

## Coordination Dynamics of Learning and Transfer Across Different Effector Systems

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If different effector systems share a common task-specific coordination dynamics, transfer and generalization of sensorimotor learning are predicted. Subjects learned a visually specified phase relationship with either the arms or the legs. Coordination tendencies in both effector systems were evaluated before and after practice to detect attractive states of the coordination dynamics. Results indicated that learning a novel relative phase with a single effector system spontaneously transferred to the other, untrained effector system. Transfer was revealed not only as improvements in performance but also as modifications of each system's initial (prelearning) coordinative landscape. What is learned, appears to be a high-level but neurally instantiated dynamic representation of skilled behavior that proves to be largely effector independent, at least across anatomically symmetric limbs.

That animals and humans can achieve the same goal using different effectors (and, conversely, different goals using the same effectors) attests to the generative and multifunctional nature of the central nervous system (CNS). A notable example is human speech: The fixing (Kelso & Tuller, 1983; MacNeilage, 1980) or sudden perturbation (Kelso, Tuller, Vatikiotis-Bateson, & Fowler, 1984) of an articulator normally involved in the production of a sound is rapidly compensated by other, putatively coupled effectors in such a way as to preserve the speaker's intent. This so-called *motor equivalence* (Hebb, 1949; Lashley, 1930) has led to the idea of a high-level, task- or function-specific structure that deals with action goals, relegating the details of muscle selection and activation to lower levels, such as the spinal interneuronal system (for a review, see Georgopoulos, 1997). Such units or modules are variously referred to as functional synergies or coordinative structures (Bernstein, 1967; Edelman, 1987; Kelso, Southard, & Goodman, 1979; Turvey, Shaw, & Mace, 1978), generalized motor programs (e.g., Rosenbaum, 1991; R. A. Schmidt & Lee, 1998), and coordinated control programs (Arbib, 1990). Common features among these notions have been discussed in Kelso (1997).

The phenomenon of motor equivalence raises a number of basic issues for all theories of motor control and learning. What kind of

abstract representation underlies stable yet flexible and adaptive skilled behavior? How does it emerge? Is this representation really separable from and independent of the effector system that executes action? Can it, in fact, be interfaced to any set of effectors? Because skilled performance is the outcome of a learning process, how might such a representation be learned? How effective is transfer or generalization of a novel skill to other, untrained effector systems? Strangely enough, these questions—although quite central to theorizing in psychology (see Fodor & Pylyshyn, 1988) and cognitive neuroscience (e.g., Keele, Cohen, & Ivry, 1990; Seal, Riehle, & Requin, 1992)—have seldom received the empirical attention they deserve. Although there appears to be general support for effector-independent representations (e.g., Jordan, 1995; Keele, Jennings, Jones, Caulton, & Cohen, 1995), this may well depend on the level of the representation itself (Wright, 1990). For instance, intermanual transfer of writing skill from the dominant to nondominant hand or transfer of mirror writing skill (e.g., Latash, 1999) may operate at a higher, more abstract level of representation, such as the overall shape of a letter. On the other hand, transfer of the same writing skill across effectors, such as writing one's name large or small (e.g., Raibert, 1977; Wright, 1990), may share a common, lower level specification for the effectors engaged. Such notions are common in current forward and inverse "internal models" of motor control, adaptation, and learning (e.g., Imamizu, Uno, & Kawato, 1998; Kawato, Furawaka, & Suzuki, 1987; Wolpert & Ghahramani, 2000) in which task variables are transformed or mapped into a space of intrinsic (e.g., joint angles) or extrinsic (e.g., endpoint motion) control variables depending on the task context. Error feedback from various sources relative to the "desired state," as well as internal feedback, is used as a means to update the internal model and adjust the motor commands to the controller.

The present approach takes a slightly different tack. Building on previous theoretical (Schöner & Kelso, 1988; Schöner, Zanone, & Kelso, 1992; Zanone & Kelso, 1994) and empirical (Zanone & Kelso, 1992, 1997; see also Fontaine, Lee, & Swinnen, 1997; Lee, Swinnen, & Verschueren, 1995; Mitra, Amazeen, & Turvey, 1998; Swinnen, Dounskaia, Walter, & Serrien, 1997) research, sensori-

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motor learning is captured in terms of *coordination dynamics*: equations of motion that govern how a system's coordination states on a given level of description evolve in time and how such coordination emerges from the nonlinear interaction among component subsystems under the influence of boundary conditions that include perceptual, intentional, and intrinsic constraints. Such dynamics are specified in terms of functionally or task-specific coordination (also called collective) variables that characterize the coordination tendencies of the system at any point in time during the learning process (see also Saltzman & Kelso, 1987). Coordination variables, values of which define the states of the coordination dynamics, have been identified in situations in which behavior changes spontaneously under the influence of an experimentally manipulated control parameter. Spatiotemporally organized behavior evolves in time according to a dynamical law that both captures and predicts the stability and change of coordination under varying task and environmental circumstances (Kelso, 2000). In recent work, laws at the behavioral level, at least in the case of unimanual and bimanual coordination, have been derived from a neurobiological account based on known cellular and neural ensemble properties of the cerebral cortex, including its heterogeneous intra- and cortico-cortical connectivity (Fuchs, Jirsa, & Kelso, 2000; Jirsa, Fuchs, & Kelso, 1998; Jirsa & Haken, 1996; Jirsa & Kelso, 2000). This multilevel approach has been able to establish an explicit connection between neural and behavioral levels of description (Jirsa, Jantzen, Fuchs, & Kelso, 2002; Kelso, Fuchs, & Jirsa, 1999; Kelso, Jirsa, & Fuchs, 1999).

Turning to the concrete case of 1:1 coordination between two component subsystems (whether the two arms, the two legs, a leg and an arm, or a stimulus and a response), the coordination dynamics has been shown to take the following form (Kelso, DelColle, & Schöner, 1990; Kelso & Jeka, 1992; see also Amazeen, Amazeen, Treffner, & Turvey, 1997; Bressler & Kelso, 2001; Carson, Goodman, Kelso, & Elliot, 1995; Fuchs & Kelso, 1994; Peper, Beek, & van Wieringen, 1995; R. C. Schmidt & Turvey, 1995):

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

This dynamical law, in which the coordination variable,  $\phi$ , is the relative phase between the two components, has been progressively established in a series of detailed experiments beginning with Kelso (1981, 1984) and theoretical steps initiated by Haken, Kelso, and Bunz (1985). It contains essentially three kinds of parameters: (a) one that reflects intrinsic frequency differences between the uncoupled individual components ( $\delta\omega$ ), (b) one that reflects external or internal factors (control parameters) the ratio of which ( $b:a$ ) has been shown to govern the strength of coupling between the components, and (c) one that reflects that all real systems contain noise or fluctuations ( $\xi_t$ ) of a given strength  $Q$  that give rise to phase variability (Kelso et al., 1990; Schöner, Haken, & Kelso, 1986). If one wishes to use Marr's (1982) notion of representation and algorithm to describe how equivalence classes of processes can be described in an explicit manner, and how several processes may use the same higher level mechanism or algorithm to accomplish a given task, then the elementary coordination dynamics of Equation 1 clearly qualifies as an abstract representation of skilled behavior. For example, the stability properties of coordination dynamics ensure that the learner is able

to maintain and adapt coordination patterns to changing circumstances, one of the hallmarks of skilled behavior. In addition, because the coordination dynamics is multistable, the learner has access to several coordination patterns for the same set of circumstances, thereby providing her or him alternative solutions to accomplish the same task. By virtue of instabilities and modifications in the coordination dynamics, an additional source of generativity is available to the learner, namely, the ability to select or choose one behavioral form from another when internal or external conditions so demand. All these features have been observed in a number of rather different experimental model systems, attesting to the so-called universal nature of the coordination dynamics (Haken, 1996; see also Kelso, 1994a, 1994b; Turvey, 1994, for reviews).

The hypothesis that visuomotor learning may be captured at the level of an abstract rule or dynamical law is supported by a series of experiments on bimanual coordination (Zanone & Kelso, 1992, 1997; see also Fontaine et al., 1997; Mitra et al., 1998; Swinnen et al., 1997) in which subjects were asked to learn a novel phase relationship between the rhythmic motion of homologous limbs. A key idea behind these experiments was that learning involves a modification of the learner's preexisting capacities in the direction of the skill to be learned (Kelso, 1990). Although other theorists also stress that learning and development proceed in the context of preexisting biases (e.g., Sporns & Edelman, 1993), they have not provided ways to evaluate this preexisting movement repertoire prior to learning. Indeed, identification of such constraints is generally lacking or, more usually, totally ignored in theories of skill acquisition and development. Because discovering the nature of preexisting capabilities is so difficult, investigators have tried to use tasks that are as novel as possible and hence unrelated to any existing coordination tendencies that the learner might possess. Ironically, this strategy may prevent us from understanding the features of the learned representation that are shared across tasks and the level at which they are specified.

In Zanone and Kelso (1992; see also Kelso, 1990), a method was developed to overcome the difficult problem of evaluating the preexisting capabilities of the learner by scanning—before learning begins and throughout the learning process—the space of the coordination variable proven to be valid for this task, namely, the relative phase between the interacting components (e.g., Fuchs & Kelso, 1994; Haken et al., 1985; Kelso, 1984; R. C. Schmidt & Turvey, 1995; Swinnen et al., 1997). This allows researchers to set the learning task on an individual basis such that it does not correspond to preexisting coordination tendencies that, whether innate or acquired, may already exist in the individual learner's repertoire. According to our theory, new task requirements may cooperate or compete with preexisting coordination tendencies, thereby influencing the nature and rate of the learning process. As the task is learned, the stability of the performed pattern increases (indexed by shifts in the mean relative phase toward the learned pattern, a sharpening of the distribution of phasing fluctuations, and faster relaxation time). At the same time, the memorized relative phase evolves on a slower time scale, biasing the performed pattern toward the to-be-learned relative phase (Schöner & Kelso, 1988; Schöner et al., 1992). An outcome of using the research strategy of coordination dynamics is that learning has been demonstrated to not only involve the acquisition of a new

pattern of behavior but also to change the entire repertoire, including formerly stable behavioral patterns themselves.

In our original work (Zanone & Kelso, 1992; see also Kelso, 1990, 1995, chap. 6), we showed not only that a new attractor is established as memorized information gains strength but also that the learning process may take the form of a nonequilibrium phase transition or bifurcation: Stabilization of the learned pattern increased the number of coordination patterns available to the learner and destabilized others (at least temporarily). Learning, in other words, not only altered behavior in the direction of the to-be-learned pattern but also changed the entire layout of the coordination dynamics (see Schöner et al., 1992, for the formal details). Regarding the issue of task equivalence and the nature of the hypothesized abstract representation of sequential behavior, two additional findings are noteworthy (Zanone & Kelso, 1997). First, we found that learning a new phase relationship occurred irrespective of any time ordering between the moving fingers. For example, when a  $90^\circ$  phasing (i.e., the left finger lagging the right by one quarter of a cycle) was learned, subjects were also able to execute a  $270^\circ$  or  $-90^\circ$  phasing pattern (i.e., the left finger leading the right by the same amount), even though the latter phasing had never been practiced. We hypothesized that such spontaneous transfer of learning in the same coordination system may be due to the preservation of symmetry (viz.,  $\pm 90^\circ$ ) in the underlying coordination dynamics.

A second result of our study (Zanone & Kelso, 1997) was that subjects performed the newly learned phase relationship through different kinematic realizations of the end effectors. Although the task requirement was always met (i.e., subjects were asked to perform a given phase relationship in synchrony with a visual model), the way it was met kinematically ranged from smooth, quasi-sinusoidal motion of both end effectors to rather jagged, discontinuous movements. Interestingly, the kinematics adopted for realizing the required task were shown to depend on the relative stability of preexisting attractive states (e.g., inphase and antiphase) in the initial coordination dynamics. For example, to accomplish a learned relative phase of  $90^\circ$  or  $270^\circ$  with the visual stimulus, subjects produced a spikelike motion of the fingers with long pauses in the component trajectories corresponding to relative inphase or antiphase motion (see Zanone & Kelso, 1997, Figures 6 and 7). Both results, symmetry preservation at the collective level and multiple realization at the end-effector level, suggested that learning occurs at the abstract level of the coordination dynamics, which itself may be considered an expression of, or representation for, motor or (more correctly, we think, in the case of learning perception-action relations) *functional equivalence*.

In short, how a pattern learned with one set of effectors can be generalized to others is a very important problem, the solution of which will help provide a deeper understanding of skill acquisition. If our hypothesis that the abstract, task-shared nature of coordination dynamics is at the origin of transfer of learning is correct, then generalization of learning should occur across different effector systems, thereby enhancing the range of functional equivalence. This means not only that two end effectors within a pair can be switched with each other (Zanone & Kelso, 1997) but also that one pair of end effectors can be exchanged for an altogether different pair to realize the same task. Specifically, we investigated whether learning a novel phase relationship with one effector system (say, the arms) transfers spontaneously to another

effector system (say, the legs), and vice versa. It is important to emphasize in terms of the research strategy of coordination dynamics that learning and transfer are assessed not (or not only) in terms of changes in performance (cf. Latash, 1999) but rather in terms of specific alterations in the layout of the coordination dynamics underlying both effector systems. This means that coordination tendencies that may be present initially in both sets of effectors prior to learning (the so-called *intrinsic dynamics*, in our terminology [Kelso, Scholz, & Schöner, 1988], or the *preexisting movement repertoire*, in the terminology of Sporns & Edelman, 1993) must be assessed before the introduction of a novel coordination task. We predicted that transfer and generalization of learning should occur across different effector systems to the extent that they share comparable coordination dynamics. Thus, if the hypothesis is correct, then both the trained and the untrained effector combination should simultaneously exhibit stabilization of the to-be-learned phasing pattern. Moreover, other phasing relations are predicted to be biased toward the to-be-learned pattern if, as our theory predicts, the entire coordination dynamics is altered by the learning process. Such a result is not typically examined in work from other traditions, because the full range of task-related coordination tendencies and how these may change with learning is not explored. That is, traditional approaches seldom measure how other timing relations, beyond the task to be learned, are influenced by the learning process (for further discussion, see R. A. Schmidt & Lee, 1998, pp. 382–383).

Whether complete transfer occurs, of course, may depend on whether the learning task is accomplished by components that are biomechanically similar (e.g., the two arms or the two legs) or different (e.g., an arm and a leg). The extended form of the coordination dynamics (Equation 1; Kelso et al., 1990) contains a term ( $\delta\omega$ ) that respects asymmetries such as those caused by biophysical differences between limbs (Jeka & Kelso, 1995; Kelso & Jeka, 1992; Sternad, Amazeen, & Turvey, 1996) or differences between stimulus and response components (Kelso et al., 1990; Wimmers, Beek, & van Wieringen, 1992), whereas the original form (Haken et al., 1985) does not. For reasons of methodological simplicity, and because our aim was to determine the relevance of these concepts for the issues of transfer and generalization, we focused on the case of learning with anatomically symmetric, but different, effectors. Given the many differences of neural and biomechanical origin between arms and legs, no one, of course, expects perfect transfer. Nevertheless, evidence that the unpracticed pattern is learned and stabilized would bolster the view that coordination dynamics constitutes a single abstract representation for an entire equivalence class of coordinated actions, specifically those dealing with the relative timing between coordinating components.

## Method

The experiment was carried out on 2 consecutive days. On the first day, after informal familiarization with the task and the experimental setup, the coordination dynamics pertaining to both effector systems (i.e., the arms and the legs) was probed for each subject between  $0^\circ$  and  $180^\circ$ . No knowledge of results (KR) was provided to subjects during these scanning probes. Then the to-be-learned pattern was set on an individual basis such that it did not correspond to an already-existing stable pattern (see the *Individual Data: Selecting the To-Be-Learned Pattern* section for further details). This new pattern was then practiced with one effector system (i.e.,

either the arms or the legs) for 20 trials, with KR given at the end of each trial. On the second day, 20 additional practice trials of the to-be-learned phasing pattern were administered. At the end of this training period, a probe of the coordination dynamics was carried out again for both practiced and unpracticed limb pairs.

