

(De)Stabilization of Required and Spontaneous Postural Dynamics With Learning

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The present research examined how learning a new ankle–hip coordination influenced the preexisting postural repertoire. Standing participants learned a new ankle–hip coordination mode (relative phase of 90°). Before and after practice, postural patterns were evaluated in two different tasks. In the required task, specific ankle–hip patterns were requested (12 relative phases in multiples of 30°). In the spontaneous task, participants performed a tracking task in which no instructions about ankle–hip coordination were given. Learning induced changes in both required and spontaneous coordination dynamics. When ankle–hip patterns were required, learning led to improvement and homogenization in performance over the entire postural repertoire. When ankle–hip patterns emerged spontaneously, in-phase and antiphase preexisting patterns destabilized and changed toward the learned pattern of 90°. These findings demonstrate that learning a new coordination pattern can induce modifications of patterns that have not been practiced. The results also suggest that the consequences of learning do not generalize across different types of tasks, even when similar coordination modes are involved. We discuss implications of these findings for the generality of learning mechanisms.

Keywords: motor learning, coordination dynamics, standing posture, ankle–hip relative phase, intention

Motor learning is a remarkable capability that makes it possible for individuals to acquire new coordination modes to optimize their behavior. The potential number of coordinative states that the human body can adopt is virtually infinite. However, typically only a few coordination modes between the body segments are used. Anatomical constraints (e.g., joint properties, muscular elasticity, strength) are not the only limits to body movements. For example, two movements performed by two different segments can be very easy to produce separately and yet prove to be very awkward to produce at the same time. Moreover, the accuracy and stability with which one can perform a given coordination pattern are heavily dependent upon the relative phase (ϕ_{rel}), that is, the

time lag between the movements of the joints. Research has shown that when two joints are oscillating together, they are strongly attracted toward two elementary coordination modes, called in-phase (ϕ_{rel} close to 0°) and antiphase patterns (ϕ_{rel} close to 180°). These two attractive states have been identified for several joint pairings, including bimanual (e.g., Kelso, 1984; Yamanishi, Kawato, & Suzuki, 1980), arm–leg (e.g., Kelso & Jeka, 1992), elbow–wrist (e.g., Kelso, Buchanan, & Wallace, 1991), ankle–wrist (e.g., Carson, Goodman, Kelso, & Elliott, 1995), and ankle–hip (e.g., Bardy, Oullier, Bootsma, & Stoffregen, 2002). Execution of patterns that differ from in-phase and antiphase often requires intensive practice.

Classically, research on motor learning has focused predominantly on the evolution of performance during practice. The main concern has been to find optimal conditions of practice for skill acquisition (e.g., random vs. blocked practice, variable vs. constant practice, optimal delay and frequency in the feedback presentation; e.g., Guadagnoli & Kohl, 2001; Wulf & Schmidt, 1989). In addition, the novelty of the to-be-learned skill was based mainly on the variation of movement parameters (i.e., scaling the timing, the force or the amplitude of an existing movement pattern; for a review, see Schmidt & Lee, 1998).

An alternative approach to motor learning has been developed from concepts relating to dynamical systems. In the dynamical approach to motor learning, skill acquisition is studied in the context of preexisting coordination tendencies (e.g., Schöner, 1989; Schöner & Kelso, 1988; Schöner, Zanone, & Kelso, 1992; Zanone & Kelso, 1992, 1994). A central idea of this view is that the learning process interacts with the preexisting behavioral rep-

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ertoire: Initial coordination tendencies both affect and are affected by the acquisition of a new coordination pattern. In this view, learning is not interpreted as the simple addition of the new mode to the preexisting capabilities but, rather, as a reorganization of the entire behavioral repertoire. A strong prediction of this approach is that learning-induced modification of the behavioral repertoire can lead to the destabilization of preexisting skills (e.g., Zanone & Kelso, 1994). In other words, coordination modes that were stable prior to learning may be less stable and less accurate after the acquisition of a new pattern.

The idea of an interaction between old and new skills originated in studies of verbal, cognitive, and motor learning that predate the application of dynamical systems theories to behavior. In particular, the destabilization hypothesis can be connected to the classical concept of retroactive interference, which refers to the negative influence of recent learning on the performance of a previously learned task (e.g., Anderson, 1995). In classical studies, participants learn a task A, then a task B, and are finally tested again on task A or B. Retroactive interference is revealed when the recently learned task (task B) impairs performance on the previously learned task (task A). Proactive interference is observed when prior learning (task A) inhibits recall of later learning (task B).¹ Because interference is expected to occur during the period in which new skills are being consolidated, interference is usually studied on short time-scales, with delays ranging from a few minutes to 1 day between learning the two tasks (e.g., Brashers-Krug, Shadmehr, & Bizzi, 1996; Goedert & Willingham, 2002; Krakauer, Ghez, & Ghilardi, 2005; Shadmehr & Brashers-Krug, 1997; Tong, Wolpert, & Flanagan, 2005; for a recent review, see Robertson, Pascual-Leone, & Miall, 2004). In contrast, the destabilization hypothesis predicts that a newly learned pattern can disrupt preferential coordination tendencies; that is, behaviors that have not been learned recently but that have been acquired years before. The difference does not rest only on the time scale on which the interaction between old and new skills is supposed to occur. Contrary to the traditional literature, the dynamical approach makes precise predictions about which motor skills will be affected by the new learning and how the entire postural repertoire will be altered (for a detailed description, see Zanone & Kelso, 1994). To summarize, destabilization can be considered as forgetting by interference (Kostrubiec & Zanone, 2002; Schöner et al., 1992) but implies more specific predictions. Finally, it must be stressed that prominent theories of motor learning from the traditional approach do not incorporate interference or impairment of preexisting skills due to learning (e.g., Adams, 1971; Logan, 1988; Schmidt, 1975; Schmidt & Lee, 1998).

The destabilization hypothesis has been supported in several studies on bimanual coordination: Zanone and Kelso have demonstrated that the antiphase pattern could be destabilized by the acquisition of a new relative phase (Kelso & Zanone, 2002; Zanone & Kelso, 1992, 1997). However, these findings have been challenged or rejected in several other studies (e.g., Fontaine, Lee, & Swinnen, 1997; Lee, Swinnen, & Verschueren, 1995; Smethurst & Carson, 2001; Swinnen, Lee, Verschueren, Serrien, & Bogaerds, 1997). In addition to the destabilization principle, the claim that the entire behavioral repertoire is modified by the acquisition of a new pattern implies that positive transfer can occur between the learned mode and other coordination modes. Consistent with this hypothesis, learning one bimanual pattern (e.g., $\phi_{rel} = 90^\circ$) is

associated with stabilization of its symmetric pattern (i.e., $360^\circ - \phi_{rel}$; in this case, $\phi_{rel,sym} = 270^\circ$), even though the symmetric pattern is not practiced (Smethurst & Carson, 2001; Zanone & Kelso, 1997).

The destabilization hypothesis is supposed to apply to a wide range of situations (e.g., Schöner & Kelso, 1988). In the existing literature, however, empirical analyses of this hypothesis have been focused almost exclusively on bimanual coordination (movements of the right and left fingers, wrists, or arms). In Faugloire, Bardy, and Stoffregen (2006), we studied the reciprocal influences of preexisting coordination tendencies and learning for the ankle–hip system during stance. This study extended the scope of application of the dynamical approach to an effector system presenting specific characteristics. In fact, the ankle–hip system differs from bimanual systems in several ways: It involves the whole body, with coupled joints (the ankle position is affected by the hip position, and vice versa), and nonhomologous segments (i.e., it is an asymmetric system). Our study consisted of four parts. First, to identify preexisting postural patterns and assess their stability, standing participants faced a square target that expanded and contracted on a screen to simulate fore–aft movements of this target. Participants were asked to maintain a constant distance between their head and the target, moving the head forward when the target contracted and backward when the target expanded (pretest). In accordance with several previous studies on postural coordination dynamics (Bardy, Marin, Stoffregen, & Bootsma, 1999; Marin, Bardy, Baumberger, Flückiger, & Stoffregen, 1999; Oullier, Bardy, Stoffregen, & Bootsma, 2002; for a review, see Bardy, 2004), we observed two ankle–hip coordination modes. Targets moving with low frequency or amplitude tended to elicit an in-phase mode,² with the ankles leading the hips with a ϕ_{rel} of about 20° . Targets moving with large amplitude or high frequency tended to elicit an antiphase mode, with ϕ_{rel} close to 180° . Second, participants attempted to learn a nonspontaneous ankle–hip relative phase of 135° over the course of 50 practice trials (each comprising 10 cycles), with performance feed-back provided after every third trial. In the third part of the design, participants performed again the initial tracking task (posttest). In accordance with the predictions of the dynamical approach to motor learning (e.g., Zanone & Kelso, 1994), the comparison between pretest and

¹ Proactive interference is similar to, and sometimes merged with, the concept of negative transfer. Proactive interference refers to the situation in which previous learning accelerates the forgetting of new learning. Negative transfer refers to the situation in which previous learning impedes the new learning. Some researchers may find a correspondence between these definitions and the competition principle defined by the dynamical approach (for an extensive presentation of the competition principle, see Zanone & Kelso, 1994). However, the competition principle specifically concerns the initial coordination tendencies and the pattern requested by the task. It also supposes a bifurcation in the coordination dynamics. Experimental results on the competition principle have been reported for bimanual coordination (e.g., Lee, Swinnen, & Verschueren, 1995; Swinnen, Lee, Verschueren, Serrien, & Bogaerds, 1997; Zanone & Kelso, 1992) and for postural coordination (Faugloire, Bardy, & Stoffregen, 2006).

² The departure from pure in-phase motion ($\phi_{rel} = 0^\circ$) found for the ankle–hip system has also been found for other asymmetric systems (i.e., with different eigenfrequencies of the limbs; e.g., Jeka & Kelso, 1995; Riley, Santana, & Turvey, 2001; Sternad, Amazeen, & Turvey, 1996).

posttest revealed that learning 135° induced either a change in the in-phase and antiphase patterns toward the learned pattern or a loss of stability of these preexisting patterns. Finally, a retention test conducted 1 week later showed that the effects of learning on the spontaneous coordination dynamics were durable.

In bimanual studies that have examined relations between learning and initial coordination tendencies, coordination modes have always been *required*; that is, participants have been instructed to produce a particular mode. In most experiments, not only was the requested relative phase explained and demonstrated prior to participants' attempts to perform it (e.g., Amazeen, 2002; Fontaine et al., 1997) but the actual performance was also paced continuously using a metronome (e.g., Smethurst & Carson, 2001; Zanone & Kelso, 1992, 1997) or using real-time feedback that indicated the discrepancy between the actual pattern and the requested pattern (e.g., Hurley & Lee, 2006; Lee et al., 1995; Swinnen et al., 1997; Wenderoth, Bock, & Krohn, 2002). By contrast, in Faugloire et al. (2006), we evaluated the influence of learning on coordination modes that emerged during a supracoordinative task; that is, a task for which the goal is not to produce a specific coordination pattern. Participants were asked to move their heads in synchrony with the visual target but were given no instructions about how to move their hips and ankles while performing the tracking task. In principle, participants might have adopted any ankle–hip pattern to achieve the task. We call the coordination patterns emerging from this task *spontaneous* patterns, as opposed to the coordination modes that are required. We regard spontaneous coordination as being important because it may be more representative of daily life. Outside the laboratory, we rarely attempt to perform coordination modes for their own sake. Rather, coordination modes emerge in the context of goals that are unrelated to the coordination pattern or the shape of movement. Examples include grasping an object, reading while standing in a vehicle, and running as fast as possible. Nevertheless, requiring particular coordination modes is scientifically interesting because it permits researchers (a) to evaluate the performance of specific coordination modes before and after learning and (b) to standardize testing procedures so as to assess the generality of the principles underlying motor learning for different effector systems.

