, the subject's performance in the first practice trial of a 135° relative phase, which was actually close to 90°, was typical of the sinelike strategy. After learning, when performance was about 135°, the adopted strategy was still of the sinelike type. Similarly, the 3 other subjects with multistable collective dynamics exhibited an in-phase strategy in the first practice trials, and still did so after learning, regardless of their respective task requirement. Thus, when a pattern other than in-phase or anti-phase was already available before practice, strategies appeared to be independent of the actual phasing requirement and the level of learning (i.e., they were idiosyncratic). As we have shown, such strategies may stem from the very stability properties of the individual coordination tendencies that existed before exposure to the learning task.

General Discussion

Our goal in this research was to characterize the processes of learning novel coordination patterns in terms of changes in hypothesized coordination dynamics. To fully understand such change, we argue that one must evaluate coordination tendencies that exist before learning for each individual learner. Taken together with our previous work (Zanone & Kelso, 1992a), a fairly coherent picture of the learning process emerges at the level of the collective variable, relative phase, that also provides a first glimpse into principles underlying transfer of learning. Moreover, in the present study we introduced a new, lower level of description to the whole process by considering how changes in coordination dynamics at the collective level correspond to specific adjustments in the component motions that also are characteristic of the individual learner. In the following, we discuss the connection between our experimental findings and their interpretation in terms of a dynamical theory of learning. We focus first on the level of the collective variable dynamics. We then address strategies that are used to satisfy learning requirements at the component level and emphasize the self-consistency between the collective and component levels of description. Finally, we briefly address some outstanding issues that remain to be resolved and place our results in the broader context of learning theory.

One of the central theoretical ideas of our approach to learning is that learning a new pattern involves alterations of the entire layout of the coordination dynamics, not only changes in the specific criterion task. Evidence from the scanning probes suggests that the learned coordination pattern becomes an attractive state of the collective variable dynamics. On the one hand, Figure 1 basically corroborates our previous findings (Zanone & Kelso, 1992a): With learning, a new attractive state of the coordination dynamics is established close to the to-be-learned relative phase. On the other hand, Figure 4 shows a different picture on two counts: First, the coordination dynamics may be multistable before learning (i.e., with attractive states other than the in-phase and anti-phase patterns). Second, learning may involve a shift of existing stable coordinative states in the direction of the to-be-learned pattern. Thus, a novel finding yielded by our study is the existence of two different routes to learning depending on the initial attractor landscape: Learning may lead to qualitative changes or to parametric changes in the initial coordination dynamics. In the former case, the attractor layout evolves from a bistable to a multistable structure, whereas in the latter case, the attractor layout is already multistable to begin with but is transformed to a different multistable structure. Interesting questions now arise: How articulated can a multistable attractor layout become with learning? Can previously stable patterns (e.g., 90°) be stabilized while new ones (e.g., 135°) are learned? Does overpractice of a pattern that already belongs to the learner's coordination tendencies before exposure to the task eventually lead to a bifurcation, annihilating other preexisting attractive states?

Independent of these issues, the present results support our key theoretical tenet that practice stabilizes the to-be-learned pattern, causing specific modifications of the entire coordination dynamics in the direction of the task requirement. Such modifications are essentially nonequilibrium phenomena (Kelso, 1990; Zanone & Kelso, 1992a) in which previously stable patterns (e.g., 180° or 90° depending on the route taken) may destabilize temporarily or permanently. As we have just seen, how such alterations actually unfold depends on the individual coordination tendencies existing before learning. These results suggest that conventional views of motor skill acquisition (see Newell, 1991; Schmidt, 1988; Schmidt & Bjork, 1992, for reviews) or dynamically oriented approaches (Beek & van Santvoord, 1992; Saltzman & Munhall, 1992; Schmidt et al., 1992; Swinnen et al., 1993; Vereijken et al., 1992) have much to gain from taking into account such preexisting constraints (here, extant coordination tendencies). So also, we contend, does developmental theory (cf. Sporns & Edelman, 1993).