### Subjects

Eighteen naive subjects (mean age = 24.2 years), all undergraduate students at Florida Atlantic University, participated in the experiment and were paid after completion of the entire experimental procedure. A prerequisite for participation was that no visual or physical impairment impeded perceiving or producing the required timing pattern. Twelve subjects were assigned to two experimental groups, in which the to-be-learned phase relationship was practiced either with the arms or with the legs. Six control subjects were not exposed to such a learning task.

### Apparatus

Subjects were seated in a specially designed multi-articulator coordination (MAC) apparatus (for a detailed description of the MAC, see Kelso & Jeka, 1992). Their arms rested against a pad in an almost vertical position, and the wrists were inserted into cuffs attached to shafts that rotated about the elbows. The subjects' ankles were inserted into similar cuffs, attached to shafts rotating about the knees. Motion of the four limbs was thereby restricted to single-joint flexion and extension motion in the parasagittal plane. The apparatus allowed subjects to move their limbs as freely as possible, with no abutment and negligible friction. The angular displacements of all four limbs were monitored by potentiometers. A visual metronome, composed of two blinking light-emitting diodes (LED), was located in front of the subjects, 3 ft (0.91 m) away. The onset of each LED was controlled by a microcomputer. Various relative phases could be displayed by manipulating the time interval between the LED onsets while maintaining the period between two successive light pulses constant. Because of the difference in the limb eigenfrequencies, we set the metronome frequency to 0.8 Hz for the legs and to 1.1 Hz for the arms.<sup>1</sup> Signals from the visual metronome and the MAC apparatus were digitized in real time at a sampling rate of 200 Hz. KR, when appropriate, was returned to the subjects on a computer screen located beside the visual metronome (for details, see Zanone & Kelso, 1992).

### Task and Procedure

Subjects were instructed to produce the required relative phase specified by the visual metronome as accurately as possible through appropriately coordinated limb movements of the arms and legs. Specifically, subjects were required to attain exact synchronization of the right and left limbs with the onset of the ipsilateral LED. With both limb pairs, the instruction was to time or synchronize peak motion of the limb (i.e., the top reversal point) precisely at the moment when the corresponding LED was turned on. Otherwise, movement kinematics (displacement, velocity, etc.) were free to vary.

First, a complete probe of each subject's coordination ability was carried out in 13 separate runs. In each such *scanning* run a different relative phase was required, which varied randomly from run to run. All the multiples of 15° in the interval between 0° and 180° were set to the subject, thereby scanning the entire interval between the inphase and antiphase patterns. Each scanning run lasted 18 s for the arms and 25 s for the legs; that is, 20 movement cycles were performed by each effector system. On the first day, the effector system that would later practice the task was scanned first, followed by the nonpracticed system. On the second day, the scans were carried out in the reverse order. This procedure minimized uncontrolled effects of probing the practiced system per se on possible transfer to the nonpracticed effector system. The specific task to be learned was individ-

ually determined on the basis of subjects' performance on the initial scanning probe (see the Results and Discussion section). That is, the relative phase pattern to be learned was chosen according to the results of the initial scanning probes of both effector systems, under the caveat that to be chosen as novel, the timing pattern to be learned did not coincide with an already-existing coordination pattern.

Each learning trial lasted 20 s when practice was with the arms and 27 s when practice was with the legs, corresponding to 22 cycles of practice per trial for each limb pair. Practice was given in four consecutive blocks of 10 trials, with an average intertrial interval of 15 s and an interblock interval of 1 min. Note that 10 practice trials correspond to 220 attempts to produce the required phasing pattern. Every learning trial was followed by KR, which provided both qualitative and quantitative information about performance.

### Measures

As a matter of convention, we defined relative phase with reference to right-hand side events. Thus, metronome and movement patterns in which the right event led with respect to the left were designated a positive relative phase, that is, ranging between 0° and +180°. Conversely, left-lead phasing patterns had negative values that varied between 0° and -180° or, equivalently, positive values between +360° and +180°. Consonant with the discrete task requirement of coinciding the movement peak with the metronome signal, our measure of the produced pattern,  $\phi$ , was a point estimate of the relative phase between limb movements. The time difference between the occurrence of the peak reversal point of the left limb and that of the right limb closest in time was expressed (in degrees) relative to the period of the corresponding right limb cycle.

## Results and Discussion

We first present individual data to illustrate the steps used in the experimental procedure, in particular, the way we selected the to-be-learned relative phase, and to provide preliminary evidence pertaining to our hypotheses regarding learning and transfer. Then we present group results to support the conclusions drawn from individual data. Finally, we present the control group data to bolster the claim that the observed effects are due to the experimental manipulation, namely, learning induced by specific practice.

### Individual Data: Selecting the To-Be-Learned Pattern

A central part of our experimental rationale was to choose the pattern to be learned with reference to the coordination capabilities of the individual learner before practice in this kind of task. In the present situation, such selection was more complicated than in previous work (Zanone & Kelso, 1992, 1997), because two effector systems must be probed instead of one, thereby creating the possibility of discrepancies in their respective underlying coordination dynamics. In the following, we illustrate how the to-be-learned relative phase was selected for 3 typical subjects, according to the results obtained from initial scanning probes of the coordination dynamics.

<sup>1</sup> The choice of a frequency specific to each effector system was an outcome of previous pilot work. We selected the average frequency at which 8 pilot subjects spontaneously oscillated their arms and the legs in the MAC apparatus.

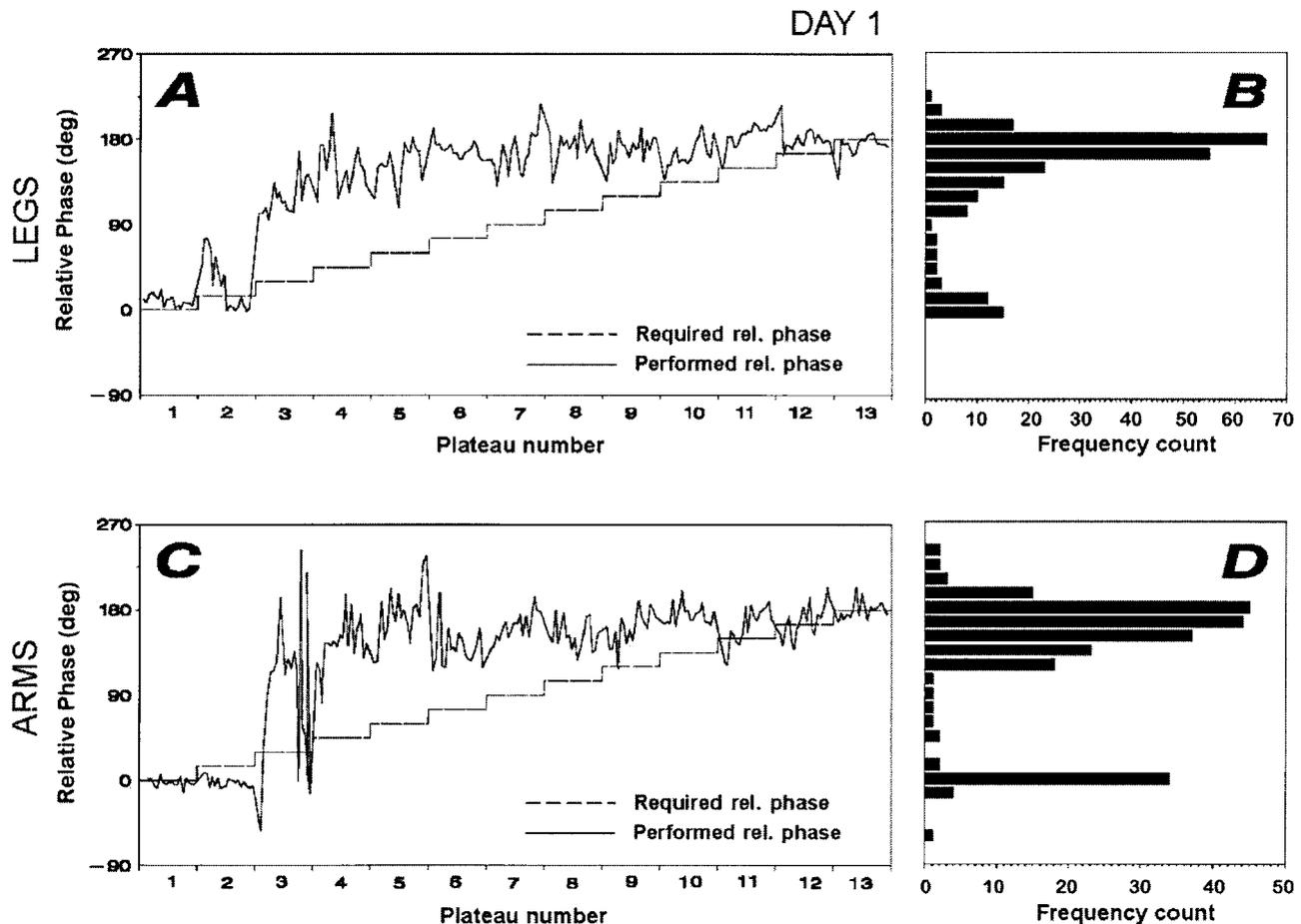


Figure 1. Initial scanning probes (Day 1) of the leg and arm coordination dynamics for a typical subject who practiced a  $90^\circ$  relative (rel.) phase with the legs. A and B show probes of the leg system, whereas C and D show probes of the arm system. The left graphs display the performed (solid lines) and the required (dashed lines) relative phases. For ease of viewing, we joined together the 13 individual trials (labeled by plateau numbers) in which a single relative phase was required at random. The right graphs display the frequency distributions of performed relative phase across all phasing requirements. Both arm and leg probes revealed coordination tendencies near  $0^\circ$  and  $180^\circ$ , suggestive of an intrinsic bistable dynamics. This probe led us to select  $90^\circ$  as the learning task. deg = degrees.

Figure 1 shows the results of the leg and arm probes carried out before learning for a subject who eventually practiced  $90^\circ$  with the legs. Figures 1A and 1C display the performed (solid line) and required (dashed line) relative phases as a function of time. Although randomly presented experimentally, for ease of viewing all 13 scanning runs for a given pair of limb effectors are shown in increasing order of the phasing requirement.<sup>2</sup> Across these plateaus of 20 cycles each, relative phase increases by  $15^\circ$ , starting at  $0^\circ$  for Step 1 and ending with  $180^\circ$  at Step 13, as shown by the dashed line. This provides a picture of the behavior expected had the phasing requirements been scaled up stepwise within a single trial. Figures 1B and 1D show the frequency histogram of the relative phase actually performed across all phasing requirements. The modes, or dominant peaks, in the histogram reflect relative phase patterns that are produced most frequently and are indicative of preexisting attractive coordination tendencies. One row of pictures (i.e., Figures 1A and 1B and Figures 1C and 1D) constitutes

the displays provided after completion of the scanning probes to the experimenters—but not to the subject—to select the to-be-learned phasing pattern. In addition, the statistics (mean and standard deviation) of the relative phase produced for each of the 13 required phasings (henceforth *plateau statistics*) were also available to the experimenters. This information allowed us to identify the phasing patterns that were performed in a reasonably accurate and consistent fashion.

Figure 1A indicates that for the first phasing requirement of  $0^\circ$  (i.e., Plateau 1) the relative phase performed with the legs was close to  $0^\circ$ . Presentation of the  $15^\circ$  requirement first entailed a noticeable perturbation, but then performance eventually returned

<sup>2</sup> This was the scanning procedure we had used in our previous work (Zanone & Kelso, 1992, 1997) to probe the nature of the underlying coordination dynamics.

to 0°. On the next required phasing (i.e., 30°), the performed relative phase shifted to near 180° (i.e., above 150°) and fluctuated there for all the following task requirements. Such a phenomenon, in which behavior appears to remain trapped in the current state or switches to another state irrespective of the actual value of the task requirement, reflects attraction to existing, so-called *intrinsic coordination tendencies* (Kelso, 1984) and attests to the inherently nonlinear nature of the underlying dynamics. Figure 1B reflects this shift between 0° and 180°, showing two modes situated around these values. Plateau statistics (not shown) revealed that the most stable phasing patterns were 9.76° and 169.11°, with standard deviations of 5.75° and 8.16°, respectively. Thus, Figures 1A and 1B suggest that the underlying dynamics for the legs are bistable, exhibiting attractive states near inphase and antiphase, with the latter pattern somewhat less stable (more variable) than the former. A similar conclusion may be drawn from the results obtained from initial scans of the arms. The time series (Figure 1C) and the

frequency histogram (Figure 1D) of performed relative phase suggest that the coordination dynamics for the arm system is bistable at inphase and antiphase (more precisely, at -2.30° and 180.38°, respectively), the former being more stable ( $SD = 4.62^\circ$ ) than the latter ( $SD = 9.44^\circ$ ).

The bistable nature of the coordination dynamics of both limb pairings renders the choice of the to-be-learned phasing pattern quite straightforward, namely, a 90° relative phase, situated in between preexisting attractive states of the coordination dynamics. Overall, 4 subjects exhibited this type of bistable coordination dynamics for both effector systems before learning. Two of them practiced the 90° relative phase with the arms, and 2 practiced it with the legs.

Figure 2 shows the results obtained from initial scanning probes of the legs and arms for a subject who eventually practiced 45° with the legs. Figure 2A indicates that besides performing inphase and antiphase fairly stably for requirements close to 0° and 180°

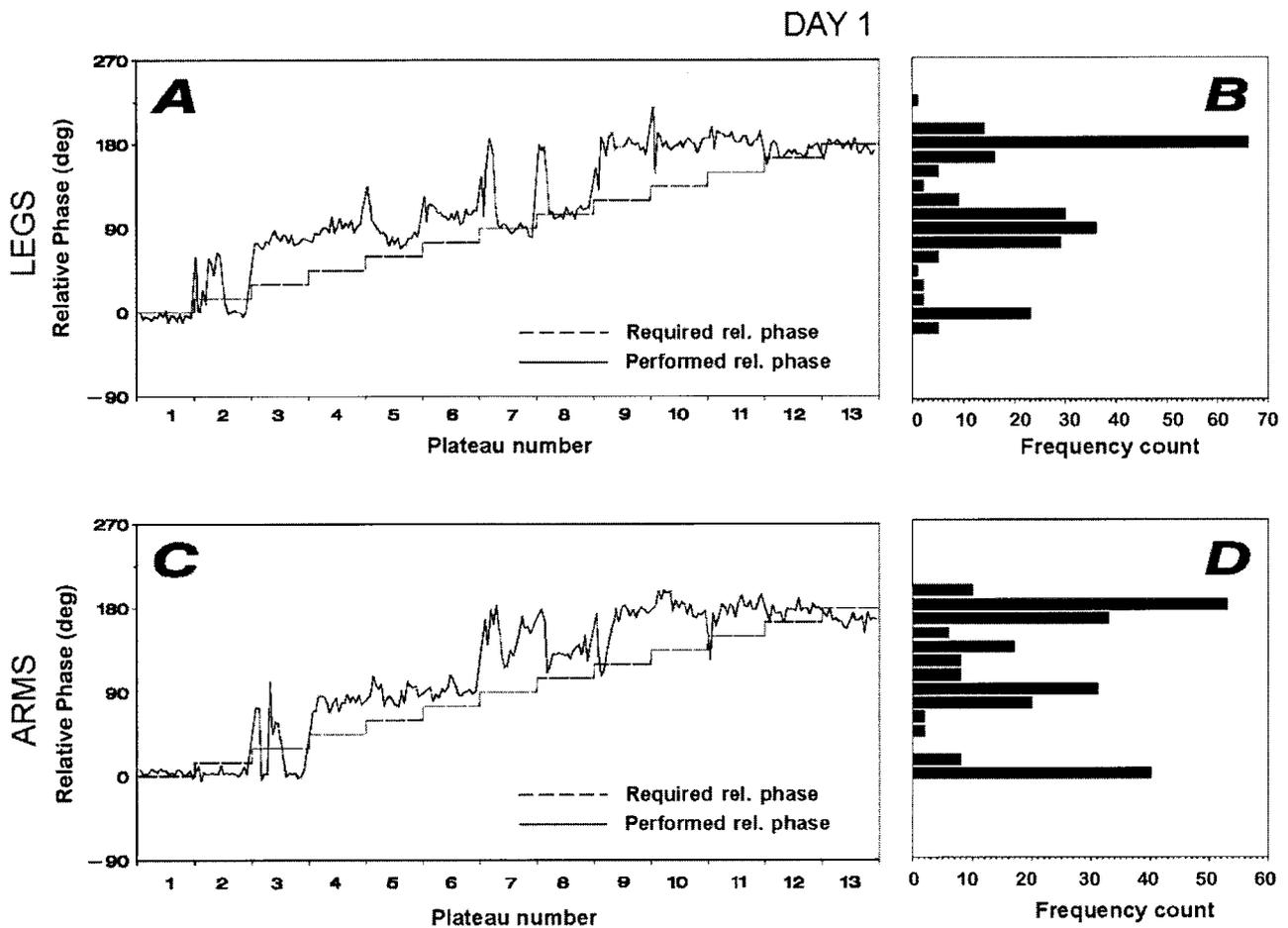


Figure 2. Initial scanning probes (Day 1) of the leg and arm coordination dynamics for a typical subject who practiced a 45° relative (rel.) phase with the legs. A and B show probes of the leg system, whereas C and D show probes of the arm system. The left graphs display the performed (solid lines) and the required (dashed lines) relative phases. For ease of viewing, we joined together the 13 individual trials (labeled by plateau numbers) in which a single relative phase was required at random. The right graphs display the frequency distributions of performed relative phase across all phasing requirements. Both arm and leg probes revealed coordination tendencies near 0°, 90°, and 180°, suggestive of multistable dynamics, which led us to select 45° as the learning task. deg = degrees.