As noted above, the dynamical perspective on motor learning predicts that learning will tend to reconfigure the entire layout of the coordination dynamics. To fully evaluate this hypothesis, it is necessary to identify the whole behavioral repertoire. A scanning procedure can be used to achieve this end (Zanone & Kelso, 1992, 1994). As used by Tuller and Kelso (1989) and Yamanishi et al. (1980), the scanning procedure consists in asking the participants to produce successively several relative phase patterns that differ by a small interval. Such a procedure combined with online visual feedback (ankle movements plotted as a function of hip movements) has proven to be an efficient method for eliciting specific ankle–hip relative phases (Faugloire, Bardy, Merhi, & Stoffregen, 2005). In the present experiment, we used the same scanning procedure to explore the postural coordinative landscape before and after the learning process.

In our previous study (Faugloire et al., 2006), we found that learning a new ankle–hip relative phase induced modification of the spontaneous in-phase and antiphase modes in the direction of the newly learned pattern. This result is consistent with, but does not directly demonstrate, the prediction of the dynamical approach

stating that learning a new pattern affects the entire repertoire of coordination patterns. In addition, even if our previous study on the postural system presented some similarities with studies on bimanual coordination, the nature of the task used for those two effector systems was qualitatively different (spontaneous vs. required). Thus, we could not evaluate the general nature of learning mechanisms and consequences across different sets of effectors. In the present study, we sought (a) to specifically address the destabilization hypothesis for the ankle–hip system, (b) to evaluate the generality of learning mechanisms over different sets of effectors by collecting postural data that would be comparable to previous studies of bimanual coordination, and (c) to estimate whether the consequences of learning would be influenced by whether or not performers deliberately attempted to execute particular coordination patterns, as such. To address these questions, we tested spontaneous patterns (with the tracking task) and required patterns (with the scanning procedure) before and after participants attempted to learn an ankle–hip relative phase of 90°. From theoretical predictions (e.g., Zanone & Kelso, 1994), previous results on spontaneous postural modes (Faugloire et al., 2006) and research on required bimanual modes (e.g., Kelso & Zanone, 2002; Zanone & Kelso, 1992, 1997), we expected a change in the attractor landscape in the direction of the new pattern. In the scanning procedure, the effect of this change would be that the learned pattern would be performed for a large range of required patterns, which could lead to the destabilization of preexisting ankle–hip attractors. In the context of spontaneous patterns, one consequence of such a change would be that the newly learned pattern would emerge during the tracking task, instead of the in-phase and antiphase patterns.

Method

Participants

Nineteen women and men volunteered to participate in the experiment. All had normal or corrected-to-normal vision, reported no balance disorder, and were naïve as to the purposes of the experiment. Each participant signed an informed consent statement after receiving oral and written descriptions of the procedure. Twelve participants, 6 women and 6 men aged between 20 and 46 years ($M = 26.83$, $SD = 8.53$), constituted the experimental group. Their mean height was 173.42 cm ($SD = 10.41$), and their mean weight was 68.58 kg ($SD = 12.48$). Seven additional participants, 3 women and 4 men aged between 22 and 36 years ($M = 28.14$, $SD = 5.52$), constituted the control group. Their mean height was 169.29 cm ($SD = 8.81$), and their mean weight was 67.21 kg ($SD = 13.69$). These participants were not exposed to the learning session.

Task and Apparatus

Participants stood barefoot, with their feet a comfortable distance apart and their hands clasped behind their back. We recorded angular positions of the ankles and hips using two electrogoniometers connected to a DataLINK unit (Biometrics, Inc., Gwent, UK). The electrogoniometers were attached to the left ankle (extending from the second metatarsus to the lower third of the tibia) and the left hip (extending from the greater trochanter to the iliac crest);

each was sampled at 50 Hz. A contact switch placed under the participant's left foot was used to detect any loss of contact (either toes or heels leaving the floor). When contact was lost more than two times within a trial, the trial was canceled and repeated. Participants were instructed to keep their legs straight, without flexion of the knees, during the entire experiment.

Learning session and scanning procedure. Participants stood 1.50 m from a large screen (3 m horizontal \times 2 m vertical). The screen displayed an ankle–hip position plane (Lissajous figure) of 0.82 m \times 0.82 m for which the abscissa and the ordinate axes corresponded to the angular position of the hip and ankle, respectively. This display consisted of a trajectory whose shape and direction indicated the required relative phase. In a Lissajous figure, each absolute value of relative phase corresponds to an elliptical shape that can range from a circle to a line segment. The distinction between two symmetric patterns, for example, 135° and -135° (which is equal to 225°), is given by the direction of movement along the shape: clockwise for values in the interval $]0^\circ, 180^\circ[$ and counter clockwise for values in the interval $]180^\circ, 360^\circ[$.

A pacesetter (a dot) moved along the ellipse (velocity = 0.2 Hz) to indicate the direction and the required velocity of the participant's movements. Within the Lissajous plot, data from the ankle and hip electrogoniometers were presented in real time (Figure 1). The ankle–hip data persisted on the screen, forming a line that was reset at the end of each cycle. Thus, participants could see their actual behavior (real-time data) in relation to the behavior that they had been asked to produce (the required pattern). In particular, they had feedback about the moment-to-moment discrepancy between the coordination actually performed and the required pattern. For the learning session (experimental group only), we required a relative phase of 90° . For the scanning procedure (experimental and control groups), we required 12 different relative phases from 0° to 330° , in multiples of 30° .

The shape of the display indicated the required value of ankle–hip relative phase. The required amplitude of hip and ankle rotations was indicated by the size of the display. For each value of required relative phases, the required rotations were 8° for the hips and 8° for the ankles. To ensure that stance could be maintained at

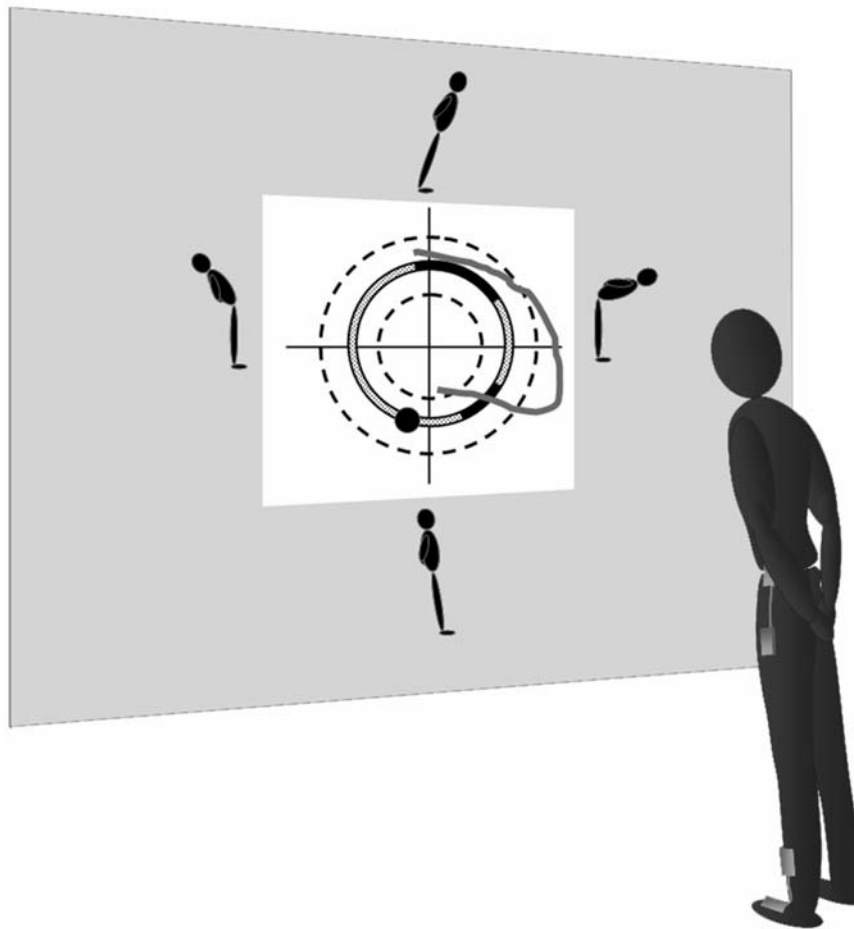


Figure 1. Experimental task in the scanning procedure and the learning session. Participants were asked to match their ankle–hip coordination (grey line) with the required pattern (ellipse with a dotted background), at the frequency imposed by the pacesetter (black circle). The color of the required pattern changed when the actual ankle–hip configuration was within the tolerance zone (dashed ellipses). In this example, the required relative phase corresponds to 90° if the pacesetter runs clockwise and to 270° if the pacesetter runs counter-clockwise.

Table 1
Procedure Followed by the Experimental Group

Activity	Day					
	1	2	3	4	5	
Test session	Pretest Tracking: 3 × 2 amplitudes Scanning: 3 × 12 patterns	Learning session	Learning session	Learning session	Posttest Tracking: 3 × 2 amplitudes Scanning: 3 × 12 patterns	Retention test Tracking: 3 × 2 amplitudes Scanning: 3 × 12 patterns
Learning session		25 trials	25 trials	10 trials		

these amplitudes for each of the coordination modes, we computed the extreme positions of the center of mass for the different ankle–hip relative phases in static conditions,³ estimating the length and mass of segments from Winter (1990) for individuals ranging from 155 cm to 190 cm and from 50 kg to 95 kg. We instructed participants to give priority to the shape of the pattern to follow rather than its position or its size in the ankle–hip space. This ensured that participants primarily focused on the relative phase (rather than, e.g., movement amplitude or position offset).

A tolerance region was shown around the target ellipse (Figure 1). When ankle–hip coordination was outside the tolerance region, the color of the target pattern was red. When ankle–hip coordination was within this region, the color of the required pattern changed from red to blue, indicating that the actual mode produced was close to the required mode. For all patterns except 0° and 180°, the target pattern described an ellipse in the display. For these patterns, we defined the tolerance region as ± 35% of the required amplitude, creating a larger ellipse around the pattern to follow and a smaller ellipse inside the pattern (see Figure 1 for an illustration on the 90° pattern). For required relative phase values of 0° or 180°, the pattern to follow corresponded to a straight diagonal line in the display. In this case, a mere change in amplitude would not have allowed deviations around the shape because it would have only influenced the length of the line. For these two patterns, the tolerance zone was therefore fixed at ± 20° of relative phase (corresponding to a thin ellipse around the straight line to follow) with an amplitude 35% higher than the required amplitude.

We began by familiarizing participants with the display and its relation to their movements. The experimenter explained the principle of the Lissajous figure, after which participants performed two familiarization tasks. First, participants executed 10 oscillations of the hips with fixed ankles (i.e., horizontal movements on the screen), and 10 oscillations of the ankles with fixed hips (i.e., vertical movements on the screen). Next, participants were asked to move their body so as to produce a rectangular shape on the screen, going back over each segment three times before tracing the next segment. Ankle and hip data collected during the familiarization period were used to offset the Lissajous figures so that participants could comfortably move in the ankle–hip space.