Another new finding of our research is the somewhat serendipitous discovery of the *spontaneous transfer of learning*. This was possible because of the careful sampling of the entire layout of the coordination dynamics, which was not accomplished in previous work (Zanone & Kelso, 1992a). A related finding in this context is that the symmetry of the coordination dynamics before learning (implicit in the case of bistability because 180° and −180° are congruent) was demonstrated for multistable dynamics as well (see Figure 4). Regardless of the initial regime of the coordination dynamics, however, we show that there is automatic stabilization of a coordination pattern that has never been practiced at all. Significantly, it is the symmetry partner of the to-be-learned pattern that exhibits transfer, suggesting that an underlying symmetry of the coordination dynamics is preserved as learning proceeds. Thus, not only does the learned pattern stabilize with learning as theory predicts but its symmetry partner also becomes an attractive state of the coordination dynamics. These results point to the abstract (but physically realized) nature of the learning process, namely, that the phase relationship is stabilized independent of component order. How abstract, transferable, and generalizable such learned relative timing is an obvious topic for future research (see Zanone & Kelso, 1994, for an expanded agenda).

As noted by Bray (1928), "it has long been known that practice of one part of the body in performing a skilled act increases the ability of the bilaterally symmetrical part in the same act" (p. 443). What we have shown here is that patterns of coordination between such symmetrical parts transfer spontaneously. Thus, we may assume that the mere transfer of performance between symmetrical parts reported by Bray pertains to the automatic stabilization of a new stable state in the underlying coordination dynamics, so that the original symmetry of the coordination dynamics and the equivalence between components are preserved. This process points to a temporal equivalence principle, namely, that the same temporal pattern can be produced through different serial ordering among the components (e.g., Jordan, 1995). In many respects, this notion is the temporal counterpart of "motor equivalence" (e.g., Hebb, 1949; Lashley, 1951), which stipulates that the same spatial goal can be achieved by different configurations among body parts. We hypothesize that the fine balance between stability and flexibility shown in both temporal and spatial equivalence arises from the abstract nature of the coordination dynamics.

A novel contribution of the current study is that a more refined understanding of the learning process is gained by considering how the learning task (a nonpreferred coordination pattern) is realized at the component level, here the fingers. Figures 5–7 show that after learning, three different coordination strategies between the components may be implemented to meet the same task requirement. This, of course, constitutes another example of temporal equivalence. Notably, such strategies are specific to the individual learner. Figures 9–11 show that these component strategies reflect idiosyncratic tendencies that are revealed at the collective level through the prelearning scanning probe. Then, when learning itself involves a qualitative change from bistable to multistable dynamics, the creation of a novel attractive state at the required relative phase implies the implementation of an altogether new coordination strategy between the components. In contrast, when learning involves the shift of a preexisting attractive state, such a parametric change in the coordination dynamics corresponds to an adjustment of the actual phasing between the components within the same coordination strategy adopted by each individual. Thus, briefly stated, dramatic changes shown in the coordination dynamics appear to necessitate dramatic changes in the component dynamics, whereas parametric changes in the collective dynamics involve parametric changes in the component dynamics. The correspondence between coordination and component dynamics demonstrated here experimentally constitutes a hallmark of the dynamic pattern approach, namely, to establish a connection between levels of description (see the introduction; for details, see Kelso, 1995).

Among coordination strategies, the most interesting are the so-called *composite strategies* (in-phase and anti-phase; Figures 6 and 7, respectively). Both show that after the subject precisely matches the task requirement by synchronizing finger peak flexion with the metronome, performance is attracted to the natural tendencies of the components to go in-phase or anti-phase. Such behavior of the components themselves reflects competition between the task constraints and the initial coordination dynamics, which were already assessed at the collective level through the bias and variability of the collective variable (e.g., see Figure 1). Such a competitive mechanism is analogous to the dual "maintenance tendency" and "magnet effect" first described by von Holst (1973) on coordinated motion of fins in the fish. The former refers to the propensity of the fins to sustain their own (uncoupled) frequency of oscillation, whereas the latter refers to the tendency of the coupled components to synchronize with each other. Because of these competing demands, a fixed phase locking between components is not attained across performance cycles, but only phase entrainment. Periods of stable relative phase are often followed by a period of phase slippage or wrapping (Kelso, Delcolle, & Schöner, 1990; see DeGuzman & Kelso, 1991, for a theoretical account). Here, epochs of stability alternate with epochs of variation within a performance cycle, a behavior that arises from competition between the discrete task constraint and existing coordination tendencies between the components. In other words, the phasing constraint introduced by the task appears to determine the component behavior at a specific point in time, namely, at the very moments when the task itself requires the synchronization of each component with its own pacing signal. This suggests the existence of "anchor points" where trajectories in phase space converge to comply with an external pacing signal.