(cf. the left and right parts of the graph), the legs performed a substantial number of movements about  $90^\circ$  for intermediate phasings (middle part of the graph). Accordingly, the histogram of the overall produced relative phase (Figure 2B) exhibits three modes centered about  $0^\circ$ ,  $90^\circ$ , and  $180^\circ$ . Plateau statistics indicated that the most stable patterns were near  $-4.75^\circ$ , between  $77.04^\circ$  and  $106.26^\circ$ , and between  $177.05^\circ$  and  $186.98^\circ$ . Thus, Figures 2A and 2B suggest that the initial coordination dynamics for the leg system is tristable within the  $0^\circ$ – $180^\circ$  range.<sup>3</sup> In previous experimental work on bimanual learning (Zanone & Kelso, 1997), such multistability was identified as an alternate prototypical regime of the coordination dynamics.

In a similar manner, Figures 2C and 2D suggest that the arm coordination dynamics is also tristable in the  $0^\circ$ – $180^\circ$  range. Plateau statistics revealed that stable coordination patterns existed about  $4^\circ$ ,  $85^\circ$ , and  $175^\circ$ . Hence, the subject depicted in Figure 2 was assigned to practice a  $45^\circ$  pattern, a relative phase located halfway between preexisting attractive states of the coordination dynamics that was not performed stably in the prelearning scanning probes. For the same reasons, 4 subjects practiced  $45^\circ$ , and 2 others practiced  $135^\circ$ , another unstable phasing pattern situated between the  $90^\circ$  and  $180^\circ$  stable states. For each requirement, half of the subjects practiced with the legs, and the other half practiced with the arms.

Figure 3 shows the results of the probes for the arm and leg systems, carried out before learning for a subject who eventually practiced a  $75^\circ$  relative phase with the arms. General features of bistable coordination dynamics were present (cf. Figure 1A), exhibited by bimodality in the two frequency histograms (Figures 3B and 3D). Examination of the statistics for the  $75^\circ$  requirement performed with the arms revealed, however, that a pattern near  $125^\circ$  was produced in a fairly stable manner (seen also in Figure 3A as a noticeable plateauing of performance). Such behavior is serendipitous, if not strange, because it is unrelated to the task requirement and fails to exhibit the property of attracting neighboring phases that typically characterizes stable behavior. Therefore, the coordination dynamics for the arm system was deemed to be basically bistable at inphase and antiphase. Because the scan of the leg system (Figures 3C and 3D) also was suggestive of bistability, the learning task might justifiably have been set at  $90^\circ$ . However, because of the anomalous behavior observed for the arm at  $125^\circ$ , the to-be-learned relative phase was moved to  $75^\circ$ , a pattern never previously performed and totally absent in the frequency histogram (Figures 3B and 3D). This maximized the distance between the task requirement and any preexisting coordination tendencies, thereby enhancing the possibility of identifying clear learning effects. Overall, only 2 subjects showed such atypical behavior and were thus assigned to practicing  $75^\circ$  with the arms and with the legs, respectively.

### *Individual Data: Effects of Learning and Transfer*

Having identified preexisting coordination tendencies in individual subjects, we now turn to the issue of how practice of the to-be-learned phasing pattern with a single effector system may affect the underlying coordination dynamics of both. Such modifications are presumed to be in the direction of the to-be-learned pattern, provided, of course, that the learning task is mastered with practice. Table 1 shows changes in performance accuracy and

variability between the first and last three learning trials, for the 3 subjects illustrated in Figures 1–3.

For all 3 subjects, the mean error (first column) drops sharply by at least  $45^\circ$  between the first and last learning trials, whereas the within-trial standard deviation (third column) decreases by approximately half. Meanwhile, the between-trials fluctuations (second and fourth columns) also diminish markedly for both scores. The data in Table 1 suggest that with practice, performance tends to stabilize close to the required values, a putative sign of learning.

How is the coordination dynamics modified as performance improves? Figure 4 shows the results of leg and arm probes, carried out after practicing a  $90^\circ$  relative phase with the legs, for the same subject whose data are presented in Figure 1. In Figure 4A, the time series of performed relative phase shows that after staying close to  $0^\circ$  for the first two phasing requirements, the leg pattern shifts to a value of about  $90^\circ$ , with fluctuations increasing as the phasing requirement approaches  $180^\circ$  (viz., with increasing time). The corresponding frequency histogram (Figure 4B) shows two modes at  $0^\circ$  and  $90^\circ$ , the latter more dominant than the former. Plateau statistics revealed that the most stable patterns are performed between  $-0.28^\circ$  and  $0.70^\circ$ , as well as in the  $97.87^\circ$ – $101.67^\circ$  range. All these features indicate that after practice, the coordination dynamics for the leg system contains attractive states near  $0^\circ$  and  $90^\circ$ .

Two points need emphasis. First, because the  $90^\circ$  pattern was not a stable state of the initial leg coordination dynamics (cf. Figures 1A and 1B), its stabilization must be due to learning through practice. Learning a novel phasing pattern appears to establish a new attractive state of the underlying coordination dynamics close to the task requirement. Second, the preexisting antiphase pattern appears to destabilize (at least temporarily) as a result of learning the  $90^\circ$  pattern. These two results are in line with the results of previous research regarding initially bistable bimanual dynamics (Zanone & Kelso, 1992, 1997; see also Fontaine et al., 1997). They suggest that the learning process essentially involves stabilizing unstable coordination states and destabilizing others, thereby modifying the layout of the underlying coordination dynamics.

Figures 4C and 4D reveal that arm coordination patterns are strongly modified after practice with the legs alone. The time series of performed relative phase, the overall frequency distribution, and the statistics suggest that attractive coordination states exist about  $0^\circ$  and  $90^\circ$  after practice (cf. Figures 1C and 1D). Because the  $90^\circ$  pattern was not practiced by the arms, its stabilization as a novel attractive state of the arm coordination dynamics reflects transfer of learning from the trained leg system. Again, such transfer involves substantial alterations of the underlying coordination dynamics, matching well those encountered in the

<sup>3</sup> For symmetry arguments, one has to posit that the symmetry partner of  $90^\circ$ , namely  $-90^\circ$  or  $270^\circ$ , is stable too, leading to multistable dynamics in the entire space of the coordination variable, relative phase, which spans from  $0^\circ$  to  $360^\circ$ . In fact, the assumption that symmetry of the underlying coordination dynamics is preserved when a phasing pattern intermediate to inphase and antiphase exists either before or after learning was demonstrated experimentally (Zanone & Kelso, 1997). In particular, what we call here *tristable* dynamics proved to be symmetric, as the intermediate attractor between inphase and antiphase was always accompanied by its symmetry partner (e.g.,  $+90^\circ$  with  $-90^\circ$ ).

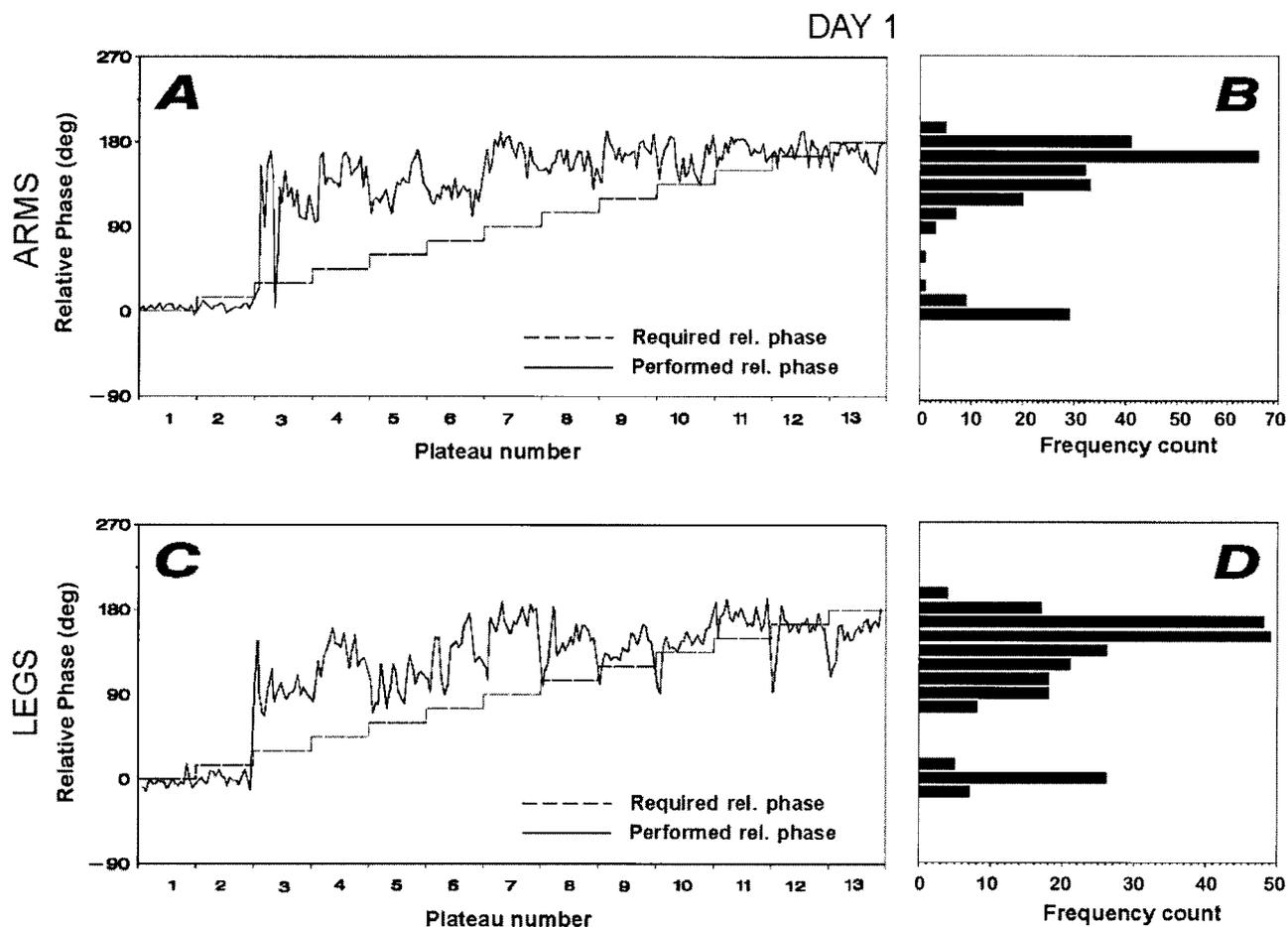


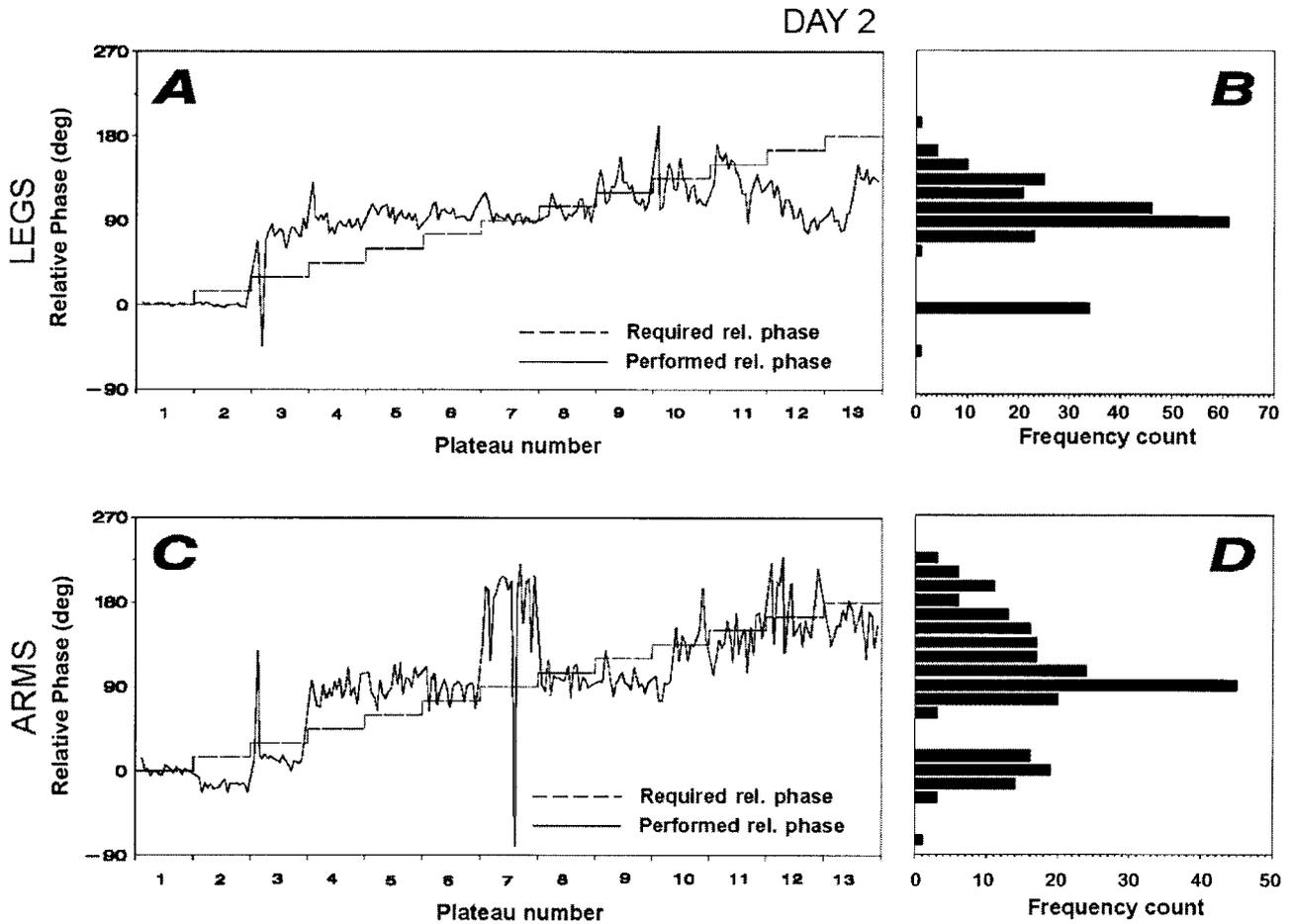
Figure 3. Initial scanning probes (Day 1) of the arm and leg coordination dynamics for a typical subject who practiced a 75° relative (rel.) phase with the arms. A and B show probes of the arm system, whereas C and D show probes of the leg system. The left graphs display the performed (solid lines) and the required (dashed lines) relative phases. For ease of viewing, we joined together the 13 individual trials (labeled by plateau numbers) in which a single relative phase was required at random. The right graphs display the frequency distributions of performed relative phase across all phasing requirements. Both arm and leg probes revealed bistable dynamics at about 0° and 180°. Panel A shows that a pattern around 125° was performed fairly stably, even if accidentally. Therefore, we set the learning task at 75°. deg = degrees.