Tracking task. For the experimental group, we used a tracking task to assess spontaneous patterns of ankle–hip coordination. In this task, the display consisted of a multicolored, square target (54 cm × 54 cm; 20.6° × 20.6°) on a black background (which replaced the Lissajous figure). Expansion and contraction of this target on the screen simulated fore–aft oscillation of a physical

object along the line of sight. Participants were instructed to keep a constant distance between their head and the apparent position of the target. Previous studies revealed that, as a function of conditions (e.g., the amplitude and frequency of target oscillation), participants exhibited in-phase or antiphase coordination of the hips and ankles in performing this task (e.g., Bardy et al., 1999, 2002). To standardize the velocity of movement for the scanning and the tracking tasks, we fixed the frequency of target oscillation at 0.2 Hz (i.e., the frequency of the pacesetter on the Lissajous figure in the learning and scanning procedures). Each participant was tested with two target amplitudes: small (8 cm peak-to-peak, or from 20.0° to 21.2° visual angle) and large (25 cm peak-to-peak, or from 18.9° to 22.3° visual angle). In earlier work using targets oscillating at 0.2 Hz, in-phase ankle–hip coordination was observed for target amplitudes below 14 cm, and antiphase coordination was observed when target amplitudes exceeded 18 cm (Bardy et al., 1999). In the tracking task, displacement of the head was measured with an electromagnetic tracking system (Flock of Birds, Ascension Technologies, Inc., Burlington, VT), which was sampled at 50 Hz. The sensor was fixed on the participants' head with a headband.

Procedure

For the experimental group, the experiment was conducted over 5 days, with sessions lasting from 35 to 60 min each day. The sequence of sessions is illustrated in Table 1. Days 1–4 were consecutive, with Day 5 following 1 week after Day 4. Day 1 included the familiarization period and the pretest. In the pretest, participants performed three trials with the target oscillating at 8 cm and three with the target oscillating at 25 cm. Each trial comprised eight cycles of target oscillation. After the familiarization period with the Lissajous display, we conducted the scanning session. Scanning consisted of three trials at each of the 12 required coordination patterns (eight cycles per trial). On Day 2, participants completed the first learning session attempting to learn the 90° pattern. This learning session consisted of 25 trials (eight cycles per trial) with the real-time visual feedback in the Lissajous figure. Day 3 was identical to Day 2, with 25 practice trials of the 90° relative phase. On Day 4, participants began with a final 10 trials of the 90° relative phase. These trials were followed by the

³ The details of the calculation can be found in the appendix of Bardy et al. (1999).

posttest, which included the tracking task (three trials for each amplitude of target oscillation) and the scanning session (three trials for each of the 12 required patterns). Day 5 (1 week later) constituted the retention test, and comprised the same tasks and the same number of trials as pre- and posttests (see Table 1). To minimize neighboring and hysteresis effects in the scanning procedure, we randomized the order of presentation of the 12 required relative phase patterns for each participant and each test session.

For the control group, the experiment was conducted over 2 days, the first session lasting 60 min and the second, 45 min. Our main purpose in using the control group was to determine whether the scanning procedure itself would lead to differences between the pretest and posttest. Participants from the control group were tested twice on the scanning procedure, with the same time interval as between the pretest and the posttest of the experimental group but without the intervening attempt to learn 90°. On the first day, control group participants performed the familiarization tasks on the Lissajous display before being tested on the scanning procedure (three trials at each of the 12 required coordination patterns, with eight cycles per trial). Three days later (corresponding to the delay between the pretest and posttest sessions of the experimental group), they completed the scanning procedure again. The order of presentation of the 12 required relative phase patterns was randomized for each participant and each test session.

Data Analysis

Prior to any computation, the electrogoniometer data were filtered with a recursive, low-pass filter, with a cutoff frequency of 2 Hz. We operationally defined ankle–hip coordination as the relative phase between ankle and hip rotations, ϕ_{rel} , and we defined the within-participants stability of ankle–hip coordination as the standard deviation of ϕ_{rel} ($SD\phi_{rel}$). We computed the point estimate of ϕ_{rel} for each trial, using the flexion peak of ankle and hip for each movement cycle. A relative phase value between 0° and 180° indicates that the ankles were leading the hips. For each trial, we computed $SD\phi_{rel}$ from the eight relative phase values per trial, in a circular fashion (Batschelet, 1981). For the learning period and the scanning procedure, we computed two additional dependent variables: the constant error (CE) of ϕ_{rel} , indicating the direction of the error, and the absolute error (AE) of ϕ_{rel} , indicating the magnitude of the error. We calculated CE for each movement cycle as the difference between the produced relative phase and the intended one. AE corresponded to the absolute value of CE for each movement cycle. For the learning period and the scanning procedure, we operationalized performance in terms of CE , AE , and $SD\phi_{rel}$, which we refer to as performance indicators. Finally, for the tracking task, we computed the gain of head movements relative to the amplitude of target oscillations. We computed the gain at each oscillation cycle as the ratio between the amplitude of the head (maximum position minus minimum position) and the amplitude of the target (maximum position minus minimum position).

Because relative phase and its derivatives ($SD\phi_{rel}$, CE , and AE) are circular variables (which implies that 0° = 360°), we used standard circular statistics to compute means, standard deviations, and 95% confidence intervals for these variables (Batschelet, 1981, pp. 7–9, 33–35, 85–87; Mardia & Jupp, 2000, pp. 15–20). Mean ϕ_{rel} , mean CE , mean AE , and 95% confidence intervals were

calculated over all cycle values. Mean $SD\phi_{rel}$ was calculated over the trial values. Rayleigh uniformity tests conducted on ϕ_{rel} values were used to determine whether postural patterns were significantly clustered around a mean value. Watson-Williams F tests, the circular equivalent of a one-factor analysis of variance (ANOVA), were used to compare ϕ_{rel} values for the spontaneous patterns (i.e., in the tracking task). Because no specific pattern of ankle–hip coordination was required in the tracking task, ϕ_{rel} values could be distributed over the entire trigonometric circle (0° through 360°).⁴

When the range of the distribution was less than 180° (which was necessarily the case for the dependent variables computed from the learning and scanning periods), the difference between circular and linear methods was negligible. Accordingly, we conducted ANOVAs on $SD\phi_{rel}$, CE , and AE , so as to be able to evaluate multiple main effects and interactions. The p value levels were corrected for possible deviations from sphericity using the Huynh-Feldt epsilon (ϵ). We report the uncorrected degrees of freedom, the ϵ value, and the p value according to the corrected degrees of freedom. For each significant effect ($p < .05$), we estimated effect size using generalized eta squared,⁵ η_G^2 . Interindividual differences are likely to occur in spontaneous patterns and in learning. For this reason, in addition to our overall analyses, we separately analyzed data for each participant. These individual analyses ensured that the general tendencies observed faithfully expressed individual behaviors.

Results

We first present the results of the experimental group for the pretest, learning, and posttest periods. Next, we report the results of the control group to ensure that the observed effects in the experimental group were due to the practice of the 90° ankle–hip pattern.

Pretest Period

Spontaneous coordination modes. We began by analyzing ankle–hip coordination of the experimental group in the pretest tracking task. Individual mean relative phases at pretest are presented in Table 2 for the two amplitudes of target oscillation.

When the amplitude of target oscillation was 8 cm, all but one of the 12 participants exhibited a significantly directional (i.e., not uniform) distribution of ϕ_{rel} (Rayleigh uniformity tests, $p < .05$). The 12th participant (Participant 11) exhibited no identifiable pattern of ϕ_{rel} . For 7 participants, the ankle–hip pattern was close to in-phase, with individual means of ϕ_{rel} from -11.07° to 59.10° . The group mean relative phase for these 7 participants was 28.81° ($SD\phi_{rel} = 41.18^\circ$). Four other participants produced an antiphase

⁴ Motivation for the use of circular statistics (both descriptive and inferential) with circular variables such as ϕ_{rel} can be found in Batschelet (1981) and Mardia and Jupp (2000).

⁵ Generalized eta squared is the effect size statistic recommended for repeated measures designs because, unlike other measures of effect size, it is comparable across studies with different designs (Bakeman, 2005; Olejnik & Algina, 2003). Note that η_G^2 is always less than partial eta squared for repeated measures ANOVAs and less than eta squared for repeated measures ANOVAs with more than one factor (e.g., Bakeman, 2005).

Table 2

Ankle–Hip Coordination in the Tracking Task, for Individual Participants of the Experimental Group: Mean Relative Phase (ϕ_{rel} ; Standard Deviation in Parentheses)

Participant	Target oscillation amplitude = 8 cm			Target oscillation amplitude = 25 cm		
	Pretest	Posttest	Retention test	Pretest	Posttest	Retention test
1	55.78 (26.84)	91.38 ^a (44.80)	107.63 ^a (26.91)	54.08 (21.94)	108.22 ^a (13.65)	129.94 ^a (24.66)
2	40.46 (38.17)	146.05 ^a (16.74)	104.36 ^a (37.23)	169.24 (9.54)	103.62 ^a (32.37)	166.53 (8.10)
3	-5.46 (30.03)	186.70 ^a (17.08)	189.60 ^a (10.34)	176.47 (13.98)	172.30 (8.94)	182.96 (7.86)
4	45.06 (44.82)	71.73 ^a (13.39)	109.57 ^a (42.01)	190.28 (18.78)	139.63 ^a (17.61)	146.57 ^a (31.72)
5	59.10 (50.00)	32.55 (36.61)	123.04 ^a (22.18)	37.50 (48.72)	71.34 ^a (28.23)	67.40 ^a (26.16)
6	175.19 (35.46)	172.99 (17.38)	190.12 (16.61)	180.44 (16.55)	175.91 (14.18)	177.24 (10.94)
7	191.37 (29.97)	172.14 (14.69)	164.41 (12.85)	175.51 (18.96)	174.16 (7.19)	181.96 (4.11)
8	199.31 (15.01)	190.66 (12.38)	192.27 (12.05)	187.04 (13.77)	104.09 ^a (48.82)	194.28 (8.27)
9	184.55 (7.46)	185.32 (6.89)	182.43 (9.90)	182.34 (8.79)	143.20 ^a (7.37)	142.37 ^a (5.87)
10	-11.07 (50.43)	14.46 (27.34)	254.24 ^a (26.35)	39.83 (23.72)	1.61 ^a (20.07)	-2.07 ^a (42.37)
11	— ^b	72.93 (53.80)	86.84 (37.03)	169.93 (33.14)	89.37 ^a (33.02)	85.23 ^a (24.78)
12	3.95 (47.93)	55.08 ^a (38.93)	56.55 ^a (23.66)	157.00 (32.53)	101.79 ^a (28.33)	87.60 ^a (40.84)

Note: Bold face indicates an in-phase pattern during the pretest. ^aSignificant change from pretest, $p < .05$. ^bRayleigh, *ns*.

pattern with individual mean ϕ_{rel} from 175.19° to 201.37°. The group mean relative phase for these 4 participants was 186.73° ($SD\phi_{rel} = 21.97^\circ$).

When the amplitude of target oscillation was 25 cm, each participant exhibited a directional distribution of ϕ_{rel} (Rayleigh uniformity tests, $p < .05$). Of the 7 participants who presented an in-phase pattern when the amplitude of target oscillation was 8 cm, 3 also presented an in-phase pattern when the amplitude of target oscillation was 25 cm. For these 3 participants, individual means of relative phase ranged from 37.50° to 54.08°; the mean relative phase of the group was 44.28° ($SD\phi_{rel} = 30.94^\circ$). The other 9 participants produced an antiphase coordination mode. Their individual means of relative phase ranged from 169.24° to 190.28°, and the mean relative phase of the group was 176.76° ($SD\phi_{rel} = 18.35^\circ$).