Such anchor points have been identified in bimanual coordination (Byblow et al., 1994) for the stable in-phase and anti-phase patterns, as well as in four-limb coordination (Jeka, Kelso, & Kiemel, 1993; Kelso & Jeka, 1992) and synchronization–syncopation tasks (Kelso et al., 1990). Here, however, an opportunity is provided to see how different and novel coordination strategies that involve such time anchoring are actually learned. Important questions are still open: To what extent are composite strategies a mere consequence of the discrete nature of the task requirements? Do they represent a necessary, if temporary, step to mastering the task? What factors determine the emergence of one or another strategy as learning proceeds? Again, a theoretical answer may be found in the (competitive or cooperative) interplay between task demands and existing coordination tendencies, a role for which has been shown here at both collective and component levels. The influence that such constraints have on the learning process is open to further investigation. The relative stability of the in-phase and anti-phase patterns is dependent on the system under study (e.g., leg vs. arm coordination) and on some experimental parameters (e.g., frequency, spatial orientation), thereby affecting the probability of occurrence of the composite strategy. On the other hand, individual components themselves (say, a finger vs. an arm vs. a leg) may display differential resistance to the breakdown of near-harmonic motion. For instance, oscillators with larger inertia tend spontaneously to exhibit a motion similar to the sinelike strategy. Similarly, the same component operating at a higher frequency will perforce behave in a smoother fashion. These factors, of course, are not mutually exclusive.

Our results raise a number of questions about learning that need to be addressed both from the experimental and theoretical points of view. A crucial issue pertains to our assumption that the newly learned pattern eventually achieves the same status as initially attractive states of the coordination dynamics. A definitive validation would be provided if the learned attractive state also manifested itself under nonspecific parametric changes, that is, when the system is driven through its stable coordinative states by manipulating a control parameter that is not related to the collective variable, as in the original Kelso paradigm. Results of recent experiments (Athènes & Zanone, 1994; Zanone, Athènes, & Kelso, 1997) provide preliminary support for this assumption. Various signs of attraction to the newly learned pattern or its symmetry partner were observed during parametrically induced phase transitions. Another, more theoretical concern pertains to our discovery that the transfer of learning follows a type of symmetry conservation. This means that the original theory (Schöner & Kelso, 1988a, 1988b; Schöner et al., 1992) must be expanded to account for such symmetric changes in the coordination dynamics. One solution is to ascribe learning and transfer effects to higher order terms (e.g., $\pi/2$-, $\pi/3$-, . . . , periodic) in the Fourier expansion of the Haken–Kelso–Bunz equation (Haken et al., 1985). Before learning, these terms are set to zero, leaving the coordination dynamics bistable at 0° and 180°, as in the original model. After learning, they assume a nonzero value because of the evolution of the memory dynamics, thereby generating a multistable regime that contains the new, learned attractive states.[10] A similar formal treatment is necessary to account for the presence of multistable coordination dynamics before learning. We hope to accommodate these effects theoretically in the near future.

What are the implications of our results and approach for motor learning theory? Despite much work on learning and transfer (e.g., Adams, 1987), progress, it seems, has been limited. Summarizing the available knowledge to date, Schmidt (1988) pointed out two findings: (a) The amount of transfer seems to be small and positive unless the tasks are practically identical and (b) the amount of transfer depends on the similarity between the tasks. However, the measures usually used in learning studies have been somewhat superficial (e.g., performance improvement in different tasks and the percentage of transfer) and often do not directly assess learning or transfer processes per se. Relatedly, no principled basis has been found to establish the degree of (dis)similarity between two tasks. In our perspective, by explicitly defining both the task demands and the individual predispositions in the space of the collective variable, it has proved possible to identify learning and transfer as alterations in the layout of underlying coordination dynamics and to evaluate the similarity between behavioral patterns in terms of distance in phase space and symmetry order. Regarding learning, we have spelled out predictions about distance effects in terms of rate or form of learning (Zanone & Kelso, 1994). The role of symmetry is less clear but nevertheless testable. One question is whether the stable patterns of dynamics with lower symmetry (e.g., π-periodic) have to be (de)stabilized for patterns defining higher symmetry dynamics (e.g., $\pi/2$-periodic) to be learned. Similar arguments may be put forth about other persisting issues in learning theory. The inability to specify the influence of task demands on initially stable coordination patterns might have hindered understanding of well-established effects on learning, such as contextual interference or variability of practice.