Table 1  
Between-Trials Statistics (in Degrees) of Within-Trial Mean Constant Errors (CEs) and Standard Deviations for Relative Phase Performed in the First and Last Three Learning Trials for Three Typical Subjects

Subject	Trials	CE		SD	
		M	SD	M	SD
1	First 3	49.10	10.66	13.61	8.44
	Last 3	4.85	5.53	4.05	0.29
2	First 3	103.933	9.92	15.76	8.71
	Last 3	22.71	0.68	8.29	1.32
3	First 3	52.34	4.07	16.78	2.60
	Last 3	-2.39	3.47	9.17	6.35

practiced limb pair. In particular, Figures 4C and 4D also suggest at least a transient destabilization of the antiphase pattern as a result of learning the 90° phasing pattern.

Figure 5 shows the results of leg and arm scanning probes, carried out after practicing a 45° relative phase with the legs alone, for the same subject as in Figure 2. Figures 5A and 5B suggest that the practiced leg system is multistable after practice, exhibiting coordination tendencies whose average values are about 4°, 55°, 125°, and 180°. Again, practice created a stable state close to the to-be-learned phasing pattern, an unequivocal sign of learning. Second, the preexisting 90° pattern (cf. Figures 2A and 2B) vanished completely, whereas the pattern at 180° remained quite prominent, a finding already reported in previous work on bimanual coordination (Zanone & Kelso, 1997). When the initial dynamics is multistable, learning appears to involve a shift of an already-existing attractive state in the direction of the task requirement. A novel finding shown in Figure 5 is that a pattern also



*Figure 4.* Final scanning probes (Day 2) of the leg and arm coordination dynamics for the same subject shown in Figure 1, who practiced  $90^\circ$  of relative (rel.) phase with the legs. A and B show probes of the leg system, whereas C and D show probes of the arm system. The left graphs display the performed (solid lines) and the required (dashed lines) relative phases. For ease of viewing, we joined together the 13 individual trials (labeled by plateau numbers) in which a single relative phase was required at random. The right graphs display the frequency distributions of performed relative phase across all phasing requirements. The leg and arm probes revealed that the to-be-learned  $90^\circ$  pattern constitutes a novel attractive state of the coordination dynamics for both the trained and untrained effector systems, attesting to learning and transfer of learning. deg = degrees.

stabilized near  $125^\circ$ , although it had never been practiced at all. Thus, spontaneous transfer of learning seems to occur within the same half of the phase diagram (i.e., between  $0^\circ$  and  $180^\circ$ , corresponding to right-lead phasing patterns), comparable to the transfer demonstrated across the two halves of the phase diagram (i.e., from right-lead patterns to left-lead patterns and vice versa; see Zanone & Kelso, 1997). Again, symmetry arguments may be invoked as a possible origin of this phenomenon, because  $55^\circ$  and  $125^\circ$  are symmetrically distributed around  $90^\circ$ .

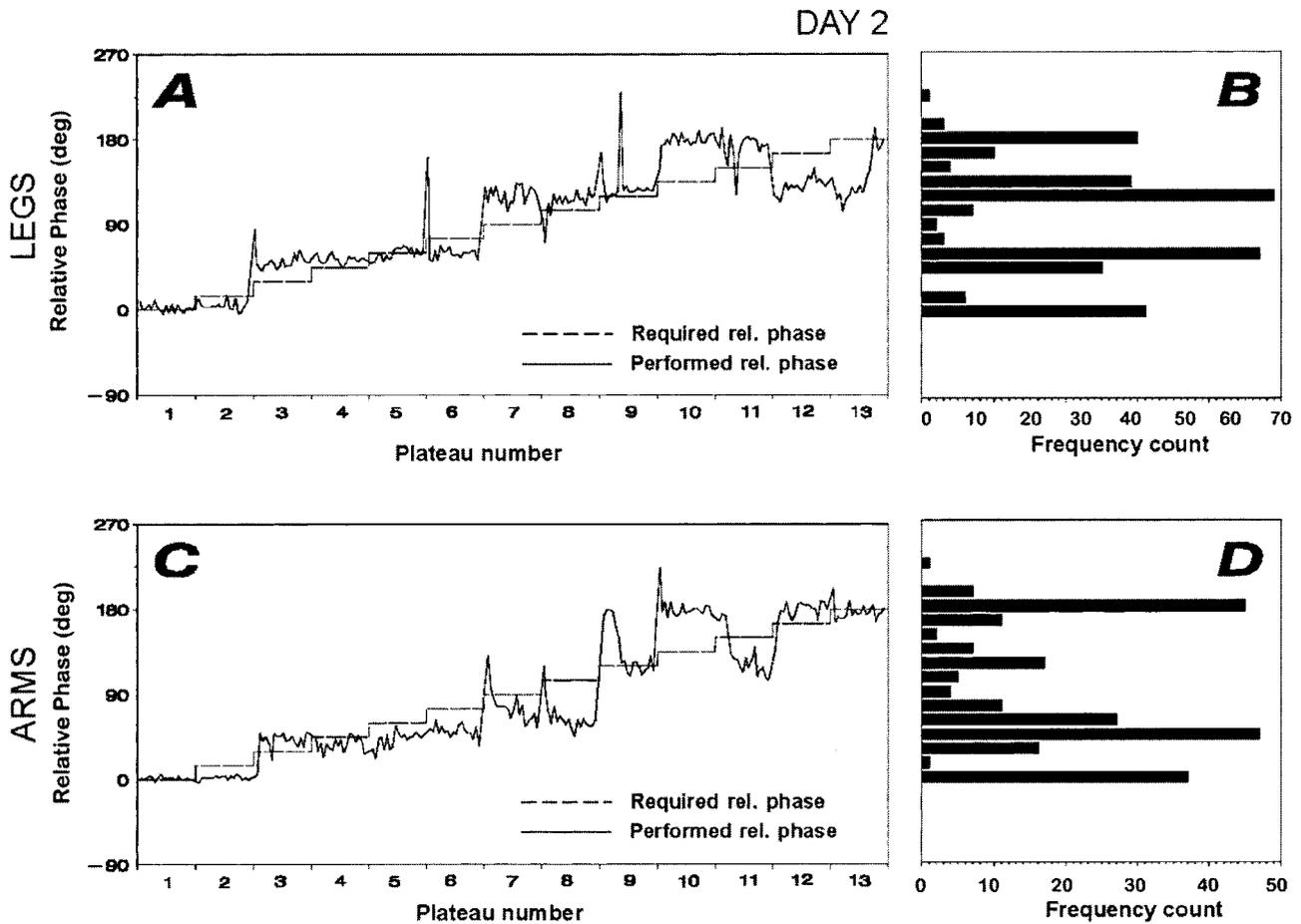
As for the nonpracticed arm system, Figures 5C and 5D display a picture that is highly compatible with the one illustrated in Figures 5A and 5B for the leg system. All the indicators suggest that a new attractive state appeared at about  $45^\circ$ , the to-be-learned relative phase, whereas the preexisting  $90^\circ$  attractive state essentially vanished (cf. Figures 2C and 2D). Good agreement between the top and bottom rows of the figures suggests that transfer of learning occurred spontaneously across initially multistable effec-

tor systems, given that the  $45^\circ$  pattern was practiced by the legs alone.

Figures 6A and 6B show the results of the postlearning probes for the arm and leg systems for a subject who practiced a  $75^\circ$  relative phase with the arms. Both parts of the figure show comparable results. After practice, stable states around  $0^\circ$  and  $90^\circ$  are noticeable (close to the to-be-learned phasing) in the coordination dynamics of both arm and leg systems, although practice was with the arms alone. Comparison with the prelearning probes of the same subject (cf. Figures 3A and 3B) suggests that learning and transfer of learning occurred with practice.

#### Group Data

The individual data provide initial support for our hypothesis that transfer of learning occurs spontaneously across comparable (i.e., symmetric) effector systems in both directions, from legs to



*Figure 5.* Final scanning probes (Day 2) of the leg and arm coordination dynamics for the same subject shown in Figure 2, who practiced 45° of relative (rel.) phase with the legs. A and B show probes of the leg system, whereas C and D show probes of the arm system. The left graphs display the performed (solid lines) and the required (dashed lines) relative phases. For ease of viewing, we joined together the 13 individual trials (labeled by plateau numbers) in which a single relative phase was required at random. The right graphs display the frequency distributions of performed relative phase across all phasing requirements. The leg and arm probes revealed that the to-be-learned 45° pattern constitutes a novel attractive state of the coordination dynamics for both the trained and untrained effector systems, attesting to learning and transfer of learning. deg = degrees.

arms and from arms to legs. In keeping with our previous work, learning and transfer of learning were assessed in terms of specific modifications of the underlying coordination dynamics—evaluated by scanning probes of relative phase—in the direction of the task requirement. Moreover, the form that such alterations take appears to depend on the nature of the coordination dynamics before any learning. We now consolidate these individual findings by presenting the group results.

A general picture of the evolution of performance with practice is provided in Figures 7A and 7B, for all subjects who practiced with the arms or the legs, respectively. In both parts of the figure, the upper curve (solid line) represents the mean error in relative phase (i.e., the average difference between the produced and the to-be-learned relative phases), collapsed across learning tasks, as a function of practice trials. The lower curve (dotted line) displays the corresponding mean within-trial standard deviation. For both curves, vertical bars indicate variability across subjects, encom-

passing  $\pm 1$  *SD*. The 40 scores per day are juxtaposed, so that the trial numbering is continuous.

Figure 7A indicates that irrespective of actual phasing requirement, mean error of arm performance (top solid curve) diminishes fivefold with practice to a value of about 7°. Variability (dashed curve) decreases by one half, reaching a final standard deviation below 10°. For both scores, between-trials fluctuations and between-subjects variability (denoted by the vertical bars) also declined. Figure 7B shows an even steeper improvement in both error and variability scores for the legs, perhaps due to the larger number of cycles per trial. These typical learning curves indicate a progressive stabilization of performance toward the criterion level. In particular, the functions presented are very similar to those found in our earlier work on learning bimanual perceptuo-motor coordination (Zanone & Kelso, 1992, 1997). Figures 7A and 7B indicate that regardless of which pattern is to be learned and which effector system is trained, subjects succeeded in learning the

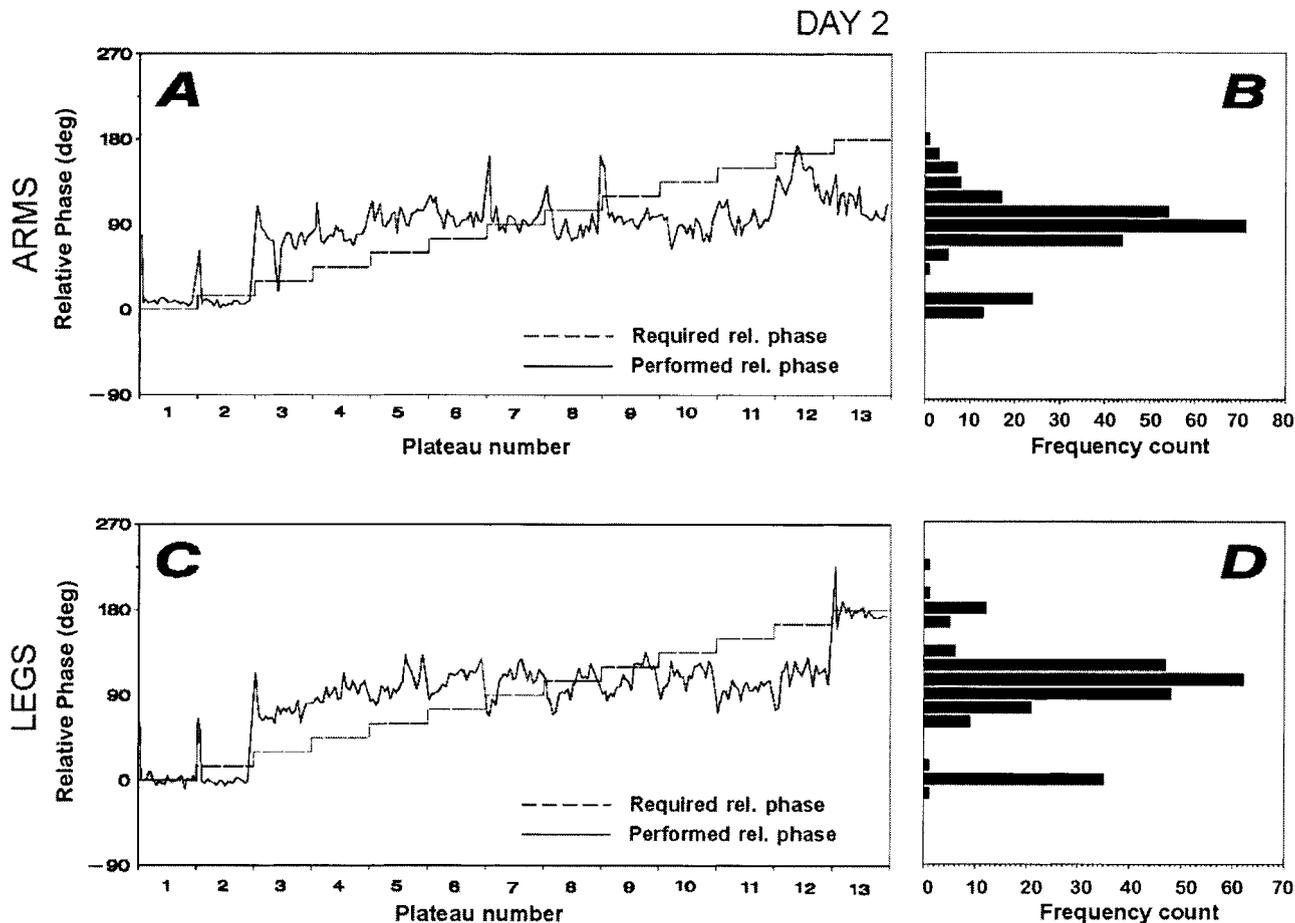


Figure 6. Final scanning probes (Day 2) of the arm and leg coordination dynamics for the same subject shown in Figure 3, who practiced a 75° relative (rel.) phasing pattern with the arms. A and B show probes of the arm system, whereas C and D show probes of the leg system. The left graphs display the performed (solid lines) and the required (dashed lines) relative phases. For ease of viewing, we joined together the 13 individual trials (labeled by plateau numbers) in which a single relative phase was required at random. The right graphs display the frequency distributions of performed relative phase across all phasing requirements. The arm and leg probes revealed that the coordination dynamics of both the trained and untrained effector systems were altered in the direction of the to-be-learned pattern, attesting to learning and transfer of learning. deg = degrees.

task within 80 trials of practice (1,760 individual cycles). Most of the improvements in performance occurred in the first daily session. Nevertheless, such change is relatively permanent, as seen in the stable performance on the second practice session, 1 day later.<sup>4</sup>

How, then, do these changes in performance due to practice relate to specific modifications of the underlying coordination dynamics? First, consider the 4 subjects who practiced 75° or 90° with the arms. Figure 8A shows the relative frequency distributions (in percentages) of all relative phases performed during the scanning probes before practice (dotted line) and after practice (solid line). Such histograms reflect the phasing patterns that are produced most often, irrespective of the task requirement. Before learning, the arms performed relative phases near inphase and antiphase more frequently than other phasing patterns. After practice, the main mode of the histogram is centered about the learning requirement, whereas the antiphase pattern is almost never pro-

duced, even when it was required. This suggests that with practice, the to-be-learned pattern was performed not only when requested (in what actually amounts to only 7.6% of the overall cycles performed during all the scanning runs) but also for other task requirements. Such changes in the histograms are supported by statistical analysis,  $\chi^2(20, N = 4) = 70.20, p < .01$ .