Required coordination modes. The mean values (collapsed across participants of the experimental group) of constant error, absolute error, and standard deviation of relative phase at pretest are illustrated with the dark curves in Figure 2. For the pretest, we conducted one-way ANOVAs with repeated measures (12 required patterns, collapsed across trials-per-pattern) on the performance indicators (CE , AE , and $SD\phi_{rel}$). We found significant effects of pattern on CE , $F(11, 121) = 4.48$, $\epsilon = .43$, $p = .002$, $\eta_G^2 = .27$, on AE , $F(11, 121) = 7.03$, $\epsilon = .68$, $p < .001$, $\eta_G^2 = .29$, and on $SD\phi_{rel}$, $F(11, 121) = 4.08$, $\epsilon = .62$, $p = .001$, $\eta_G^2 = .20$. These analyses reveal that both the accuracy and stability of coordination differed across required patterns of relative phase. The constant error exhibits a negative slope crossing the abscissa for a required pattern of 180° (dark curve in Figure 2A). This negative slope shows that CE was minimal when the antiphase pattern was required; and, more important, it shows that the 180° required relative phase attracted neighboring patterns. The negative CE for required patterns greater than 180° and the positive CE for requested patterns less than 180° indicate that participants tended to produce 180° in every condition, regardless of the required pattern. Across values of required relative phase, AE and $SD\phi_{rel}$ exhibited similar characteristics. When required relative phase was in the range 180° to 210°, the magnitude of error and the variability of ϕ_{rel} were minimal. Error and variability tended to increase (i.e.,

performance was poorer) as required relative phases moved away from the 180° to 210° range.

There were individual differences in the strength of attraction to the antiphase pattern. The mean values presented by the dark curves in Figure 2 accurately express the behavior of 5 participants. Each of these 5 participants exhibited negative slope of CE , with the CE curve crossing 0 at around 180° of required ϕ_{rel} . For each of these 5 participants, AE and $SD\phi_{rel}$ showed a V shape with minimal values around 180° to 210°. Four other participants also exhibited a negative slope of CE , but with a smaller slope. For these participants, CE was close to 0 for several values of required relative phase in the range 60° to 210°; over the same range, AE was also minimal and undifferentiated. These 4 participants were accurate for patterns close to antiphase but also for a relatively wide range of required relative phases. Finally, for the 3 remaining participants, CE was low for almost all required patterns and AE varied erratically without any preferential pattern. In contrast to spontaneous patterns observed in the tracking task, in the scanning procedure no participant exhibited an accurate and stable in-phase pattern when relative phases around 0° to 60° were required. Specificity of coordination dynamics to the nature of the task will be addressed in the Discussion section.

Learning Period

Learning trials were grouped into blocks of five. Figure 3 presents group mean values of CE , AE , and $SD\phi_{rel}$ when participants attempted to move with ankle–hip relative phase of 90°. The figure includes the 12 blocks of practice trials in the learning period and the 90° condition from the scanning procedure performed during the retention test. Repeated measures ANOVAs (12 blocks of practice) revealed significant improvements in CE , $F(11, 121) = 3.68$, $\epsilon = .34$, $p < .02$, $\eta_G^2 = .12$, AE , $F(11, 121) = 5.05$, $\epsilon = .23$, $p < .01$, $\eta_G^2 = .14$, and $SD\phi_{rel}$, $F(11, 121) = 6.32$, $\epsilon = .68$, $p < .001$, $\eta_G^2 = .19$. Figure 3 indicates that the performance reached at the end of the practice period was maintained 1 week after practice (retention test). Statistical analyses including the retention test are presented in the next section.

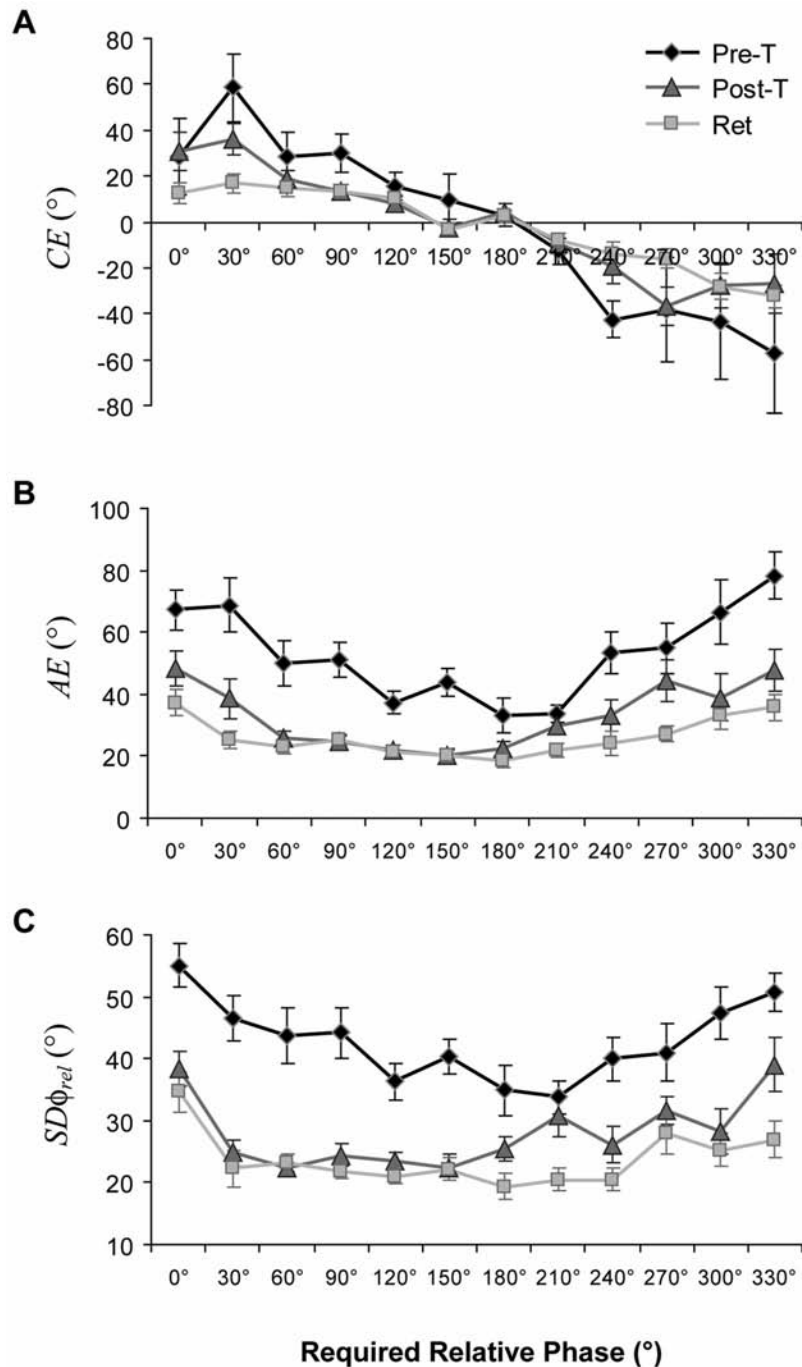


Figure 2. Mean values of the performance indicators for each required relative phase at pretest, posttest, and retention test for the experimental group. A: Constant error, CE , indicating the direction of error. B: Absolute error, AE , indicating the magnitude of error. C: Standard deviation of relative phase, $SD\phi_{rel}$, indicating the stability of the performed pattern. The error bars represent standard error (between-subjects variability).

Test Periods: Consequences of Learning 90°

Consequences of learning on spontaneous patterns (tracking task). For group analyses, we included only those participants who produced an in-phase pattern when the amplitude of target

motion was 8 cm ($n = 7$), and an antiphase pattern when the amplitude of target motion was 25 cm ($n = 9$). Data from those participants are presented in Figure 4. Watson-Williams tests (paired comparisons) revealed that learning involved a modification of the spontaneous patterns in the direction of the learned

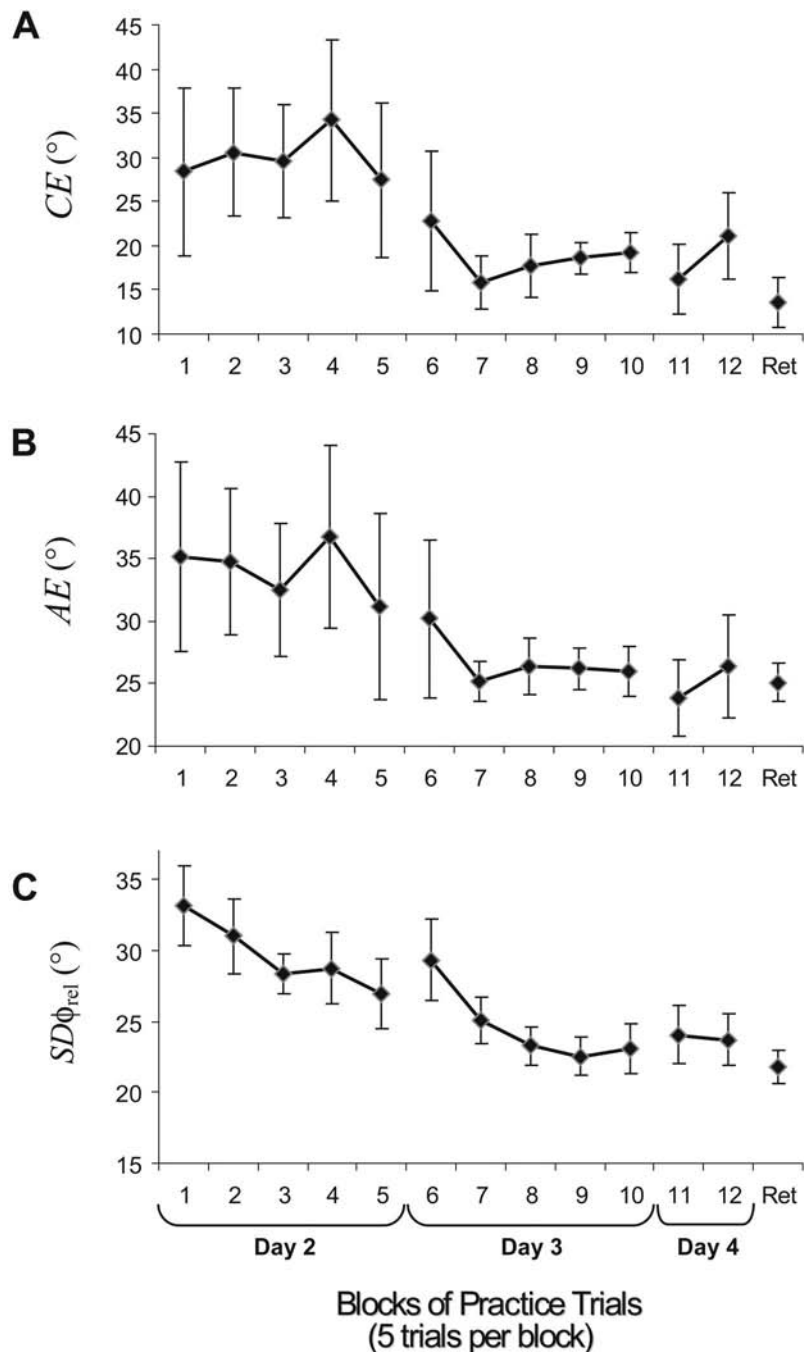


Figure 3. Evolution of (A) mean constant error, CE , (B) mean absolute error, AE , and (C) mean standard deviation of relative phase, $SD\phi_{rel}$, during the learning period of 90° for the experimental group. Each block of practice included five trials and the retention test (Ret) included three trials. The error bars represent standard error (between-subjects variability).

pattern. When the amplitude of target oscillation was 8 cm, the mean relative phase was 28.81° at pretest ($SD\phi_{rel} = 41.17^\circ$), 99.39° at posttest ($SD\phi_{rel} = 27.82^\circ$), and 127.63° at the retention test ($SD\phi_{rel} = 26.84^\circ$); each of these differed from both of the others, all $F_s(1, 292) > 10.62$, $ps < .01$. When the amplitude of target oscillation was 25 cm, the mean relative phase was 176.76°

at pretest ($SD\phi_{rel} = 18.35^\circ$), 142.73° at posttest ($SD\phi_{rel} = 21.88^\circ$), and 162.85° at the retention test ($SD\phi_{rel} = 15.69^\circ$); each of these differed from both of the others, all $F_s(1, 376) > 12.13$, $ps < .001$. For individuals in both the in-phase and antiphase groups, within-participants $SD\phi_{rel}$ was low or tended to decrease across test sessions (see $SD\phi_{rel}$ values above), but between-