What are some of the implications of our results and approach for learning theory in general? We have shown that organisms (here people) enter the learning situation with a certain degree of preorganization that clearly constrains the learning process. Actually, we have shown that such individual predispositions may predict the form that learning takes and the coordination strategy that eventually realizes the task. Although different in origin, our approach emphasizing the role of individual constraints in learning is continuous with others, especially biological constraint perspectives (e.g., Bolles, 1970; Garcia & Garcia, 1985; Germana, 1989; Timberlake, 1993). In the latter, constraints are partially innate and species specific and reflect evolutionary processes shaping the organism's ability to survive in a specific environment. Thus, learning is a fine-tuning, selective process operating on an existing functional organization. For us, whether coordinative constraints are innate or attributable to previous experience is not a crucial distinction. What is important is that whatever is learned is determined relative to constraints that can be identified and measured. Stimuli are not just arbitrary bits of information to associate with responses. What is informationally relevant to the organism in our theory depends on existing organization, here operationalized in terms of behavioral patterns and conceptualized as an attractor layout or coordination dynamics. Theoretically, competitive and cooperative mechanisms can be evaluated only in relation to existing coordination

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[10] In particular, the removal of a $\pi/2$-periodic term added for capturing the pair of stable states at ±90° established by learning and transfer leads to a subcritical pitchfork bifurcation, analogous to that occurring in the parametrically induced phase transition from bistable to monostable dynamics reported by Kelso (1984).

tendencies, making the individual learner the significant unit, not the group or the species.

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Appendix

Dynamics and Relative Phase Measures

We investigated learning at both levels of the collective and component dynamics, for which we used point-estimate and continuous measures of the collective variable, relative phase (ϕ), respectively. In the text (see the section on the link between the component and collective levels), we showed that both measures are adept at characterizing the learner's behavior and at revealing learning effects in a consistent manner. As far as learning a new coordination pattern is concerned, both tell the same story, except for a difference in the temporal and spatial graining: Learning establishes a new stable phasing pattern at the required value. At the collective level, the learned pattern is mostly revealed by attraction of the surrounding relative phases in parameter space, whereas at the component level, learning is shown by the actual achievement of the discrete coordinative task specified by the metronome. The goals of the Appendix are (a) to elaborate on the theoretical link between the collective and component levels, beyond the experimental evidence already provided, and to show the equivalence, hence the pertinence of their respective measurement for capturing the underlying coordination dynamics and (b) to establish the adequacy of the Haken, Kelso, and Bunz (1985) model (the HKB model) for the somewhat peculiar behaviors classified as different coordination strategies (see Figures 5–7). We emphasize the intuitive and logical aspects of the argument rather than its formal development, which may be found elsewhere (Fuchs, Jirsa, Haken, & Kelso, 1996; Fuchs & Kelso, 1994).

A *dynamical system* is a system of equations determining the evolution of a vector, $\mathbf{x} = (x_1, x_2, x_3, \ldots)$, with time. If $\mathbf{x}$ is a continuous function of time, its dynamics may be defined as an ordinary differential equation (ODE):

$$\dot{\mathbf{x}} = \mathbf{F}(\mathbf{x}), \qquad \text{(A1)}$$

where $\dot{\mathbf{x}}$ denotes the derivative with respect to time and $\mathbf{F}(\mathbf{x})$ the vector field. If $\mathbf{x}$ is a discrete function of time, another class of dynamical systems describes the dynamics of $\mathbf{x}$ as a difference equation or (iterative) map:

$$\mathbf{x}_{t+n} = \mathbf{G}(\mathbf{x}_t), \qquad \text{(A2)}$$

where $\mathbf{x}$ at a given time t is determined by precedent $\mathbf{x}$, n iterations away. In the simplest case where $n = 1$, the system's current state defines its immediate successor.