Figure 8C shows the same data in another form, with specific reference to the task requirement. The mean error in relative phase (i.e., the difference between the produced and required relative phases) for the arm probes carried out before and after practice (dashed and solid lines, respectively) is plotted as a function of the

<sup>4</sup> We demonstrated persistence of such improvements with practice (Zanone & Kelso, 1992) through a recall procedure carried out 1 week after the learning procedure. Comparable scores were obtained for all subjects between the last practice trials and the recall trials.

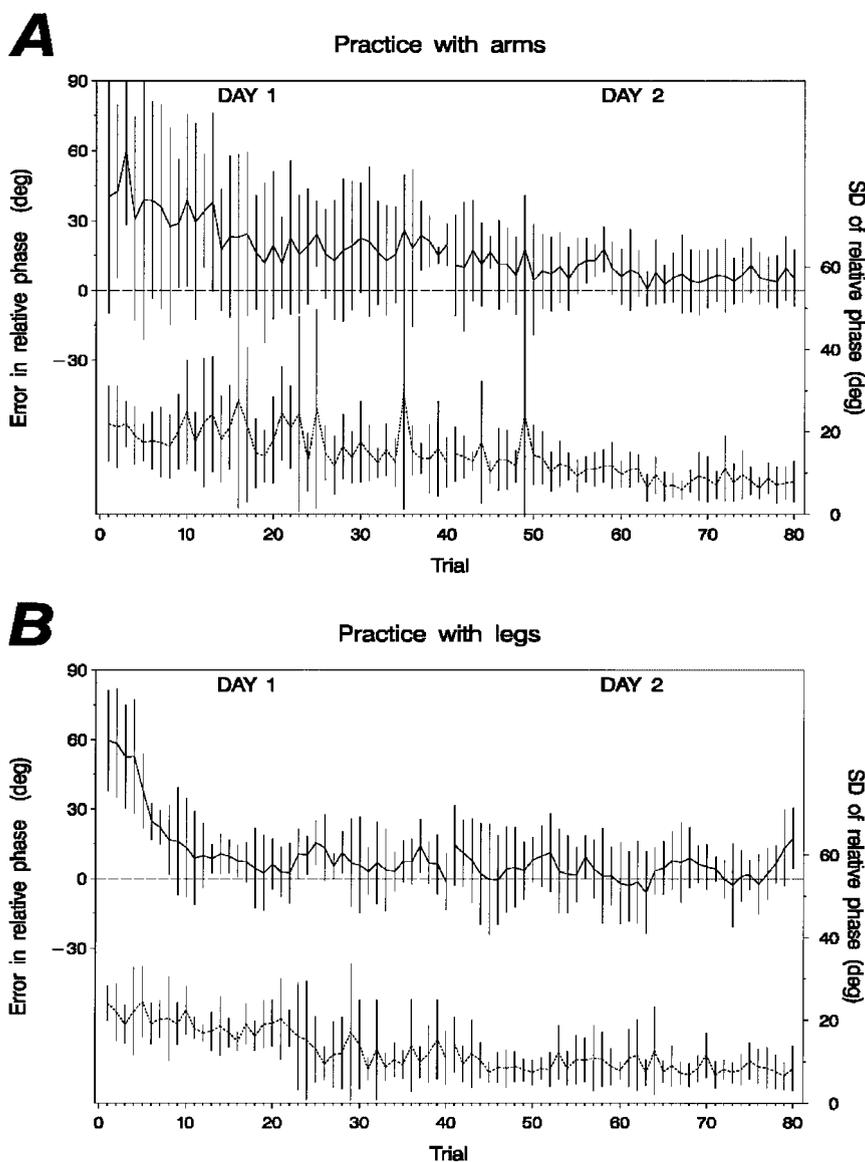
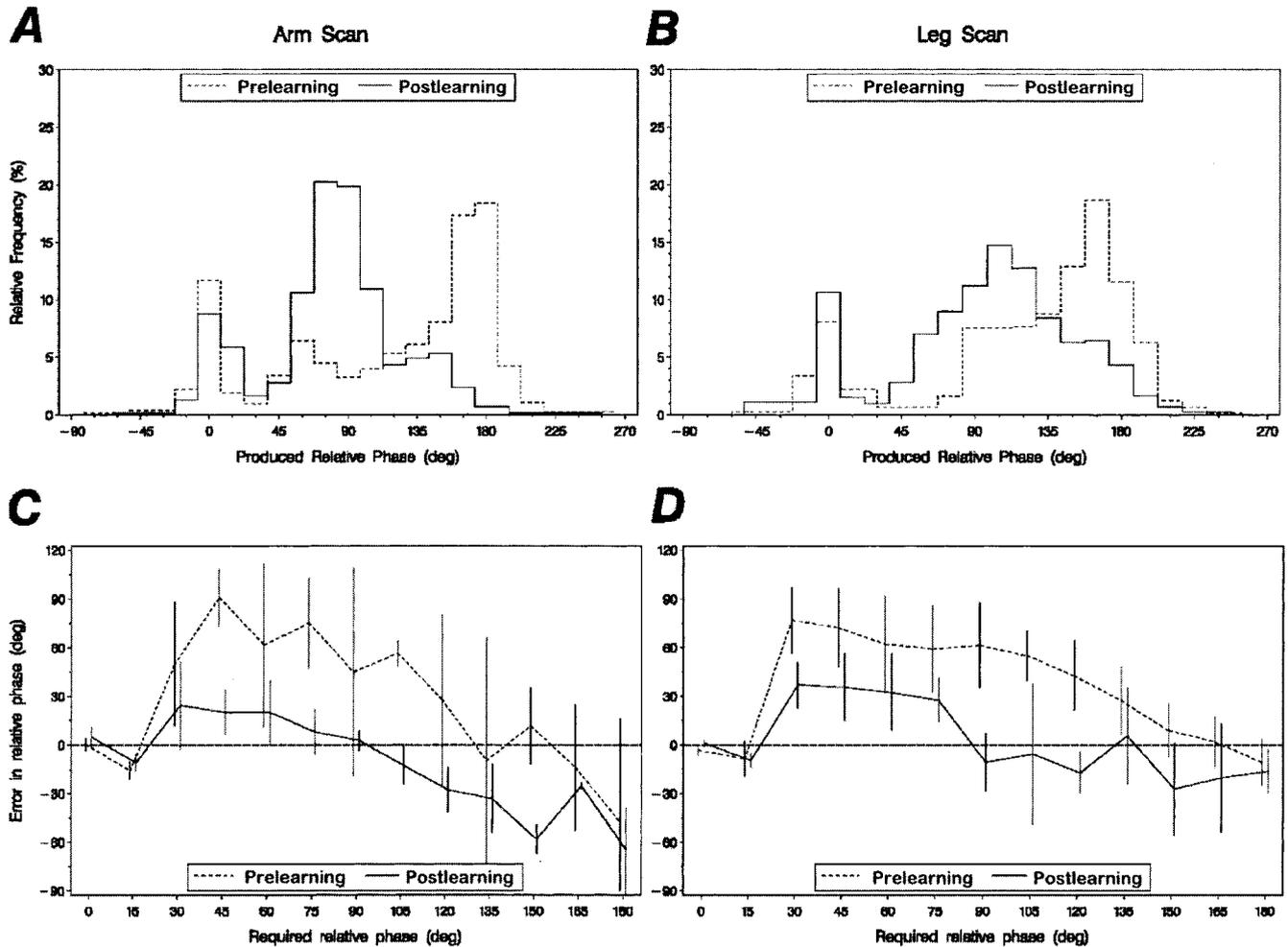


Figure 7. Performance improvements with practice. A: Practice with the arms. B: Practice with the legs. The top, solid curves represent the mean errors in relative phase (i.e., performed minus required), collapsed across subjects, as a function of practice trials. The bottom, dashed curves represent the corresponding within-trial standard deviations. Vertical bars denote between-subjects standard deviations. The general pattern of results for both effector systems complies with typical learning curves, suggesting that the task was mastered by the end of the learning procedure. deg = degrees.

required relative phase. A positive (negative) value means that the required relative phase was overestimated (underestimated). Vertical bars encompass  $\pm 1$  between-subjects *SD*. In the prelearning probe (dashed line), the mean error exhibits a humped shape as a function of the required relative phase. Mismatch is lowest for the  $0^\circ$  or  $180^\circ$  requirements, with a marked increase for intermediate values. The negative slope between  $45^\circ$  and  $180^\circ$  reflects a general attraction to the antiphase pattern, because intermediate relative phases are overshoot in that direction.<sup>5</sup> Likewise, the negative slope between  $0^\circ$  and  $15^\circ$  suggests attraction to the inphase pattern. Such attraction of nearby phasing requirements to  $0^\circ$  and  $180^\circ$  reflects

the stability of the inphase and antiphase patterns before learning and suggests that these patterns are attractive states of the underlying coordination dynamics (Beek, Peper, & Stegeman, 1995; Carson et al., 1995; Fontaine et al., 1997; Kelso, 1984; Lee et al., 1995; Schöner et al., 1992; see Zanone & Kelso, 1992, for more details). After practice (solid line in Figure 8C), the mean error is

<sup>5</sup> The negative slope in the error curve about a given value reflects exactly the same phenomenon causing the plateaus in performance near a phasing value that can be seen in Figures 1–6, namely, attraction.



*Figure 8.* Group changes with learning. Pre- and postlearning scanning probes of the arm and leg coordination dynamics for subjects who practiced a 75° or 90° pattern with the arms. A and B show the frequency distributions of the performed relative phases for all phasing requirements constituting probes of the arm and leg systems, respectively, before (dashed lines) and after (solid lines) practice of a 75° or 90° phasing with the arms. C and D show the average errors between the performed and required relative phases as a function of the phasing requirement in the prelearning (dashed lines) and postlearning (solid lines) probes, collapsed across the same subjects and effector systems. Vertical bars denote between-subjects standard deviations. Zero crossing of the error curve with a negative slope is indicative of attractive states of the underlying coordination dynamics. Comparison of the results of pre- and postlearning probes in A and C suggests that learning involves stabilizing the new pattern as an attractive state of the coordination dynamics of the practiced (arm) system. Comparison of the results of pre- and postlearning scanning probes in B and D shows that learning also entails stabilizing the new pattern as a stable state of the coordination dynamics of the unpracticed (leg) system. deg = degrees.

low not only around 0° but also around 90°. Moreover, a negative slope spans all the way from 60° to 150°. Overestimation of the required pattern below 90° and underestimation above it implies that the pattern actually performed is biased toward 90°, indicating that the learned state has become attractive to its neighbors. In accordance with the individual data, learning a new pattern of coordination involves stabilizing a value of the coordination dynamics close to the task requirement.

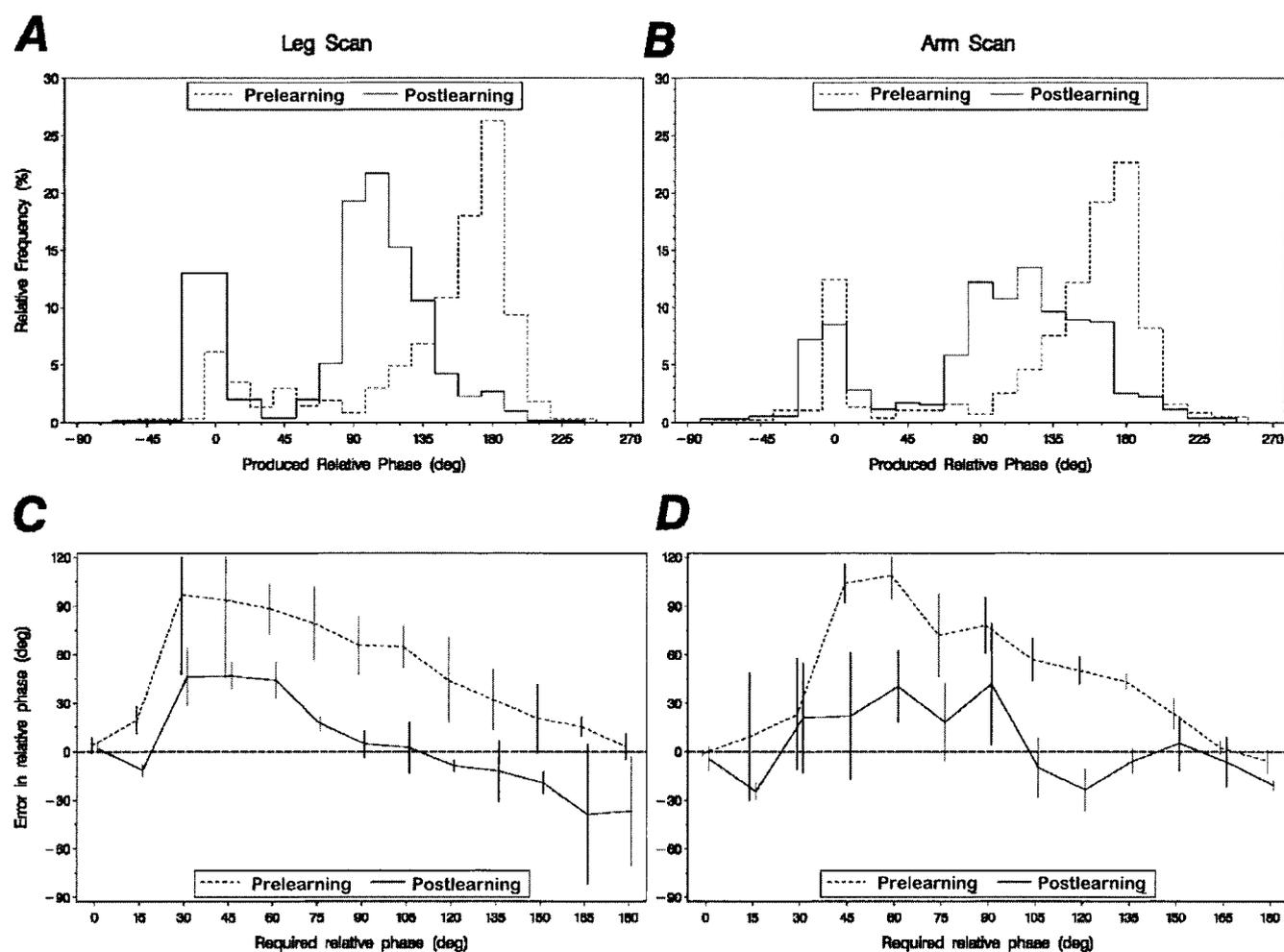
Figures 8B (histogram) and 8D (error curve) show the results of the leg probes conducted before learning (dashed line) and after learning (solid line). Figure 8B shows that the initial frequency

distribution exhibits two dominant modes at 0° and 180°, whereas after practice of the 75° or 90° pattern with the arm system, a new mode appears close to the to-be-learned value. Such a significant change in the frequency distributions was confirmed statistically,  $\chi^2(18, N = 4) = 34.78, p < .01$ . The negative slopes and zero crossings seen in Figure 8D also suggest that 0° and 180° correspond to the initial attractive states of the leg coordination dynamics and that the pattern around 90° is stabilized with practice. Overall, these findings are quite comparable to those reported in Figures 8A and 8C regarding the arm coordination dynamics, although the leg system did not practice the task at all. The

practiced pattern becomes a stable state of the dynamics of both effector systems, a clear sign of transfer of learning.

Consider now the two subjects who practiced  $75^\circ$  or  $90^\circ$  with the legs. Figures 9A and 9C show the frequency distributions and the error curves for the relative phases performed by the legs during the prelearning (dashed line) and postlearning (solid line) probes, respectively. The modes and zero crossing in each figure suggest that prior to practice, the initial coordination dynamics for the leg system was bistable at inphase and antiphase. After practice, a new attractive state emerges close to the task requirement, whereas the antiphase pattern again appears to destabilize. Such differences in the frequency histograms are confirmed statistically,

$\chi^2(17, N = 2) = 86.77, p < .01$ . These are the basic features of learning a new coordination pattern that we have seen before. Figures 9B and 9D show the results of the probes for the arm system conducted before learning (dashed line) and after learning (solid line). Although the pattern to be learned was not practiced by the arms, both parts of the figure show changes in the underlying coordination dynamics analogous to those undergone by the legs (cf. Figures 9A and 9C), again substantiated by statistical testing,  $\chi^2(20, N = 2) = 71.30, p < .01$ . This result indicates that spontaneous transfer occurred from the leg system to the arm system, leading to similar modifications in their respective coordination dynamics.