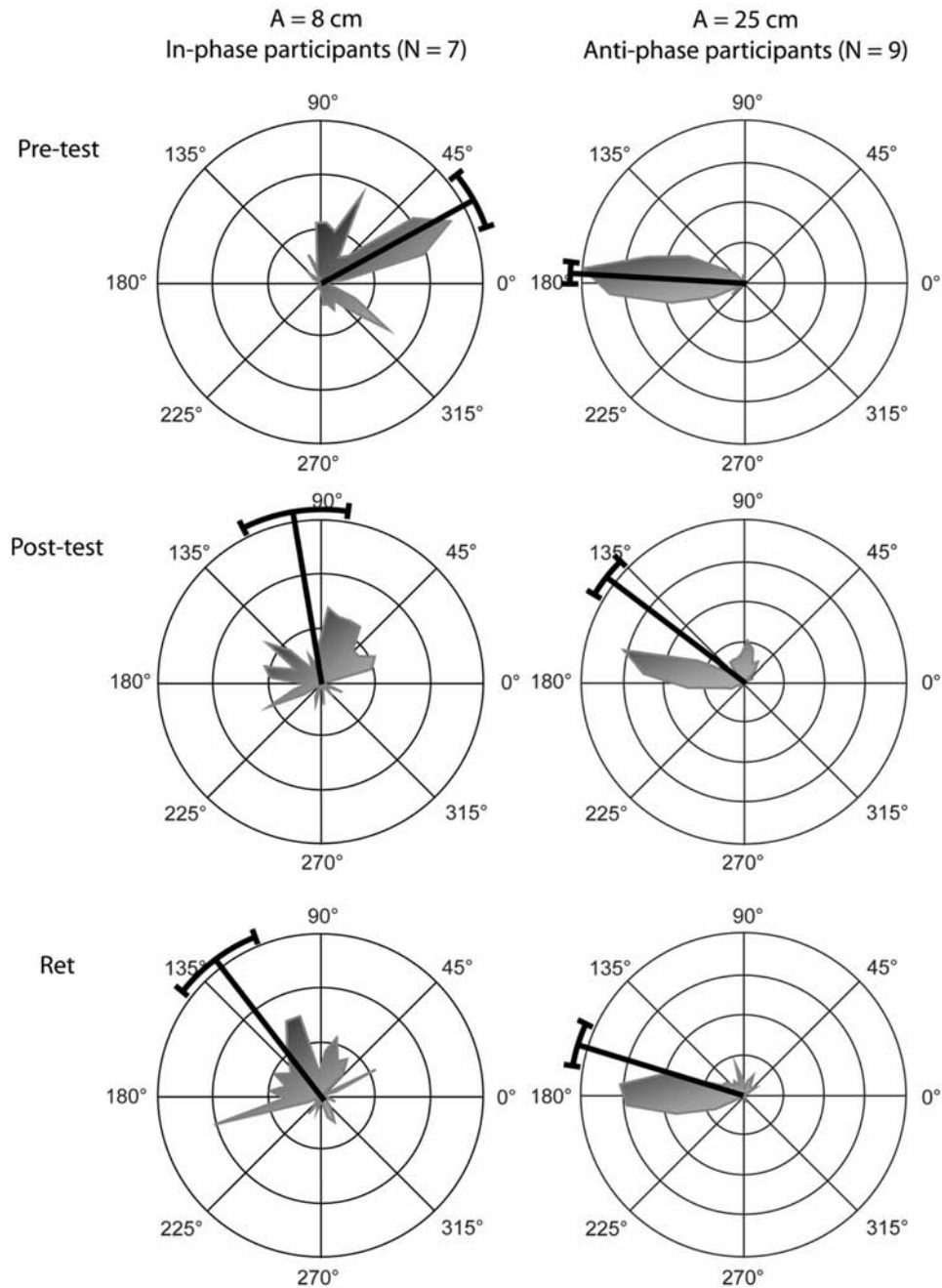


Figure 4. Frequency distributions for spontaneous relative phase (tracking task) at pretest, posttest, and retention test (Ret) for the experimental group. Left panel: Seven participants who produced an in-phase pattern at pretest for the small amplitude of target oscillation ($A = 8$ cm). Right panel: Nine participants who produced an antiphase pattern at pretest for the large amplitude of target oscillation ($A = 25$ cm). Each concentric circle corresponds to 5% of the total distribution of observed relative phase values. The dark radial line and the arc of circle represent the circular mean direction and its 95% confidence interval, respectively.

participants $SD\phi_{rel}$ substantially increased across test sessions. For the in-phase group, between-participants $SD\phi_{rel}$ was 28.26° at pretest, 59.42° at posttest, and 60.31° at the retention test. For the antiphase group, between-participants $SD\phi_{rel}$ was 9.59° at pretest, 36.31° at posttest, and 38.98° at the retention test. The between-

participants $SD\phi_{rel}$ data reveal an important differentiation of individual behaviors after the learning period of the 90° pattern.

Individual mean relative phases of the experimental group are summarized in Table 2. Watson-Williams tests conducted individually showed that Participants 1, 2, 4, 5, 8, 9, 11, and 12 exhibited

a significant change in spontaneous relative phase in the direction of the learned pattern for at least one of the two amplitudes of target motion. For Participants 1, 2, 4, 5, and 12, the modification occurred in both the 8-cm and 25-cm conditions. Participants 3, 6, and 7 showed no difference in spontaneous coordination or switched between two preexisting patterns. Participant 10 exhibited unexpected modifications for both target amplitudes. In the 8-cm condition, this participant changed from an in-phase pattern at pretest and posttest to $\phi_{rel} = 254^\circ$ at the retention test. This value close to the symmetric pattern of 90° , namely 270° , might be the expression of a positive transfer from the learned pattern to its symmetric pattern, as observed in bimanual studies (Smethurst & Carson, 2001; Zanone & Kelso, 1997). In the 25-cm condition, an in-phase pattern was observed at each test. Among participants who, from pretest to posttest, changed their spontaneous pattern in the direction of the learned pattern, only two (Participants 2 and 8) were attracted back to their initial mode at the retention test, and then only in the 25-cm condition. For nearly all other changes in the initial pattern, either no significant difference was found between posttest and retention test or the spontaneous pattern got closer to the learned pattern at the retention test (the sole exception was Participant 1 in the 25-cm condition). In conclusion, whereas learning the 90° pattern induced durable modifications of the spontaneous patterns in the direction of the learned relative phase in most participants, there were important interindividual differences.

Consequences of learning on required patterns (Lissajous task). To compare the absolute error before (pretest) and after learning 90° (posttest or retention test) for each participant of the experimental group, we conducted individual Watson-Williams tests for each required ankle-hip pattern. For 11 patterns, at least 8 participants (67%) exhibited an improvement in accuracy after learning, all $F_s(1, 40) > 4.29$, $ps < .05$. For the remaining pattern (210°), 5 participants (42%) exhibited improvement after learning, all $F_s(1, 40) > 4.32$, $ps < .04$. All participants exhibited a significant improvement in accuracy for at least 8 of the 12 patterns, all $F_s(1, 40) > 4.29$, $ps < .05$. Because individual performances were consistent, we present only the group analyses below.

The evolution of performance on the Lissajous task is illustrated in Figure 2 for the group of 12 participants. For each performance indicator (CE , AE , and $SD\phi_{rel}$), we conducted Pattern (12 required relative phases) \times Test (pretest, posttest and retention test) ANOVAs with repeated measures on both factors. For CE , the analysis revealed a significant main effect of pattern, $F(11, 121) = 15.57$, $\epsilon = .53$, $p < .001$, $\eta_G^2 = .32$. The main effect of test and the Pattern \times Test interaction were not significant, $F(2, 22) = 2.56$, $\epsilon = .69$, $p = .12$, and $F(22, 242) = 1.50$, $\epsilon = .24$, $p = .20$, respectively. These results indicate that the tendency to overestimate the relative phase values below 180° and to underestimate them above 180° persisted over the test sessions. For AE , the ANOVA revealed a significant main effect of pattern, $F(11, 121) = 14.84$, $\epsilon = .37$, $p < .001$, $\eta_G^2 = .26$, a significant main effect of test, $F(2, 22) = 52.26$, $\epsilon = .97$, $p < .001$, $\eta_G^2 = .34$, and a significant Pattern \times Test interaction, $F(22, 242) = 2.36$, $\epsilon = .71$, $p = .004$, $\eta_G^2 = .07$. Similarly, for $SD\phi_{rel}$, the ANOVA revealed a significant main effect of pattern, $F(11, 121) = 11.99$, $\epsilon = .76$, $p < .001$, $\eta_G^2 = .19$, a significant main effect of test, $F(2, 22) = 106.90$, $\epsilon = .64$, $p < .001$, $\eta_G^2 = .41$, and a significant Pattern \times Test interaction, $F(22, 242) = 1.75$, $\epsilon = .80$, $p = .03$,

$\eta_G^2 = .06$. The main effects of pattern indicate that the movement accuracy and stability differed for different required values of ankle-hip relative phase. The main effects of test show that overall performance improved from the pretest to the posttest and the retention test. In other words, learning $\phi_{rel} = 90^\circ$ enhanced performance of the different ankle-hip patterns. Finally, the interaction effects reveal that differences in performance among the required patterns tended to decrease over the test periods: Learning $\phi_{rel} = 90^\circ$ led performance to be uniform over the various coordination modes.

To better distinguish the evolution of performance for the different patterns, we conducted Newman-Keuls post hoc analyses on AE and $SD\phi_{rel}$. We found that all patterns but four (120° , 180° , 210° , and 270°) significantly improved in accuracy (AE) from pretest to posttest, $ps < .02$, and that all patterns but three (120° , 180° and 210°) became more accurate from pretest to retention test, $ps < .001$. The analyses conducted on $SD\phi_{rel}$ revealed that all patterns but three (180° , 210° , and 270°) significantly improved in stability from pretest to posttest, $ps < .02$, and that every pattern, with no exception, became more stable from pretest to retention test, $ps < .02$.

The post hoc analyses also allowed us to determine whether the 180° pattern was performed more accurately than the other patterns for the different test sessions. At pretest, $\phi_{rel} = 180^\circ$ was more accurate than eight of the other required patterns (0° , 30° , 60° , 90° , 240° , 270° , 300° , and 330° , $p < .05$). At posttest, $\phi_{rel} = 180^\circ$ was more accurate than four of the required patterns (0° , 270° , 300° , and 330° , $p < .05$), whereas at retention test, 180° was more accurate than only one of the required patterns (0° , $p < .05$). These results confirm that, over the test sessions, the antiphase pattern lost its superiority, suggesting that learning the 90° pattern lead to increasingly uniform performance across all patterns. This outcome is contrary to our expectation that the learned pattern would be performed for a large range of required patterns, which could have explained the emergence of this learned pattern in a supra-coordinative task such as the tracking task. The homogenization in performance we observed on the Lissajous task cannot account for the changes observed in spontaneous in-phase and antiphase patterns toward the learned coordination. We will return to this point in the Discussion section.

Figure 5 presents the relative phases produced when the patterns of 0° and 180° were required. These diagrams allow a direct comparison of the in-phase and antiphase patterns produced in the required and in the spontaneous conditions (see Figure 4). When the pattern of 0° was required, the mean relative phase was 28.72° at pretest ($SD\phi_{rel} = 55.04^\circ$), 30.93° at posttest ($SD\phi_{rel} = 38.43^\circ$) and 12.38° at the retention test ($SD\phi_{rel} = 34.65^\circ$). When the 180° relative phase was required, the mean relative phase was 183.01° at pretest ($SD\phi_{rel} = 34.97^\circ$), 184.17° at posttest ($SD\phi_{rel} = 25.43^\circ$) and 182.51° at the retention test ($SD\phi_{rel} = 19.36^\circ$).