There is, however, an intimate relationship between ODEs (Equation A1) and maps (Equation A2) in the particular case of periodically forced systems. Using a technique called *Poincaré section,* a continuous ODE can be "reduced" to a discrete map. We illustrate the process with our experimental model system, coordination between fingers, formalized by the HKB model. Such a coordination system may be conceived of as nonlinearly coupled nonlinear oscillators, in which the fingers reciprocally drive (viz. force) each other. The phase of the right and left individual fingers in the $\dot{x}$–x plane (i.e., θ_r, θ_l , respectively) varies from 0° to 360° over one respective period of time ($1/\omega_r$, $1/\omega_l$, where ω_r, ω_l are the respective frequencies of each component). The trajectory (i.e., the ensemble of the values taken over time) for each phase corresponds to a full circle. How such phases actually evolve with time is determined by the ODEs of each component. The relative phase ($\phi = \theta_l - \theta_r$) of this pair of oscillators may be represented on a doughnut-shaped torus formed by two such circles, one, say θ_l, running orthogonally along the circumference of the other, θ_r. Such a torus contains all possible trajectories of the relative phase between the oscillators. Again, the actual trajectories are determined by various parameters in the system of ODEs defining the entire dynamics (e.g., coupling strength, eigenfrequencies, etc.). If one intersects half of the torus by a transverse plane, the trajectory of relative phase pierces this surface each time the phase of the right oscillator (θ_r) achieves a complete revolution. Of course, such intersecting points will all lie on a circle, representing the possible values of the other oscillator's phase (θ_l) at that moment. Thus, the process amounts to stroboscopically sampling the phase of an oscillator each time the other has reached a given phase. Most important is that the discrete evolution of the intersecting points is governed by the dynamics of the continuous system. Of course, the continuous trajectory of relative phase between the intersection points is lost. Yet, the essential features of the (common) dynamics—namely, attractive states—are preserved, and may be observed as clusters of points on the θ_l circle in the Poincaré section plane. In conclusion, a map proves to be a valid means to characterize a continuous dynamical system such as bimanual coordination studied here. Discretization of time and reduction of the system's dimensionality are exactly what has been accomplished in our study by using the point-estimate measure of relative phase as a collective variable (see Figures 5–7).

By definition, the passage from an ODE to a map gets rid of the details of the actual motion of the oscillators, however important such details may be behaviorally (as we have seen in the current study of the component level). Consequently, the harmonicity of the oscillators does not constitute a requirement for performing a Poincaré section. The only prerequisite, of course, is that the motion be periodic, without which the strobing essential to generate a return map is not possible.

The second issue addressed in this Appendix is the mapping between the theoretical and experimental relative phases (see Fuchs et al., 1996, for a complete treatment). In fact, for (continuous) relative phase to be always constant, the oscillators must be harmonic (pure sine–cosine functions). For nonlinear oscillators, relative phase generally exhibits fluctuations, like those shown in the middle of Figures 5–7. (An exception occurs when the oscillators go in-phase or anti-phase and their phase portrait is symmetrical with respect to the origin. This is why, although the HKB model posits nonlinear van-der-Pol oscillators [a best estimate of the slightly nonharmonic motion usually exhibited by the fingers in the first experiments by Kelso and colleagues], the relative phase proves to be stable at in-phase and anti-phase.) Consequently, the most harmonic motion illustrated in Figure 5 shows the least jagged continuous relative phase time series. The theoretical problem to be solved is how a continuous relative phase that appears to fluctuate with time can be consistent with the assumed stability of the collective variable, which is evaluated, in our case, using the point-estimate measure.

Three methods are available to compare experimental data and theoretical results. The first two procedures, which are general, involve the calculation of the relative phase equation of motion in phase space or a nonlinear transformation of time, respectively (see Fuchs et al., 1996). The third, more simple method applies here. The basic idea is to introduce a phase for each frequency component taken from the Fourier decomposition of each oscillator motion. In the case of a harmonic oscillator, the solution contains only one frequency (ω) and one phase (ψ_0):

$$x(t) = A\cos(\omega t + \psi_0), \tag{A3}$$

where A is a constant denoting the amplitude of the motion.