*Figure 9.* Pre- and postlearning probes of the arm and leg coordination dynamics for subjects who practiced a  $75^\circ$  or  $90^\circ$  pattern with the legs. A and B show the frequency distributions of the performed relative phases for all phasing requirements constituting scanning probes of the leg and arm systems, respectively, before (dashed lines) and after (solid lines) practice of a  $75^\circ$  or  $90^\circ$  phasing with the arms. C and D show the average errors between the performed and required relative phases as a function of the phasing requirement in the prelearning (dashed lines) and postlearning (solid lines) probes, collapsed across the same subjects and effector systems. Vertical bars denote between-subjects standard deviations. Zero crossing of the error curve with a negative slope is indicative of attractive states of the underlying coordination dynamics. Comparison of the results of pre- and postlearning probes in A and C shows that learning involves stabilizing the new pattern as a stable state of the coordination dynamics of the practiced (leg) system. Comparison of the results of pre- and postlearning probes in B and D shows that learning also entails stabilizing the novel pattern as an attractive state of the coordination dynamics of the unpracticed (arm) system. deg = degrees.

That learning and transfer involve similar changes in the attractor layout was corroborated by a statistical analysis in which we compared the mean error obtained with both limbs when the required phasing pattern was set to 0°, 180°, and to the to-be-learned value (75° or 90°), across days of practice. A  $2 \times 2 \times 3$  (Limb  $\times$  Day  $\times$  Pattern) analysis of variance with repeated measures on day and pattern revealed that the effects of day and pattern were significant,  $F(1, 10) = 8.09$ ,  $p < .02$ , and  $F(2, 20) = 47.60$ ,  $p < .01$ , respectively, as was their interaction,  $F(2, 20) = 6.23$ ,  $p < .01$ . Note that neither the effect of limb nor any interaction with limb was significant. Thus, differential effects due to day and pattern were comparable across effector systems.

Taken together, Figures 8 and 9 and the related analyses confirm our main experimental hypotheses. First, irrespective of the system practicing the task, learning involves alterations of the underlying coordination dynamics in the direction of the task requirement, such that the newly learned pattern becomes a stable state of the dynamics. Second, such modifications also occur spontaneously in the dynamics of the effector system that did not practice the learning task, suggesting automatic transfer of learning. One reason for transfer may be the similarity of both effector systems' dynamics before learning: Both were bistable at inphase and antiphase prior to practice. Moreover, these group data support our previous findings (Zanone & Kelso, 1992; see also Lee et al., 1995) that stabilizing a new attractive state may involve—at least temporarily—loss of stability of an initially stable state (i.e., 180°).

Figures 10A and 10B show the results of the probes obtained for the 4 subjects who practiced 45°, regardless of which effector system (arm vs. leg) actually practiced the task. Figure 10A displays the frequency histograms of the relative phase performed by the effector system that was actually exposed to training. The distribution suggests that before learning (dashed line), stable patterns exist around 0°, 90°, and 180°. After practice (solid line), the most noticeable feature is the shift of the mode centered about 90° toward 45°, the task requirement. Consonant with the individual data shown in Figure 5A, learning led to the stabilization of a new attractive state at the required value of 45°, accompanied by the virtual disappearance of the initially stable state at 90°. This finding agrees with our previous results (Zanone & Kelso, 1997) showing that when the initial dynamics are multistable, learning a new pattern involves the shift of a preexisting nearby attractive state toward the task requirement. The group data for the practiced effector systems (see Figure 10A) also show a less prominent mode around 120°. As suggested in the individual data (Figure 5A), it seems that learning also stabilizes one of the symmetry partners of the learned 45° pattern, namely, 135°. This may be a phenomenon similar to the spontaneous transfer between symmetry partners with inverse sign (e.g.,  $\pm 135^\circ$ ) demonstrated in our earlier study (Zanone & Kelso, 1997).

Figure 10B shows the frequency distributions of the performed relative phase during scans of the effector system that was not trained at 45°. The histogram for the prelearning probe (dotted line) exhibits two modes, at 0° and 180°, plus a less well-defined mode approximately centered around 110°. After learning 45° with the other effector system, this intermediate mode shifts toward a central value of 60°, close to the learning requirement. Thus, the frequency distribution of the untrained effector systems matches that of the trained effector systems (cf. Figures 10A and 10B), suggesting spontaneous transfer of learning, regardless of whether

the arms or the legs actually practiced the to-be-learned relative phase. A test on the overall distribution data—that is, pooling all subjects together—showed a significant effect of learning and transfer,  $\chi^2(18, N = 4) = 68.17$ ,  $p < .01$ .

Figures 11A and 11B show the results of the scans obtained for the 2 subjects who practiced the 135° phasing pattern, regardless of which effector system (arm or leg) actually practiced the task. For the effector system that practiced the task (Figure 11A), the frequency histogram before practice (dashed line) indicates that the coordination dynamics has a multistable character with attractive states located about 0°, 90°, and 180°. After practice (solid line), the intermediate mode shifts to the value set as the learning task. Note that the initial 180° mode has apparently been incorporated into the new mode around 135°. Figure 11B shows a comparable frequency distribution for the effector system that did not practice the learning task. Once again, transfer of learning from the trained to the untrained effector systems is evident, irrespective of whether the arms or the legs practiced the task. A test on the overall data indicated a significant effect of learning and transfer,  $\chi^2(18, N = 2) = 48.12$ ,  $p < .01$ .

In summary, the results for the subjects who learned 135° or 45° are quite consistent. Unlike the case of initially bistable dynamics (Figures 8 and 9), change consists of the shift of an already-existing attractive state (viz., 90°) toward the pattern to be learned. Such shifts have proven to be a typical route to learning associated with multistable coordination tendencies (Zanone & Kelso, 1997). It is interesting that the present results show that the intermediate stable pattern can be moved around in both directions (i.e., toward 45° or 135°) in the space of the coordination variable, relative phase, to meet the learning task requirements.

### Control Groups

The foregoing conclusions are valid insofar as the effects attributed to learning and transfer of learning do not arise from the mere use of the experimental equipment and/or from exposure to the series of scanning runs used to probe the coordination dynamics of the two limb pairings.

Figures 12A and 12B show the frequency distributions of the relative phases performed by 6 control subjects during scanning probes of the arm and leg systems, carried out on the first (dashed line) and second (solid line) day. Figure 12A shows that the histograms are almost identical on both days. Figure 12B displays the same results regarding the leg system, indicating that the underlying coordination dynamics remained virtually unchanged. A chi-square test ( $df = 20$ ,  $N = 6$ ) on the overall data for the control groups yielded a nonsignificant value of 7.53 ( $p > .05$ ). The negligible differences exhibited across days for both effector systems in the control group further attest to the notion that the results of the main experiment are a specific outcome of the learning process.

### Summary

The ensemble of results reported here provides new findings and corroborates previous findings concerning the dynamics of learning and transfer. On the one hand, we provide strong evidence that learning a new phase relationship with one effector system (the arms) automatically transfers to another effector system (the legs),

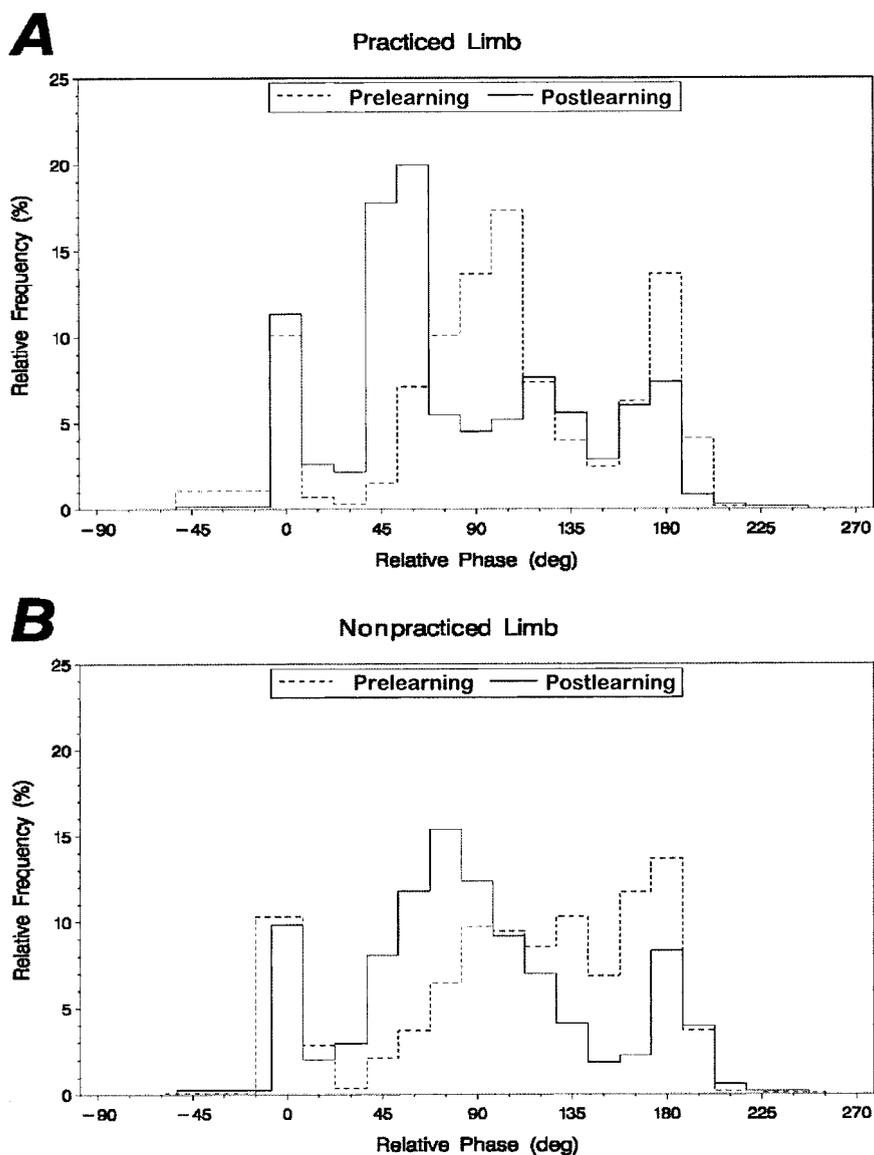


Figure 10. Pre- and postlearning probes of the practiced and unpracticed effector systems for subjects who practiced the  $45^\circ$  pattern. A and B show the frequency distributions of the performed relative phases for all phasing requirements used to probe the effector systems that did and did not practice the  $45^\circ$  phasing task, respectively. Comparison of the results of prelearning (dashed lines) and postlearning (solid lines) probes indicates that learning involves stabilizing the to-be-learned pattern as a stable state of the coordination dynamics, irrespective of which effector system practiced the task. deg = degrees.

and vice versa. On the other hand, the basic mechanism through which learning occurs is established further on two counts. First, we have shown that learning and transfer of learning involve systematic modifications of the coordination dynamics of both effector systems. Irrespective of differences in limb patterning before exposure to a novel learning task, the learned pattern becomes a novel attractive state of the underlying coordination dynamics of both effector systems.<sup>6</sup> Second, the coordination dynamics prior to learning determines the form that the learning process may take. When coordination tendencies are initially bistable (i.e., the inphase and antiphase are attractive states), the

newly learned stable pattern is accompanied by the transient destabilization of a preexisting attractive state (i.e.,  $180^\circ$ ). When coordination tendencies are initially multistable (i.e., an attractive state also exists about  $90^\circ$ ), shifts (or drifts) toward the to-be-

<sup>6</sup> Again, initial probes of the underlying coordination dynamics are crucial to assert the novelty of a phasing pattern. The learned pattern was certainly novel, because the task was set such that it did not correspond to any attractive states of the coordination dynamics that were present before practice.

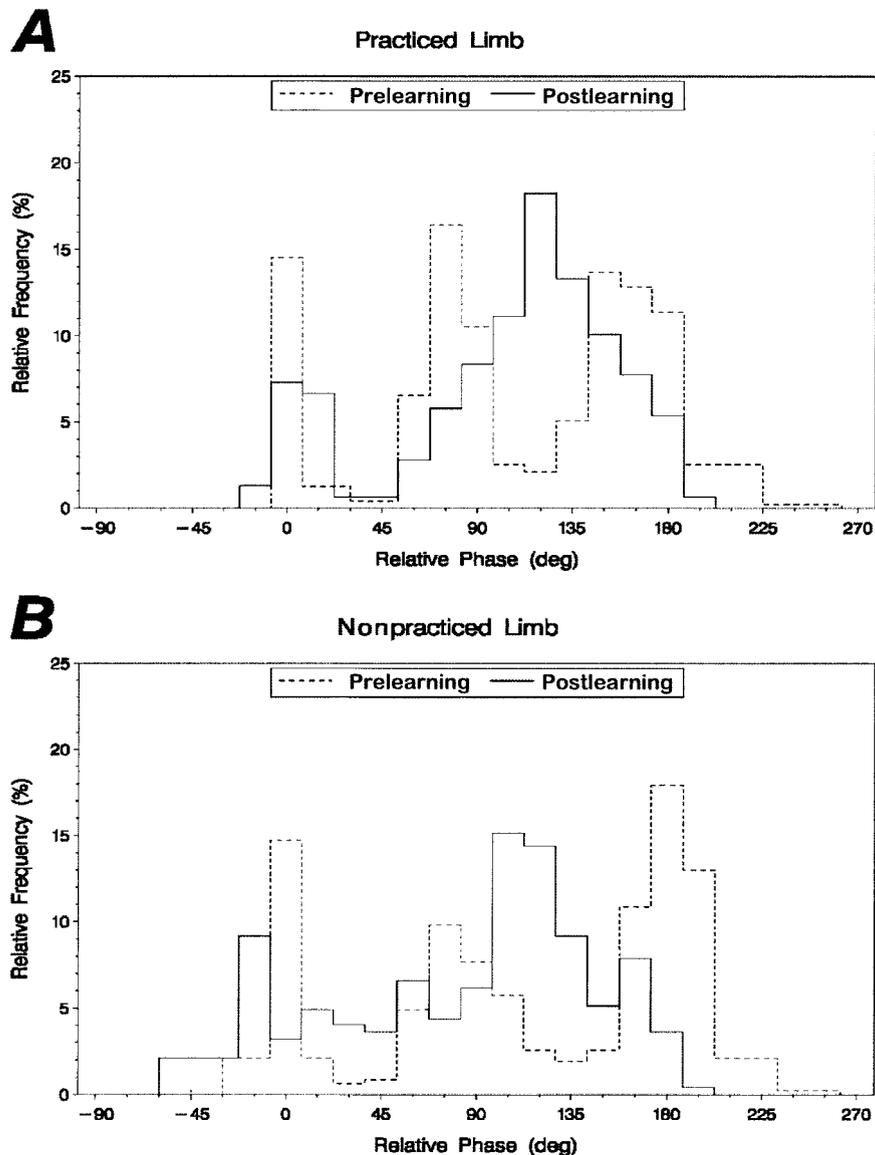


Figure 11. Pre- and postlearning probes of the trained and untrained effector systems for subjects who practiced the 135° pattern. A and B show the frequency distributions of the performed relative phases for all phasing requirements used to probe the effector systems that did and did not practice the 135° phasing task, respectively. Comparison of the results of prelearning (dashed lines) and postlearning (solid lines) probes shows that learning involves stabilizing the to-be-learned pattern as a stable state of the coordination dynamics, irrespective of which effector system practiced the task. deg = degrees.

learned value occur, leaving preexisting coordination tendencies more or less unchanged.