We compared ϕ_{rel} as well as $SD\phi_{rel}$ in the required and spontaneous conditions for the in-phase pattern (0° required vs. in-phase pattern for target amplitude of 8 cm) and antiphase pattern (180° required vs. antiphase pattern for target amplitude of 25 cm). For the in-phase pattern, Watson-Williams tests conducted on ϕ_{rel} revealed that mean relative phase differed between spontaneous and required conditions at posttest and retention test, all $F_s(1, 397) > 75.01$, $ps < .001$, but not at pretest, $F(1, 397) < 1$, $p = .90$. The same tests conducted on

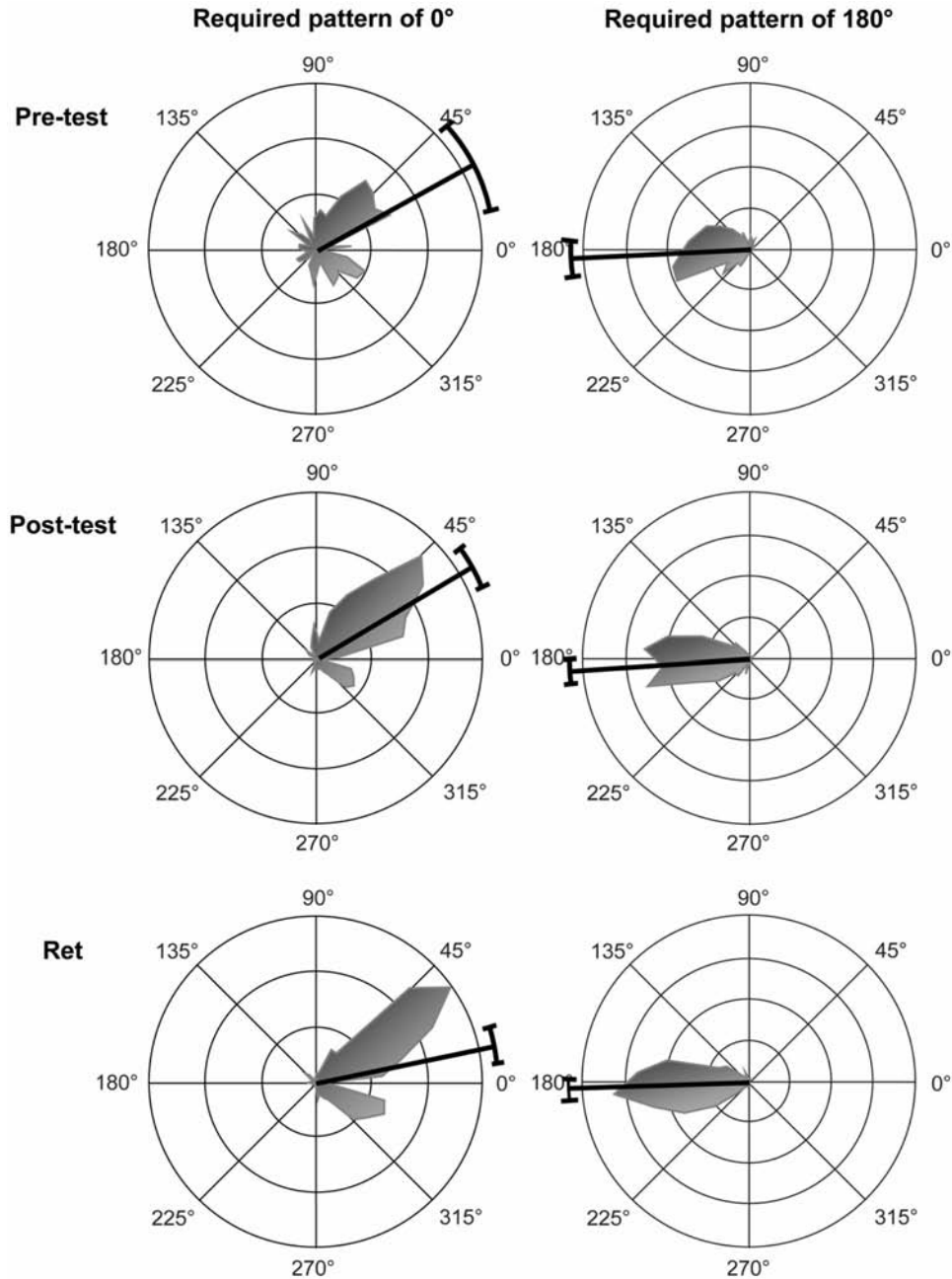


Figure 5. Frequency distributions for required relative phases of 0° (left panel) and 180° (right panel) at pretest, posttest, and retention test (Ret) for the experimental group. Each concentric circle corresponds to 5% of the total distribution of observed relative phase values. The dark radial line and the arc of circle represent the circular mean direction and its 95% confidence interval, respectively.

$SD\phi_{rel}$ revealed that the coordination pattern was less stable in the required condition than in the spontaneous condition at pretest and posttest, all $F_s(1, 55) > 8.97$, $p_s < .001$. This difference did not reach significance at retention test, $F(1, 55) = 3.89$, $p = .054$. For the antiphase pattern, Watson-Williams tests conducted on ϕ_{rel} revealed that mean relative phase differed between spontaneous and required condition at posttest and retention test, all $F_s(1, 439) > 27.89$, $p_s < .001$, but not at pretest, $F(1, 439) = 2.92$, $p = .09$.

The same tests conducted on $SD\phi_{rel}$ revealed that the coordination pattern was less stable in the required condition than in the spontaneous condition at pretest, $F(1, 61) = 21.67$, $p < .001$, but not at posttest and retention test, all $F_s(1, 61) < 1.64$, $p_s > .20$. These results show that both in-phase and antiphase patterns were less stable at pretest in the required condition than in the spontaneous condition and that mean relative phase became significantly different between those two conditions at posttest and retention test.

Contrary to the spontaneous condition, the mean relative phase did not deviate from its initial value between pretest and posttest for either the 0° or 180° required patterns, Watson-Williams, all $F_s(1, 502) < 1, p_s > .70$. In addition, between-participants $SD\phi_{rel}$ did not increase in the required condition, contrary to the spontaneous condition, but decreased from pretest (52.67° and 16.46° for required patterns of 0° and 180°, respectively) to posttest (27.42° and 12.78° for required patterns of 0° and 180°, respectively) and retention test (14.68° and 9.08° for required patterns of 0° and 180°, respectively).

Head Amplitude During the Tracking Task

The mean gains between target motion and head motion are presented in Figure 6 for the two amplitudes of target oscillation (8 cm and 25 cm) and the three test sessions. An Amplitude (2) × Test (3) ANOVA with repeated measures showed a significant main effect of amplitude on head-target gain, $F(1, 11) = 242.66, \epsilon = 1, p < .001, \eta_G^2 = .64$. The main effect of test and the Amplitude × Test interaction were not significant, $F(2, 22) = 3.05, \epsilon = 1, p = .07$, and $F(2, 22) < 1, \epsilon = .78, p = .70$, respectively. The mean gain over the test session was 2.39 when the target oscillated at 8 cm, and 1.20 when the target oscillated at 25 cm. The higher gain of head movements for the small amplitude is in accordance with previous results (e.g., Bardy et al., 1999). The consistency of head-target gain over the different test periods indicates that head motion was not dependent on (or responsible for) the changes in spontaneous patterns induced by learning.

Control Group

In the scanning procedure, the experimental group exhibited improvement over tests in the performance indicators (CE, AE , and $SD\phi_{rel}$) for all required ankle-hip patterns. Despite the familiarization period of 15 min, one may wonder whether this improvement was related to the fact of exposure to the experimental situation rather to learning the 90° pattern. The control group was included to evaluate this possibility.

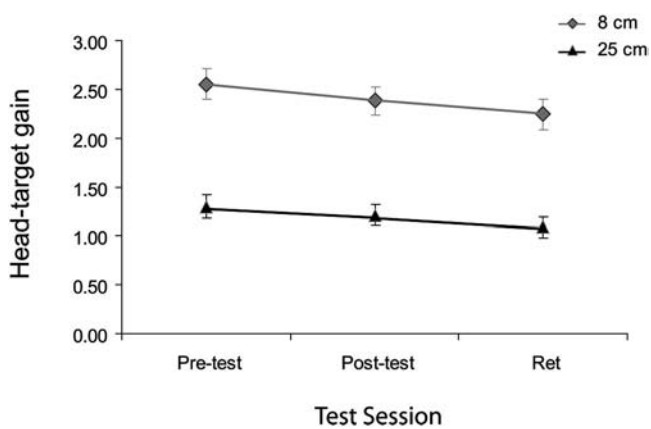


Figure 6. Head-target gain of the experimental group for both amplitudes of target oscillation (8 cm and 25 cm) during the tests sessions (pretest, posttest, and retention test). The error bars represent standard error (between-subjects variability).

Figure 7 illustrates the evolution of performance on the Lissajous task for the control group. For each performance indicator (CE, AE , and $SD\phi_{rel}$), we conducted Pattern (12 required relative phases) × Test (first and second scanning probes) ANOVAs with repeated measures on both factors. As for the experimental group, the analyses on the control group revealed a significant main effect of pattern for $CE, F(11, 66) = 29.92, \epsilon = .27, p < .001, \eta_G^2 = .74$, for $AE, F(11, 66) = 15.93, \epsilon = .45, p < .001, \eta_G^2 = .51$, and for $SD\phi_{rel}, F(11, 66) = 10.64, \epsilon = 1, p < .001, \eta_G^2 = .49$. However, contrary to the experimental group, the main effects of test, all $F_s(1, 6) < 1.66, p_s > .24$, and the Pattern × Test interactions, all $F_s(11, 66) < 1.04, p_s > .42$, were not significant for any of the performance indicators. The absence of differences in performance between the two scanning sessions for the control group strongly suggests that the improvements observed over the test sessions for the experimental group were due to learning the 90° pattern rather than to experience with the experimental situation per se.

Discussion

In this experiment, we tested the dynamics of spontaneous and required ankle-hip coordination patterns before and after participants learned a new coordination mode (ankle-hip relative phase of 90°). The acquisition of the new pattern strongly influenced coordination dynamics, but we found no direct relationship between (a) the changes in performance of spontaneous and required modes of ankle-hip coordination, (b) our results on required modes and the theoretical predictions of the dynamical approach, (c) our results in postural learning and results from studies of bimanual learning.

Preexisting Coordination Dynamics

For spontaneous patterns (i.e., in the tracking task), the majority of participants exhibited the expected coordination mode at pretest for each of the two amplitudes of target oscillation: in-phase when the amplitude of target oscillation was small and antiphase when it was large. In accordance with previous results (e.g., Bardy et al., 1999), some participants did not produce an in-phase mode for the 8-cm condition, and some did not produce an antiphase mode for the 25-cm condition. The amplitude (or frequency) at which the bifurcation from one ankle-hip pattern to the other occurs is variable and depends on various participant-related factors.