Likewise, for a nonharmonic oscillator, which contains many harmonics (or subharmonics), one has a single frequency and phase for each Fourier component:

$$x(t) = \sum_n A^{(n)} \cos(n\omega t + \psi_0^{(n)}). \tag{A4}$$

In general, the calculations of the explicit amplitudes and phases, hence of the relative phase, give rise to huge expressions due to the nonlinearities of the oscillators and the coupling between them. However, if the time series of both oscillators have the same power spectrum (up to a constant factor), and the relation

$$\phi^n = \psi_r^{(n)} - \psi_l^{(n)} = n\phi, \forall n \tag{A5}$$

holds, then the continuous relative phase is well defined. (The demonstration, which necessitates only college-level algebra, is not given here.) The first condition requires that the two time series have the same main frequency component and harmonics, to a common scaling in amplitude. The second condition stipulates that the relative phase between pairs of successive harmonics increases as a multiple of the base relative phase, ϕ. If both conditions are satisfied, then the two time series are simply shifted in time. Therefore, the relative phase, ϕ, is the time shift divided by the time period T multiplied by 2π (viz. 360°).

Let us return to our data. The behaviors illustrated in Figures 5–7 typical of the sinelike, in-phase, and anti-phase strategies were subjected to a Fourier transform, shown in the top, middle, and bottom rows, respectively, in Figure A1. The left and middle columns show the power spectra of the right and left finger motion, respectively. The right column plots the relative phase between each pair of frequency components. The first two columns demonstrate that for all strategies, the power spectra for the right and left fingers are quite comparable. In particular, the main frequency component is, of course, at 1.25 Hz, that of the metronome. The spectra also exhibit a harmonic at 2.5 Hz and, for the in-phase strategy (middle row), a barely noticeable extra harmonic at 3.75 Hz. The graphs of the right column in Figure A1 show that for all strategies, the relative phase between the main frequency components (1.25 Hz) of the right and left finger motion and that of the first harmonic component (shown by the solid circles) are close to 270° and 180°, respectively. Thus, the two conditions stipulated above are indeed satisfied, demonstrating that for all strategies the time series are merely shifted in time by 270° of relative phase. Note that the same analysis conducted on the time series presented in the top windows of Figures 9–11 gave similar results (data not shown). Therefore, further theoretical treatment of the data, in our case through the HKB model or derivatives therefrom, is perfectly legitimate.

More generally, the relative phase between two periodic time series is customarily assigned to that between their main frequency components, which carry most of the power in the Fourier spectrum. This is how biological signals at all levels of description (e.g., opening of membrane ion channels, neuron firing, electromyographic or electroencephalographic activity, motor performance), albeit fundamentally nonharmonic (e.g., randomlike time series, bursts of spikes, jerky signals), are amenable to formalization. In particular, their modeling in terms of relative phase dynamics has proved successful and insightful, emphasizing the central role of phase attraction in mutual synchronization, a ubiquitous property