### General Discussion

An important issue in theories of skill acquisition and learning concerns the nature of what is being learned. The present research addressed this issue from the perspective of coordination dynamics, a lawful representation that is hypothesized to govern how the central nervous system assembles coordinated patterns of activity on different levels of description. How abstract this representation

is may be ascertained by determining the effectiveness of transfer or generalization from one (trained) effector system to another (untrained) effector system. Previous work on bimanual coordination has established that learning involves modifications of the preexisting coordination dynamics in the direction of the learning task (Kelso, 1990; Schöner et al., 1992; Zanone & Kelso, 1992, 1997) and that transfer may occur spontaneously between two components within the same effector system (Zanone & Kelso, 1994, 1997). Through the window of interlimb coordination, we conducted an experiment to test whether transfer of learning also occurs across different effector systems, causing similar alterations

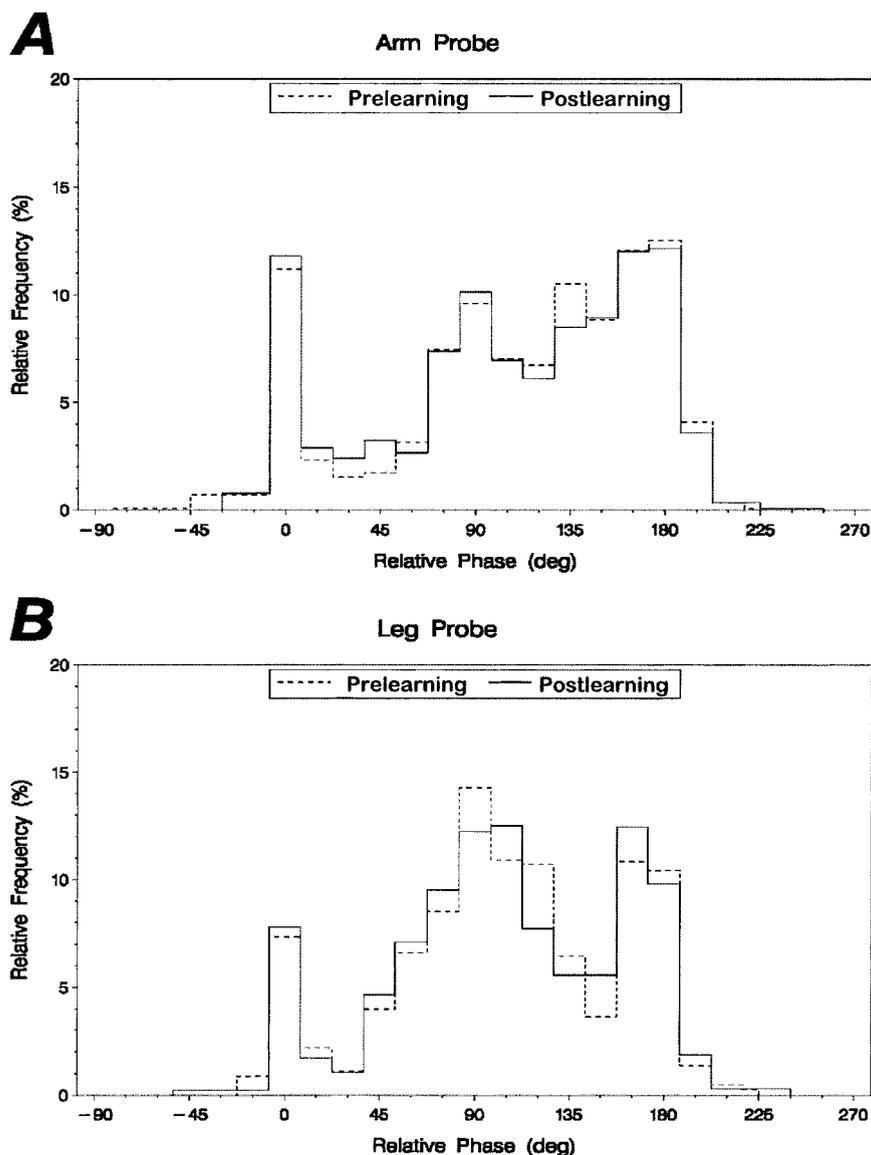


Figure 12. Pre- and postlearning probes of both effector systems for control subjects who did not practice any phasing pattern. A and B show the frequency distributions of the performed relative phases for all phasing requirements used to probe the arm and leg systems, respectively, before (dashed lines) and after (solid lines) practice, for all the control subjects. Comparison of the results of pre- and postlearning probes for both effector systems shows negligible differences in the underlying coordination dynamics. deg = degrees.

in their respective coordination dynamics. The task was to learn a specific phase relationship through practice with the arms or the legs. To assess modifications induced by learning and transfer, we evaluated the coordination dynamics of both effector systems before and after practice through scanning probes aimed at revealing underlying attractive or stable states of the coordination dynamics (see also Tuller & Kelso, 1989; Yamanishi, Kawato, & Suzuki, 1980).

The results indicated that learning a novel relative phase with one effector system spontaneously transferred to the other, untrained effector system. Not only was transfer seen as performance improvements in both systems when the to-be-learned phasing was

required but it was also revealed by qualitative modifications of their underlying coordination dynamics. That is, the dynamics of both the trained and untrained limb pairs exhibited either comparable phase transitions, themselves a signature of learning (Kelso, 1990; Zanone & Kelso, 1992), or similar shifts in preexisting attractive states, a further, parametric sign of learning (Zanone & Kelso, 1997). Irrespective of the form taken by the learning process, the visually specified phasing pattern was learned and remembered, creating a new attractive state in both the practiced and unpracticed coordination dynamics.

An important provision we took was that the pattern selected as a learning task did not coincide with already-existing attractive

states (or preferences) of the underlying coordination dynamics. Theoretically, before learning, any contribution to the coordination dynamics due to the novel task requirement should compete with preexisting, so-called intrinsic coordination tendencies. Such competitive interaction between behavioral task demands and individual coordination tendencies is hypothesized to lead to the observed bias and increase in variability of the performed pattern. The present results suggest that a common mechanism underlies learning and transfer, namely, reduction of the competition that initially arises between task requirements and intrinsic coordination tendencies. How such competition is instantiated in the CNS is an interesting question. It is now well established that different behavioral phasing patterns have their expression in spatiotemporal patterns of brain activity, quantified (using time-averaging techniques) in terms of spatial modes and their time-dependent amplitudes (e.g., Fuchs, Mayville, et al., 2000; Fuchs, Kelso, & Haken, 1992; Jirsa et al., 1998; Kelso et al., 1992, 1998) or (in the frequency domain) as patterns of power and coherence, particularly in the beta (15–30 Hz) range (Chen, Ding, & Kelso, 1999; Jantzen, Fuchs, Mayville, & Kelso, 2001; Mayville et al., 2001). A reasonable hypothesis is that competitive processes in learning may be captured in terms of mode competition in the brain. Still other evidence found using positron emission tomography indicates that activity in the parietal cortex remains high after transfer has occurred from fingers to arms in a sequencing task (Grafton, Hazeltine, & Ivry, 1998), suggesting that parietal areas are involved in generating the sequence at an abstract level independent of the effectors used. As expected, other neural areas, such as the sensorimotor cortex, are quite effector specific.

Scanning probes of subjects' coordination abilities before and after practice corroborate the idea that what is learned is not only the practiced coordination pattern but also an entire dynamics of coordination. The relevant coordination variable of these task-specific dynamics is the relative timing or phasing between the limbs. We ruled out the alternate possibility that an absolute time interval between the limbs was actually learned and transferred, because the two effector systems performed the learning task and scanning probes at different movement frequencies. Were an absolute timing acquired, the learned and transferred relative phases should differ systematically, which was not the case here.

A closer look at the results indicates that although the effects of learning and of transfer on the coordination dynamics are qualitatively equivalent—namely, stabilization of an attractive state coincident with the learning requirement—small but detectable quantitative differences may be spotted in terms of strength and localization of attractive coordination patterns. First, the transferred pattern (viz., pertaining to the untrained effector system) appears to be less stable than the learned attractor (viz., pertaining to the practiced system). This may be readily seen in terms of variability, with the learned pattern usually exhibiting a smaller standard deviation than the transferred one. Moreover, the span of the negative slope effect, a sign of attraction to the learned pattern in parameter space, is more limited for the transferred than for the learned attractor. Second, whereas the learned pattern stabilizes very close to the required phasing (generally within less than 10°), the transferred pattern is typically located a bit farther away. Note that in the case of initially multistable dynamics, the shift of the 90° pattern toward the required state is not always complete. Such slight quantitative discrepancies between practiced and unprac-

ticed systems are to be expected given the limited amount of practice, the many superficial differences between arms and legs, and the different ways these anatomical structures could be controlled. The remarkable result, however, is the extent to which the two effector systems are similar in terms of changes in coordination with learning.

The status of the antiphase pattern deserves closer scrutiny (see also Fontaine et al., 1997; Lee, 1998). Except for the case of learning a 45° phasing pattern, our findings indicate that the 180° pattern is performed less stably or accurately after learning, being (at least temporarily) drawn into the newly created basin of attraction of the learned pattern. Why the temporary destabilization of the antiphase pattern appears more systematic here than in previous studies is an open question. We have reported similar findings in earlier work (Zanone & Kelso, 1992, 1997). In probes where subjects were asked to execute a large variety of relative phases, the antiphase pattern destabilized with the creation of a nearby (e.g., 90° or 135°) novel attractive state through learning. In contrast, the 180° pattern appears to remain a stable state when the 45° pattern is learned. This suggests a limit on the extent over which competitive processes may operate: When the newly learned pattern is far enough from the intrinsic 180° phasing pattern, the latter does not diminish as an attractive state, even though it may become more variable. An important methodological point is that such a result cannot be interpreted as a *history effect* (Zanone & Kelso, 1997), meaning that when the target relative phase is incremented gradually, subjects tend to stay longer in the pattern currently performed regardless of the actual task requirement. In the present study, we assigned the different phasing requirements in a random and not in a stepwise fashion, thereby eliminating the possibility of hysteresis. Such methodological matters aside, there is absolutely no reason to expect that subjects, if asked to produce an antiphase pattern between the arms or between the legs spontaneously or from memory, could not do it. Generally speaking, it seems likely that the influence of the newly learned pattern on one of the intrinsic coordination tendencies is transient and context dependent (see also Tsutsui, Lee, & Hodges, 1998, for another kind of evidence of context effects on learning bimanual coordination).

At a conceptual level, the finding that similar alterations occur in the coordination dynamics of both the trained and untrained effector systems suggests that learning and transfer involve a common mechanism—neurally instantiated, of course (cf. Grafton et al., 1998; Jantzen et al., 2001)—that exists at a rather abstract level of system functioning. In previous work (Zanone & Kelso, 1997), we demonstrated that the realization of the learned phasing pattern was independent of any lead-lag relationship between the components and independent of their kinematic implementation. Here, we found that the realization of such a pattern is also largely independent of the effector system used to perform the task (or, conversely, is shared by both effector systems). By definition, such flexibility in the motor implementation of the same task is a signature of motor (or, as we prefer to call it, *functional*) equivalence (Kelso et al., 1984). Such equivalence may be possible only because what is learned and remembered corresponds to task-level attractive states of the coordination dynamics based on perception of the task. This statement is not intended to minimize specific neuromuscular-skeletal factors that have been shown to sculpt the

coordination dynamics (Carson & Riek, 1998; Jeka & Kelso, 1995; Kelso, Fink, DeLaplain, & Carson, 2001; Kelso & Jeka, 1992).

The idea that actions are specified in terms of attractive states of an underlying coordination dynamics may shed light on how the CNS specifies a motor command. A command may have less to do with a top-down prescription dictating the behavior of the individual components than with the propensity of a complex system to exhibit but a limited set of attractive coordination states. The parameters of the coordination dynamics are based on the ongoing integration of information from a variety of sources that jointly constrain behavior and behavioral choice, including the perceptual requirements of the task and the subject's intentions, prior experiences, and movement history. In this picture, learning qua the emergence of novel collective states in response to new environmental constraints provides an essential means of behavioral flexibility.

In the framework of coordination dynamics, which factors influence whether transfer occurs between different effector systems? In our study, the practiced and unpracticed effector systems initially shared several characteristics. First, both the trained and untrained systems are described by the dynamics of the same task-specific coordination variable: relative phase. Thus, task and coordination tendencies of both effector systems are captured in the same space of variables. Second, although it varied on a subject-by-subject basis, each limb pair exhibited similar initial coordination dynamics. Arm and leg systems were always bistable (i.e., attraction to inphase and antiphase only) or multistable (with another attractive state). Thus, a second condition for extensive transfer may be the similarity of the initial coordination dynamics. Although modified with learning, such similarity persisted even when a novel coordination state was stabilized with learning and constituted our main criterion for transfer. Third, the coordination dynamics of both systems were symmetric; that is, the left and right components can be permuted without changing the underlying dynamics.<sup>7</sup> Of course, to say that the arms or the legs form a bilaterally symmetric system is trivial on the surface. In the present context, however, symmetry requirements are more stringent, on two counts. On the one hand, the very coordination between the components is symmetric; that is, the behavior of the right limb relative to the left is perfectly equivalent to that of the left limb with respect to the right. On the other hand, this remains so even after learning, because the spatiotemporal symmetry of the coordination dynamics is preserved. Further investigation awaits as to which of the foregoing prerequisites is necessary for transfer of learning to occur. One may wonder, for instance, whether there is transfer between a symmetric system—say, the arms—and an asymmetric system—say, the homolateral arm and leg.<sup>8</sup>

Finally, it may be useful to discuss briefly how the present work relates to more classical views of skill acquisition and learning. In most, if not all, previous views the outcome of learning is addressed in terms of abstract, task-specific entities such as schemas, images of achievement, and generalized motor programs (e.g., Bartlett, 1932; Bernstein, 1967; R. A. Schmidt, 1975). For example, the aim of schema theory was to explain how variable experiences with a skill allow a learner to parameterize it in the form of a generalized motor program (GMP). This generative, rulelike feature of schema theory is intrinsic to even the most elementary form of the coordination dynamics. Equation 1, for example, incorporates not only the so-called invariance properties of the

GMP but also the important dynamic features of multistability, metastability, state transitions, and hysteresis that are crucial for both stability and flexibility (Kelso, 1997; Mitra et al., 1998). For neurobehavioral dynamical systems (Kelso, 1991), these features correspond to multifunctionality (different behavioral patterns for the same parameter values), switching or decision making (one behavioral pattern is selected over another at critical parameter values), and a primitive kind of memory (the history of system behavior affects the current state). Whereas data suggesting that the temporal structure of movement is preserved across various kinds of parameterizations is used as *prima facie* evidence for a GMP (as it was for the earlier notion of coordinative structure; e.g., Kelso et al., 1979; Turvey et al., 1978), coordination dynamics rationalizes why this is so in terms of the fundamental concept of stability. This issue is not merely semantic but has conceptual and methodological consequences as well. For example, in coordination dynamics loss of stability provides a selection mechanism in the form of bifurcations or phase transitions for the emergence of novel behavioral patterns. Fluctuations or variability in a movement's spatiotemporal structure are not errors or noise in the output of the motor program but rather a fundamental way for the system to test its own stability under the current circumstances. Thus, in coordination dynamics, fluctuations are an essential part of the decision-making mechanism that determines whether the system switches behavior (e.g., Kelso, Scholz, & Schöner, 1986; Schöner, Haken, & Kelso, 1986).

These theoretical differences notwithstanding, a persistent issue in cognitive science has been to define equivalence classes of processes to understand how two different processes may be accomplished by the same higher level mechanism or algorithm. Viewed in the context of perceptual-motor control and learning, this problem reduces to identifying the ensemble of coordinated behaviors that share the same task- or function-specific coordination dynamics. By showing task level transfer, the present study provides an indication of just how abstract and generalizable the coordination dynamics is. It may well be that coordination dynamics and its recent theoretical extensions—for example, those that model observations of human brain and behavioral activity in terms of dynamic neural fields (Fuchs, Jirsa, & Kelso, 2000; Jirsa et al., 1998; Jirsa & Haken, 1996; Jirsa & Kelso, 2000; Kelso, Fuchs, & Jirsa, 1999; Kelso, Jirsa, & Fuchs, 1999)—may mark the genuine arrival of a new kinematics and dynamics for psychological states and cognitive processes (Churchland, 1988). We shall have to wait and see.

<sup>7</sup> See Footnote 3. Such symmetry intuitively reflects the commonsensical notion that arms and legs are bilaterally symmetric.

<sup>8</sup> In fact, there is evidence that learning overcomes initial asymmetries (in the form of a 25° phase lead at 1.0 Hz) between arms and legs (Brown, Carver, & Kelso, 1999).