For required patterns (i.e., in the Lissajous task), the scanning procedure revealed that there was a strong attraction to the antiphase pattern at pretest. The fact that the in-phase pattern was not better performed than other patterns at pretest contrasts with the results obtained for the tracking task in the present experiment and in previous studies (Bardy et al., 1999, 2002; Oullier et al., 2002) but replicates previous findings obtained with a similar design (Faugloire et al., 2005). The absence of a stable in-phase pattern with the Lissajous task is a first indicator that there may be important differences between the dynamics of required and spontaneous patterns of coordination. In Faugloire et al. (2005), we argued that requiring coordination patterns could disrupt natural behaviors. For example, Wulf and Prinz (2001) found that performance improved when subjects were asked to concentrate on how their actions affected the environment, relative to when they were told to focus on the movement itself. Wulf, McNevin, and Shea

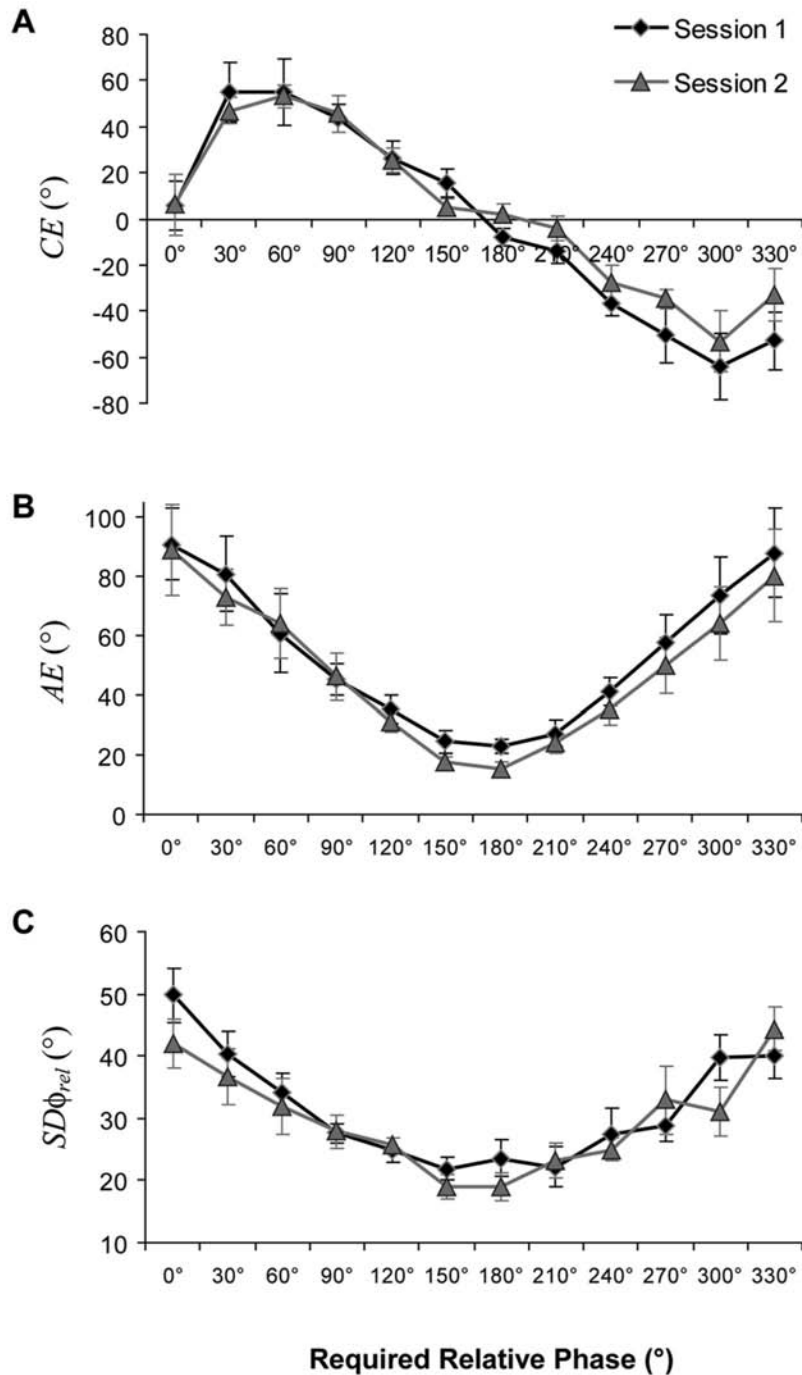


Figure 7. Performance on the 12 required coordination modes for the control group during the first scanning probe (Session 1) and the second scanning probe (Session 2), 3 days after. A: Constant error, CE . B: Absolute error, AE . C: Standard deviation of relative phase, $SD\phi_{rel}$. The error bars represent standard error (between-subjects variability).

(2001) proposed a constrained action hypothesis, arguing that an internal focus of attention (i.e., focus on body movements) can constrain and disrupt automatic control processes that naturally rule the self-organization of the motor system. Similarly, Hodges and Franks (2002) suggested that explicit instructions can lead

individuals to attempt conscious control over processes that typically are controlled by lower, less cognitive levels of the motor system. Whether this principle can explain our results is unclear at this stage, but the fact remains that when particular patterns of relative phase were required, participants' performance of the

in-phase pattern was not better than their performance of other patterns, whereas they spontaneously produced the in-phase pattern (and not others) when no instructions about ankle–hip coordination were given.

The scanning procedure also revealed that some participants were able to perform several patterns quite accurately in addition to the antiphase mode. Again, this result differs from the results on spontaneous coordination dynamics that we obtained in the present experiment and in previous studies: During the tracking task, only the in-phase and antiphase have been observed (e.g., Bardy et al., 1999, 2002).

Change in Coordination Dynamics Due to Learning

Learning the novel 90° ankle–hip relative phase induced important changes in the patterns of coordination produced at posttest, as measured in both the tracking and Lissajous tasks. We discuss the results obtained for each task separately and then offer a more general interpretation.

Our results for the spontaneous ankle–hip modes are in accordance with predictions of the dynamical approach to motor learning. As a new coordination mode was learned, its emergence competed with preexisting in-phase and antiphase patterns. Important individual differences were observed in how the learning period influenced preexisting spontaneous modes. At posttest, some participants presented a coordination mode that was close to the learned relative phase of 90°, some participants produced an intermediate state between the 90° pattern and one of the preexisting modes, whereas the rest did not show any change in spontaneous coordination. The theoretical point of view that learning interacts with preexisting capabilities imparts particular importance to individual differences. Individuals present specific coordination dynamics that may depend on multiple factors (e.g., innate characteristics, anthropometric features, past experience). According to the dynamical approach, the consequences of learning (on both the to-be-learned pattern and the preexisting coordination repertoire) depend upon preexisting tendencies. If initial coordination dynamics differ across individuals, then it is expected that the consequences of learning for coordination dynamics will also differ. Despite the potential value of this principle, in the present study we could not identify general rules relating preexisting tendencies to the effects of learning (results showing such a relation can be found in Zanone & Kelso, 1997, and Kelso & Zanone, 2002). It is likely that several factors, such as the learning rate, anthropometric features, or psychological determinants, interact with preexisting tendencies to influence the nature of the changes in coordination dynamics.

Overall, changes in the spontaneous pattern in the direction of the learned relative phase were observed for 8 of the 12 participants for at least one of the two amplitudes of target oscillation. This change is remarkable in two respects. First, the learning of the new relative phase (90°) generalized to a task of a very different nature. During the learning session, participants were specifically asked to produce a relative phase of 90°. Learning this 90° pattern appeared to transfer, at posttest, to the tracking task, in which ankle–hip coordination was unconstrained. Second, for most participants who exhibited a change in spontaneous coordination at posttest, the modification persisted 1 week after the end of practice.

Concerning the required coordination modes (i.e., the scanning procedure), the learning period induced a general improvement of the 12 ankle–hip patterns. Unsurprisingly, individual differences were less important in the required condition than in the tracking task, when participants had no instruction on the coordination pattern to produce. At both the posttest and the retention test, antiphase was no longer significantly more accurate than other patterns. Learning the 90° relative phase induced an improvement and homogenization in the performance of all required patterns. This result is not consistent with predictions of the dynamical approach to motor learning (e.g., Zanone & Kelso, 1994) or with results from studies of bimanual coordination. Our scanning procedure and our experimental design were similar to those used in studies of bimanual coordination (Kelso & Zanone, 2002; Lee et al., 1995; Smethurst & Carson, 2001; Swinnen et al., 1997; Zanone & Kelso, 1992, 1997). Despite this similarity, the improvement in performance that we observed for each required coordination mode contrasted with effects observed with bimanual coordination, that is, the destabilization effect (e.g., Kelso & Zanone, 2002; Zanone & Kelso, 1992, 1997) or the absence of modification of preexisting modes (e.g., Fontaine et al., 1997; Lee et al., 1995; Smethurst & Carson, 2001; Swinnen et al., 1997).

The positive transfer on all required patterns that we observed is quite different from the kinds of transfer usually studied in the literature. In traditional research on transfer (e.g., Hall & Magill, 1995; Wright & Shea, 2001; Wulf & Schmidt, 1989; Wulf, Schmidt, & Deubel, 1993), modification of the tasks has usually been achieved either by varying the overall duration, force, or amplitude of the movement (i.e., the movement parameters; Schmidt, 1975), or by changing the relative timing of the movement (i.e., the time ratios of the different elementary actions of the motor sequence). In our study, the computation of relative phase is independent of the speed (as long as it is similar across measured joints), force, and amplitude of movement. The transfer we report is, thus, different from parameter learning. In addition, in the present study, relative phase relates to the timing relation between the movements of two segments, whereas relative timing refers to the temporal structure of the different movement elements. We report a transfer from one intersegmental coordination mode to other, new ones, which is quite different from reorganizing the time dedicated to successive parts of a movement.

Participants from the control group (who were not exposed to the learning session) showed no difference in performance between the first and the second scanning procedures. Therefore, it is unlikely that the general improvement of required patterns was due to a better mastery of the Lissajous device. Rather, it seems that learning an ankle–hip relative phase of 90° led not only to improvement of this particular coordination mode but also to better control of ankle and hip movements in general. It may be that practicing any novel ankle–hip pattern would have led to general improvement and the homogenization of performance that we observed.

Studies of hand function in the elderly have found that training on a single task can improve manual dexterity in general (e.g., Kornatz, Christou, & Enoka, 2005; Ranganathan, Siemionow, Sahgal, Liu & Yue, 2001). For example, Ranganathan et al. (2001) trained elderly participants in skilled finger movements and examined the consequences of this training on hand function. They found that training on a ball-rolling task (similar to the so-called

baoding balls) induced improvement in tasks that were nonspecific to the training task (e.g., tasks involving finger-pinch). They concluded that training on the ball-rolling task could improve general factors of manual dexterity, such as the ability to control submaximal pinch force, hand steadiness, speed of movement, and motoneuron excitability. A similar process might have induced the general improvement in performance that we found in the present study. Practicing one particular value of ankle–hip relative phase may have enhanced general motor control properties, such as a decrease in joint stiffness, increase in muscle coordination, or sensibility to kinesthetic information. Why similar improvements have not been observed in studies of bimanual motor learning in young adults is an interesting question. Ankle–hip and bimanual systems have very different characteristics (e.g., mechanically coupled vs. independent joints) and functions (e.g., proximal vs. distal motion, fine manipulation vs. antigravity function) that can contribute to explain the difference between those two effector systems. Interestingly, the positive transfer we observed supports and extends recent results from Buchanan and colleagues on elbow–wrist coordination (Buchanan, Zihlman, Ryu, & Wright, 2007). Buchanan et al. (2007) showed an increase in the stability of the antiphase pattern after learning a relative phase of 90° and proposed that the direct mechanical linkage in the elbow–wrist system (coupled joints) may account for the different consequences of learning on the antiphase pattern between their study and bimanual studies. This assertion may also apply to the ankle–hip system. Future research will be needed to assess the specific consequences of learning for different sensori-motor systems.