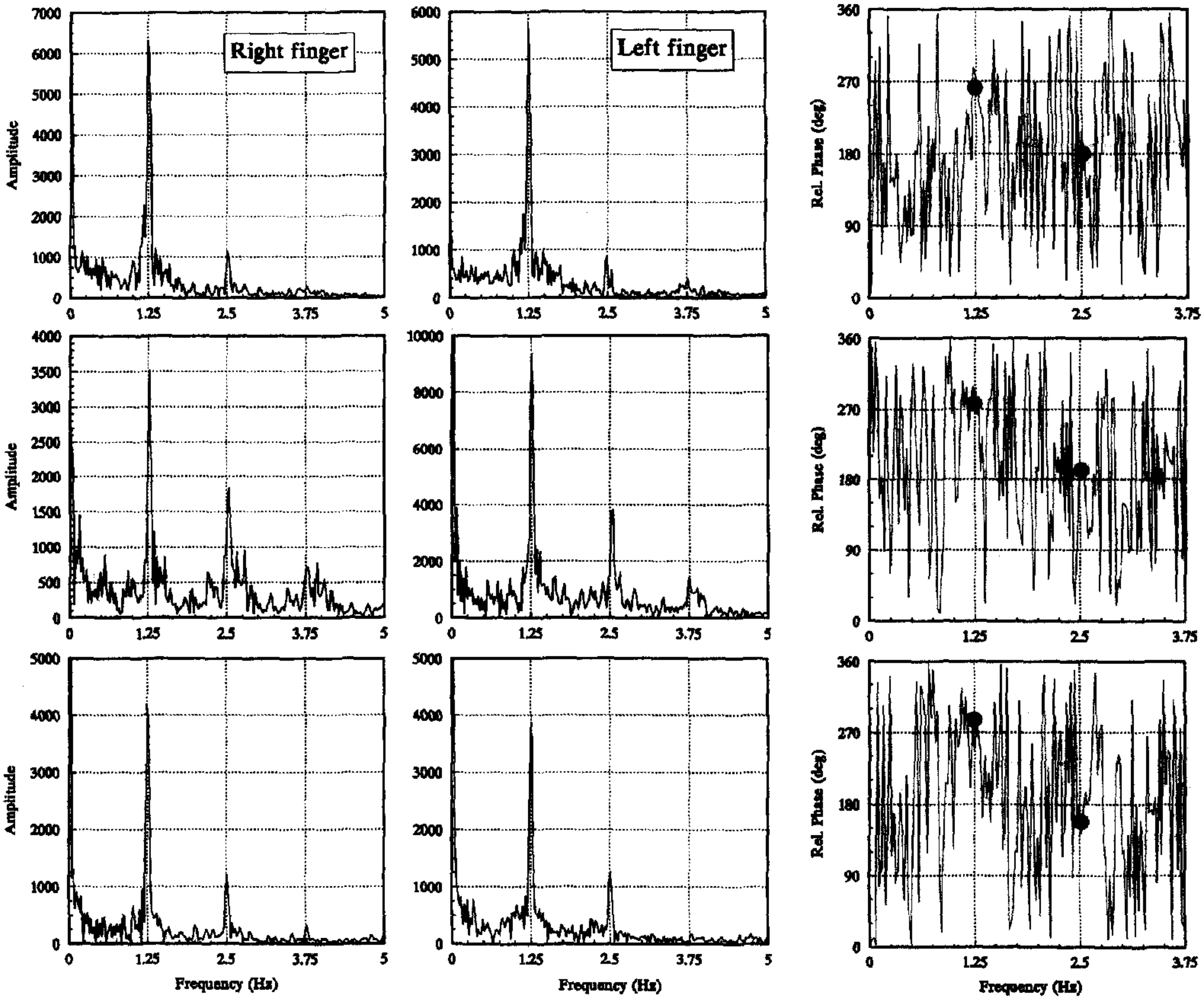

Figure A1. Fourier analysis of finger motions for different coordination strategies. The top, middle, and bottom rows concern the analysis of the time series shown in Figures 5–7 (bottom window) typical of sinelike, in-phase, and anti-phase strategies, respectively. The left and middle graphs show the power spectra of the right and left finger motions, respectively. The right graphs show the relative (Rel.) phase between each pair of corresponding Fourier components. The relative phase for the main frequency component (1.25 Hz) and its first harmonic is represented by solid circles. The figure demonstrates that in all cases, the finger motions are actually shifted by 270° of relative phase, thereby being amenable to a theoretical formalization like the model of Haken, Kelso, and Bunz (1985).

of biological systems (e.g., Mirollo & Strogatz, 1990; Rand, Cohen, & Holmes, 1988).

Therefore, there is no contradiction between the stability of the theoretical relative phase and the actual fluctuations of the calculated continuous relative shown in Figures 5–7. In this article, our intention was to characterize the qualitatively different behaviors through which subjects succeeded in meeting the task requirements. Although this is not the relative phase used for formalization, the continuous relative phase calculated following the Kelso et al. (1986) procedure (see the Method section) is actually very good at distinguishing among the three different strategies. The reason is that when the components do not move, both individual phases in the $\dot{x} - x$ plane remain the same, and the relative phase between the components corresponds to their relative positions during such rest periods. However, the mapping between theoretical and experimental relative phases is realized through the pointwise measure, which is indeed stable after learning. Again, this proves the pertinence of the point-estimate measure as a collective variable.

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