## References

- Amazeen, E. L., Amazeen, P. G., Treffner, P. J., & Turvey, M. T. (1997). Attention and handedness in bimanual coordination dynamics. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 1552–1560.
- Arbib, M. A. (1990). Programs, schemas, and neural networks for control

- of hand movements: Beyond the RS framework. In M. Jeannerod (Ed.), *Attention and performance XIII* (pp. 111–138). Hillsdale, NJ: Erlbaum.
- Bartlett, F. C. (1932). *Remembering: A study in experimental and social psychology*. Cambridge, England: Cambridge University Press.
- Beek, P. J., Peper, C. E., & Stegeman, D. F. (1995). Dynamical models of movement coordination. *Human Movement Science, 14*, 573–628.
- Bernstein, N. (1967). *The coordination and regulation of movements*. Oxford, England: Pergamon.
- Bressler, S. L., & Kelso, J. A. S. (2001). Cortical coordination dynamics and cognition. *Trends in Cognitive Sciences, 5*, 26–36.
- Brown, L. E., Carver, F., & Kelso, J. A. S. (1999). How learning may overcome intrinsic biophysical differences among individual effectors in a coordination task. *Medicine and Science in Sports and Exercise, 31*(Suppl. 5), S206.
- Carson, R. G., Goodman, D., Kelso, J. A. S., & Elliot, D. (1995). Phase transitions and critical fluctuations in rhythmic coordination of ipsilateral hand and foot. *Journal of Motor Behavior, 27*, 211–224.
- Carson, R. G., & Riek, S. (1998). The influence of joint position on the dynamics of perception–action coupling. *Experimental Brain Research, 121*, 103–114.
- Chen, Y., Ding, M., & Kelso, J. A. S. (1999). Alpha (10 Hz), Beta (20 Hz) and Gamma (40 Hz) networks in the human brain and their functions in a visuomotor coordination task revealed by MEG. *Society for Neuroscience, 25*, 1893.
- Churchland, P. M. (1988). *Matter and consciousness*. Cambridge, MA: MIT Press.
- Edelman, G. M. (1987). *Neural Darwinism*. New York: Basic Books.
- Fodor, J., & Pylyshyn, Z. (1988). Connectionism and cognitive architecture: A critical analysis. *Cognition, 28*, 3–17.
- Fontaine, R. B., Lee, T. D., & Swinnen, S. P. (1997). Learning a new bimanual coordination pattern: Reciprocal influences of intrinsic and to-be-learned patterns. *Canadian Journal of Experimental Psychology, 51*, 1–9.
- Fuchs, A., Jirsa, V. K., & Kelso, J. A. S. (2000). A theory of the relation between human brain activity (MEG) and hand movements. *NeuroImage, 11*, 359–369.
- Fuchs, A., & Kelso, J. A. S. (1994). A theoretical note on models of interlimb coordination. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 1088–1097.
- Fuchs, A., Kelso, J. A. S., & Haken, H. (1992). Phase transitions in the human brain: Spatial mode dynamics. *International Journal of Bifurcation and Chaos, 2*, 917–939.
- Fuchs, A., Mayville, J., Cheyne, D., Weinberg, H., Deecke, L., & Kelso, J. A. S. (2000). Spatiotemporal analysis of neuromagnetic events underlying the emergence of coordinative instabilities. *NeuroImage, 12*, 71–84.
- Georgopoulos, A. P. (1997). Neural networks and motor control. *Neuroscientist, 3*, 52–60.
- Grafton, S. T., Hazeltine, E., & Ivry, R. B. (1998). Abstract and effector-specific representations of motor sequences identified with PET. *Journal of Neuroscience, 18*, 9420–9428.
- Haken, H. (1996). *Principles of brain functioning*. Berlin, Germany: Springer.
- Haken, H., Kelso, J. A. S., & Bunz, H. (1985). A theoretical model of phase transition in human hand movements. *Biological Cybernetics, 51*, 347–356.
- Hebb, D. O. (1949). *The organization of behavior: A neuropsychological theory*. New York: Wiley.
- Imamizu, H., Uno, Y., & Kawato, M. (1998). Adaptive internal model of intrinsic kinematics involved in learning an aiming task. *Journal of Experimental Psychology: Human Perception and Performance, 24*, 812–829.
- Jantzen, K. J., Fuchs, A., Mayville, J. M., & Kelso, J. A. S. (2001). Neuromagnetic activity in alpha and beta bands reflects learning-induced increases in coordinative stability. *Clinical Neurophysiology, 112*, 1685–1697.
- Jeka, J. J., & Kelso, J. A. S. (1995). Manipulating symmetry in the coordination dynamics of human movement. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 360–374.
- Jirsa, V. K., Fuchs, A., & Kelso, J. A. S. (1998). Neural field theory connecting cortical and behavioral dynamics: Bimanual coordination. *Neural Computation, 10*, 2019–2045.
- Jirsa, V. K., & Haken, H. (1996). Field theory of electromagnetic brain activity. *Physical Review Letters, 77*, 960–963.
- Jirsa, V. K., Jantzen, K. J., Fuchs, A., & Kelso, J. A. S. (2002). Spatiotemporal forward solution of the EEG and MEG using network modeling. *IEEE Transactions on Biomedical Imaging, 21*, 1–12.
- Jirsa, V. K., & Kelso, J. A. S. (2000). Spatiotemporal pattern formation in neural systems with heterogeneous connection topologies. *Physical Reviews E, 62*, 8462–8465.
- Jordan, M. (1995). The organization of action sequences: Evidence from a relearning task. *Journal of Motor Behavior, 27*, 179–192.
- Kawato, M., Furawaka, T., & Suzuki, R. (1987). A hierarchical neural network model for the control and learning of voluntary movements. *Biological Cybernetics, 56*, 1–17.
- Keele, S. W., Cohen, A., & Ivry, R. (1990). Motor programs: Concepts and issues. In M. Jeannerod (Ed.), *Attention and performance XIII* (pp. 77–110). Hillsdale, NJ: Erlbaum.
- Keele, S. W., Jennings, P., Jones, S., Caulton, D., & Cohen, A. (1995). On the modularity of sequence representation. *Journal of Motor Behavior, 27*, 17–30.
- Kelso, J. A. S. (1981). On the oscillatory basis of movement. *Bulletin of the Psychonomic Society, 18*, 63.
- Kelso, J. A. S. (1984). Phase transitions and critical behavior in human bimanual coordination. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology, 15*, R1000–R1004.
- Kelso, J. A. S. (1990). Phase transitions: Foundations of behavior. In H. Haken (Ed.), *Synergetics of cognition* (pp. 249–268). Berlin, Germany: Springer.
- Kelso, J. A. S. (1991). Behavioral and neural pattern generation: The concept of neurobehavioral dynamical system (NBDS). In H. P. Koepchen (Ed.), *Cardiorespiratory and motor coordination* (pp. 224–238). Berlin, Germany: Springer-Verlag.
- Kelso, J. A. S. (1994a). Elementary coordination dynamics. In S. Swinnen, H. Heuer, J. Massion, & P. Casaer (Eds.), *Interlimb coordination: Neural, dynamical, and cognitive constraints* (pp. 301–318). San Diego, CA: Academic Press.
- Kelso, J. A. S. (1994b). The informational character of self-organized coordination dynamics. *Human Movement Science, 13*, 393–413.
- Kelso, J. A. S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge, MA: MIT Press. (Paperback published 1997)
- Kelso, J. A. S. (1997). Relative timing in brain and behavior: Some observations about the generalized motor program and self-organized coordination dynamics. *Human Movement Science, 16*, 453–460.
- Kelso, J. A. S. (2000). Principles of dynamic pattern formation and change for a science of human behavior. In L. R. Bergman, R. B. Cairns, L.-G. Nilsson, & L. Nystedt (Eds.), *Developmental science and the holistic approach* (pp. 63–83). Mahwah, NJ: Erlbaum.
- Kelso, J. A. S., Bressler, S. L., Buchanan, S., DeGuzman, G. C., Ding, M., Fuchs, A., & Holroyd, T. (1992). A phase transition in human brain and behavior. *Physics Letters A, 169*, 134–144.
- Kelso, J. A. S., DelColle, J. D., & Schöner, G. S. (1990). Action–perception as a pattern formation process. In M. Jeannerod (Ed.), *Attention and performance XIII* (pp. 139–169). Hillsdale, NJ: Erlbaum.
- Kelso, J. A. S., Fink, P., DeLaplain, C. R., & Carson, R. G. (2001). Haptic information stabilizes and destabilizes coordination dynamics. *Proceedings of the Royal Society of London, Series B, 268*, 1207–1213.
- Kelso, J. A. S., Fuchs, A., & Jirsa, V. K. (1999). Traversing scales of brain

- and behavioral organization: I–III. In C. Uhl (Ed.), *Analysis of neurophysiological brain functioning* (pp. 73–125). Berlin, Germany: Springer.
- Kelso, J. A. S., Fuchs, A., Lancaster, R., Holroyd, T., Cheyne, D., & Weinberg, H. (1998, April 23) Dynamic cortical activity in the human brain reveals motor equivalence. *Nature*, *392*, 814–818.
- Kelso, J. A. S., & Jeka, J. J. (1992). Symmetry breaking dynamics of human multilimb coordination. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 645–668.
- Kelso, J. A. S., Jirsa, V. K., & Fuchs, A. (1999). From level to level in brain and behavior. In M. T. Bachelard & L. T. Wille (Eds.), *Statistical physics on the eve of the 21st century* (pp. 113–130). Singapore: World Scientific.
- Kelso, J. A. S., Scholz, J. P., & Schöner, G. (1986). Non-equilibrium phase transitions in coordinated biological motion: Critical fluctuations. *Physics Letters A*, *118*, 279–284.
- Kelso, J. A. S., Scholz, J. P., & Schöner, G. (1988). Dynamics governs switching among patterns of coordination in biological movement. *Physics Letters A*, *134*, 8–12.
- Kelso, J. A. S., Southard, D., & Goodman, D. (1979, March 9). On the nature of human interlimb coordination. *Science*, *203*, 1029–1031.
- Kelso, J. A. S., & Tuller, B. (1983). “Compensatory articulation” under conditions of reduced afferent information: A dynamic formulation. *Journal of Speech and Hearing Research*, *26*, 217–224.
- Kelso, J. A. S., Tuller, B., Vatikiotis-Bateson, E., & Fowler, C. (1984). Functionally specific articulatory cooperation following jaw perturbations during speech: Evidence for coordinative structures. *Journal of Experimental Psychology: Human Perception and Performance*, *10*, 812–832.
- Lashley, K. S. (1930). Basic neural mechanisms in behavior. *Psychological Review*, *37*, 1–24.
- Latash, M. L. (1999). Mirror writing: Learning, transfer, and implications for internal inverse models. *Journal of Motor Behavior*, *31*, 107–115.
- Lee, T. D. (1998). On the dynamics of motor learning research. *Research Quarterly for Exercise and Sport*, *69*, 334–337.
- Lee, T. D., Swinnen, S. P., & Verschueren, S. (1995). Relative phase alterations during bimanual skill acquisition. *Journal of Motor Behavior*, *27*, 263–274.
- MacNeilage, P. F. (1980). Distinctive properties of speech motor control. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 607–621). Amsterdam: North Holland.
- Marr, D. (1982). *Vision*. San Francisco: Freeman.
- Mayville, J. M., Fuchs, A., Ding, M., Cheyne, D., Deecke, L., & Kelso, J. A. S. (2001). Event-related changes in neuromagnetic activity associated with syncope and synchronization tasks. *Human Brain Mapping*, *14*, 65–80.
- Mitra, S., Amazeen, P., & Turvey, M. T. (1998). Intermediate motor learning as decreasing active (dynamical) degrees of freedom. *Human Movement Science*, *17*, 17–65.
- Peper, C. E., Beek, P. J., & van Wieringen, P. C. W. (1995). Frequency-induced phase transitions in bimanual tapping. *Biological Cybernetics*, *73*, 301–309.
- Raibert, M. H. (1977). *Motor control and learning by the state-space model* (Tech. Rep. No. AI-TR-439). Cambridge: Artificial Intelligence Laboratory, Massachusetts Institute of Technology.
- Rosenbaum, D. A. (1991). *Human motor control*. San Diego, CA: Academic Press.
- Saltzman, E. L., & Kelso, J. A. S. (1987). Skilled actions: A task dynamic approach. *Psychological Review*, *94*, 84–106.
- Schmidt, R. A. (1975). A schema theory of discrete motor skill learning. *Psychological Review*, *82*, 225–260.
- Schmidt, R. A., & Lee, T. (1998). *Motor control and learning: A behavioral emphasis*. Champaign, IL: Human Kinetics.
- Schmidt, R. C., & Turvey, M. T. (1995). Models of interlimb coordination—Equilibria, local analysis, and spectral patterning: Comment on Fuchs and Kelso (1994). *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 432–443.
- Schöner, G., Haken, H., & Kelso, J. A. S. (1986). A stochastic theory of phase transitions in human hand movement. *Biological Cybernetics*, *53*, 247–257.
- Schöner, G., & Kelso, J. A. S. (1988). A synergetic theory of environmentally-specified and learned patterns of movement coordination. *Biological Cybernetics*, *58*, 71–80.
- Schöner, G., Zanone, P.-G., & Kelso, J. A. S. (1992). Learning as change of coordination dynamics: Theory and experiment. *Journal of Motor Behavior*, *24*, 29–48.
- Seal, J., Riehle, A., & Requin, J. (1992). A critical re-examination of the concept of function within the neocortex of the monkey. *Human Movement Science*, *11*, 47–58.
- Sporns, O., & Edelman, G. M. (1993). Solving Bernstein’s problem: A proposal for the development of coordinated movement by selection. *Child Development*, *64*, 960–981.
- Sternad, D., Amazeen, E. L., & Turvey, M. T. (1996). Diffusive, synaptic, and synergetic coupling: An evaluation through inphase and antiphase rhythmic movements. *Journal of Motor Behavior*, *28*, 255–270.
- Swinnen, S. P., Dounskaia, N., Walter, C. B., & Serrien, D. (1997). Preferred and induced coordination modes during the acquisition of bimanual movements with a 2:1 frequency ratio. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 1087–1110.
- Tsutsui, S., Lee, T. D., & Hodges, N. J. (1998). Contextual interference in learning new patterns of bimanual coordination. *Journal of Motor Behavior*, *30*, 151–157.
- Tuller, B., & Kelso, J. A. S. (1989). Environmentally-specified patterns of movement coordination in normal and split-brain patients. *Experimental Brain Research*, *75*, 306–316.
- Turvey, M. T. (1994). From Borelli (1680) and Bell (1826) to the dynamics of action and perception. *Journal of Sports and Exercise Psychology*, *12*, 564–583.
- Turvey, M. T., Shaw, R. E., & Mace, W. M. (1978). Issues in the theory of action: Degrees of freedom, coordinative structures, and coalitions. In J. Requin (Ed.), *Attention and performance VII* (pp. 557–559). Hillsdale, NJ: Erlbaum.
- Wimmers, R. H., Beek, P. J., & van Wieringen, P. C. W. (1992). Phase transitions in rhythmic tracking movements: A case of unilateral coupling. *Human Movement Science*, *11*, 217–226.
- Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3*, 1212–1217.
- Wright, C. E. (1990). Generalized motor programs: Reexamining claims of effector independence in writing. In M. Jeannerod (Ed.), *Attention and performance XIII* (pp. 294–320). Hillsdale, NJ: Erlbaum.
- Yamanishi, J., Kawato, M., & Suzuki, R. (1980). Two coupled oscillators as a model for the coordinated finger tapping of both hands. *Biological Cybernetics*, *37*, 219–225.
- Zanone, P.-G., & Kelso, J. A. S. (1992). Evolution of behavioral attractors with learning: Nonequilibrium phase transitions. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 403–421.
- Zanone, P.-G., & Kelso, J. A. S. (1994). The coordination dynamics of learning. In S. Swinnen, H. Heuer, J. Massion, & P. Casaer (Eds.), *Interlimb coordination: Neural, dynamical, and cognitive constraints* (pp. 462–490). San Diego, CA: Academic Press.
- Zanone, P.-G., & Kelso, J. A. S. (1997). The coordination dynamics of learning and transfer: Collective and component levels. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 1454–1480.

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