Spontaneous Versus Required Coordination Modes

Hodges and Franks (2002, p. 256) stated, “The fact that the movement pattern is the goal of the task puts this task into a special category that has sometimes been defined as a ‘closed skill.’ . . . Whether findings generated from these types of tasks are equally applicable to skills that are not constrained by specific movements is not clear.” Even though we would rather have used the terms of morphokinesis and topokinesis (Paillard, 1991),⁶ the problem expressed by Hodges and Franks apply fairly well to the diverging results we observed between spontaneous and required coordination dynamics. With respect to ankle–hip coordination, the goals of the tracking task and the Lissajous task differed qualitatively. The instructions of the tracking task focused participants’ attention on relations between movement of their head and the visual target, whereas in the Lissajous task, attention was explicitly focused on the activity of the hips and ankles. Several studies have shown that attention and intention of the performer have a strong influence on the performance and learning of motor coordination (e.g., Hodges & Franks, 2002; Hodges & Lee, 1999; Wulf & Prinz, 2001; for a review, see Lee, 2004). The results of the present study are in accordance with these findings. Our tracking task is unusual relative to most studies relating motor learning to preexisting patterns; it permitted us to evaluate coordination patterns that emerge when participants’ conscious intentions are not focused on ankle–hip coordination. We found that learning a novel pattern of ankle–hip coordination ($\phi_{rel} = 90^\circ$) had different effects on later performance of spontaneous and required coordination patterns. After learning, the spontaneous modes were characterized by significant individual differences, whereas performance of required coordina-

tion patterns differed very little across individuals. Moreover, we could draw no correspondence between the spontaneous patterns and the required coordination dynamics we tested during the same time period. First, the in-phase pattern spontaneously produced during the tracking task before learning could not be successfully performed when it was required in the Lissajous task. Second, the pattern of results we observed after learning the 90° relative phase in the required condition (positive transfer of learning to every ankle–hip phase relations leading to an homogenization in performance) could not explain the destabilization of preexisting modes in the spontaneous condition (change from in-phase and antiphase modes toward the learned pattern). Third, our results showed that learning a new (required) postural coordination favors its appearance in a supra-coordinative task (i.e., the tracking task) to the detriment of initial spontaneous patterns, but that these initial patterns could still be performed in an accurate and stable manner when required. Thus, the nature of learning-induced destabilization depends on the nature of the task at hand. Our results suggest that what is observed for a specific kind of task cannot be directly generalized to others even if the coordination mode involved is similar.

Conclusion

We asked standing participants to learn a new pattern of ankle–hip coordination ($\phi_{rel} = 90^\circ$), and we evaluated how the learning of that new pattern influenced the performance of other patterns, both patterns that tend to emerge spontaneously (in-phase and antiphase, in the tracking task) and patterns that participants were asked to perform (in the Lissajous task). This design permitted us to bring a fresh perspective to our understanding of the consequences of learning on the behavioral repertoire. Some of our results were not predicted by the dynamical approach (e.g., Zanone & Kelso, 1994); but, on balance, the present study demonstrates the relevance of considering learning in the context of preexisting capabilities. In the Lissajous task, we found that learning had important consequences on the entire postural repertoire. We also found that the consequences of learning differed across tasks and were not the same for the postural system as had been reported in studies of bimanual coordination. Our results are consistent with several findings on the sensitivity of coordination dynamics to circumstances, such as neuromuscular-skeletal constraints (e.g., Carson, 2004; Carson, Smethurst, Oytam, & de Rugy, 2007), perceptual parameters (e.g., Mechsner, 2004), focus of attention (e.g., Temprado, 2004), and intention (e.g., Lee, 2004). The new insights we have gained through the study of the ankle–hip system underscore the value of enlarging the range of conditions over which motor learning is studied to better understand the process and consequences of skill acquisition.

⁶ Originally (Gentile, 1972), *closed skills* referred to situations in which environmental conditions are certain or remain unchanged whereas *open skills* referred to situations in which environmental conditions change over time and are unpredictable. *Morphokinetics* and *topokinetics skills* are defined in terms of the nature of the goal for the performer (Paillard, 1991): The goal of morphokinetic skills is to (re)produce a specific form whereas the goal of topokinetic skills is spatially located in the external environment (in that case, the performer can produce different movements to reach the goal).

References

- Adams, J. A. (1971). A closed-loop theory of motor learning. *Journal of Motor Learning*, 3, 111–150.
- Amazeen, P. G. (2002). Is dynamics the content of a generalized motor program for rhythmic interlimb coordination. *Journal of Motor Behavior*, 34, 233–251.
- Anderson, J. R. (1995). *Learning and memory: An integrated approach*. New York: Wiley.
- Bakeman, R. (2005). Recommended effect size statistics for repeated measures designs. *Behavior Research Methods*, 37, 379–384.
- Bardy, B. G. (2004). Postural coordination dynamics in standing humans. In V. K. Jirsa & J. A. S. Kelso (Eds.), *Coordination dynamics: Issues and trends* (pp. 103–121). New York: Springer Verlag.
- Bardy, B. G., Marin, L., Stoffregen, T. A., & Bootsma, R. J. (1999). Postural coordination modes considered as emergent phenomena. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 1284–1301.
- Bardy, B. G., Oullier, O., Bootsma, R. J., & Stoffregen, T. A. (2002). Dynamics of human postural transitions. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 499–514.
- Batschelet, E. (1981). *Circular statistics in biology*. New York: Academic Press.
- Brashers-Krug, T., Shadmehr, R., & Bizzi, E. (1996). Consolidation in human motor memory. *Nature*, 382, 252–255.
- Buchanan, J. J., Zihlman, K., Ryu, Y. U., & Wright, D. L. (2007). Learning and transfer of a relative phase pattern and a joint amplitude ratio in a rhythmic multijoint arm movement. *Journal of Motor Behavior*, 39(1), 49–67.
- Carson, R. G. (2004). Governing coordination. Why do muscles matter? In V. K. Jirsa & J. A. S. Kelso (Eds.), *Coordination dynamics: Issues and trends* (pp. 141–154). New York: Springer Verlag.
- 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., Smethurst, C. J., Oytam, Y., & de Rugy, A. (2007). Postural context alters the stability of bimanual coordination by modulating the crossed excitability of corticospinal pathways. *Journal of Neurophysiology*, 97, 2016–2023.
- Faugloire, E., Bardy, B. G., Merhi, O., & Stoffregen, T. A. (2005). Exploring coordination dynamics of the postural system with real-time visual feedback. *Neuroscience Letters*, 374, 136–141.
- Faugloire, E., Bardy, B. G., & Stoffregen, T. A. (2006). The dynamics of learning new postural patterns. *Journal of Motor Behavior*, 38, 299–312.
- Fontaine, R. J., Lee, T. D., & Swinnen, S. P. (1997). Learning a new bimanual pattern: Reciprocal influence of intrinsic and to-be-learned patterns. *Canadian Journal of Experimental Psychology*, 51, 1–9.
- Gentile, A. M. (1972). A working model of skill acquisition with application to teaching. *Quest*, 17, 3–23.
- Goedert, K. M., & Willingham, D. B. (2002). Patterns of interference in sequence learning and prism adaptation inconsistent with the consolidation hypothesis. *Learning & Memory*, 9, 279–292.
- Guadagnoli, M. A., & Kohl, R. M. (2001). Utilization of knowledge of results for motor learning. *Journal of Motor Behavior*, 33, 217–224.
- Hall, K. G., & Magill, R. A. (1995). Variability of practice and contextual interference in motor skill learning. *Journal of Motor Behavior*, 27, 299–309.
- Hodges, N. J., & Franks, I. M. (2002). Learning as a function of coordination bias: Building upon prepractice behaviours. *Human Movement Science*, 21, 231–258.
- Hodges, N. J., & Lee, T. D. (1999). The role of augmented information prior to learning a bimanual visual-motor coordination task: Do instructions of the movement pattern facilitate learning relative to discovery learning? *British Journal of Psychology*, 90, 389–403.
- Hurley, S. R., & Lee, T. D. (2006). The influence of augmented feedback and prior learning on the acquisition of a new bimanual coordination pattern. *Human Movement Science*, 25, 339–348.
- 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.
- Kelso, J. A. S. (1984). Phase transitions and critical behavior in human bimanual coordination. *American Journal of Physiology: Regulatory, Integrative, and Comparative*, 15, R1000–R1004.
- Kelso, J. A. S., Buchanan, J. J., & Wallace, S. A. (1991). Order parameters for the neural organization of single, multijoint limb movement patterns. *Experimental Brain Research*, 85, 432–444.
- 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., & Zanone, P. G. (2002). Coordination dynamics of learning and transfer across different effector systems. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 776–797.
- Kornatz, K. W., Christou, E. A., & Enoka, R. M. (2005). Practice reduces motor unit discharge variability in a hand muscle and improves manual dexterity in old adults. *Journal of Applied Physiology*, 98, 2072–2080.
- Kostrubiec, V., & Zanone, P. G. (2002). Memory dynamics: Distance between the new task and existing behavioural patterns affects learning and interference in bimanual coordination in humans. *Neuroscience Letters*, 331, 193–197.
- Krakauer, J. W., Ghez, C., & Ghilardi, M. F. (2005). Adaptation to visuomotor transformations: Consolidation, interference, and forgetting. *The Journal of Neuroscience*, 25, 473–478.
- Lee, T. D. (2004). Intention in bimanual coordination performance and learning. In V. K. Jirsa & J. A. S. Kelso (Eds.), *Coordination dynamics: Issues and trends* (pp. 41–56). New York: Springer Verlag.
- Lee, T. D., Swinnen, S. P., & Verschueren, S. (1995). Relative phase alterations during bimanual skill acquisition. *Journal of Motor Behavior*, 27, 263–274.
- Logan, G. D. (1988). Toward an instance theory of automatization. *Psychological Review*, 95, 492–527.
- Mardia, K. V., & Jupp, P. E. (2000). *Directional statistics*. Chichester, England: Wiley.
- Marin, L., Bardy, B. G., Baumberger, B., Flückiger, M., & Stoffregen, T. A. (1999). Interaction between task demands and surface properties in the control of goal-oriented stance. *Human Movement Science*, 18, 31–47.
- Mechner, F. (2004). A perceptual-cognitive approach to bimanual coordination. In V. K. Jirsa & J. A. S. Kelso (Eds.), *Coordination dynamics: Issues and trends* (pp. 177–195). New York: Springer Verlag.
- Olejnik, S., & Algina, J. (2003). Generalized eta and omega squared statistics: Measures of effect size for some common research designs. *Psychological Methods*, 8, 434–447.
- Oullier, O., Bardy, B. G., Stoffregen, T. A., & Bootsma, R. J. (2002). Postural coordination in looking and tracking tasks. *Human Movement Science*, 21, 147–167.
- Paillard, J. (1991). Motor and representational framing in space. In J. Paillard (Ed.), *Brain and space* (pp. 163–82). Oxford: Oxford University Press.
- Ranganathan, V. K., Siemionow, V., Sahgal, V., Liu, J. Z., & Yue, G. H. (2001). Skilled finger movement exercise improves hand function. *Journal of Gerontology: Medical Sciences*, 56, M518–22.
- Riley, M. A., Santana, M. V., & Turvey, M. T. (2001). Deterministic variability and stability in detuned bimanual rhythmic coordination. *Human Movement Science*, 20, 343–369.
- Robertson, E. M., Pascual-Leone, A., & Miall, R. C. (2004). Current concepts in procedural consolidation. *Nature Reviews Neuroscience*, 5, 576–582.
- 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* (3rd ed.). Champaign, IL: Human Kinetics.
- Schöner, G. (1989). Learning and recall in a dynamic theory of coordination patterns. *Biological Cybernetics*, 62, 39–54.
- Schöner, G., & Kelso, J. A. S. (1988). A synergetic theory of environmentally-specified and learned patterns of movement coordination. I. Relative phase dynamics. *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.
- Shadmehr, R., & Brashers-Krug, T. (1997). Functional stages in the formation of human long-term motor memory. *The Journal of Neuroscience*, 17, 409–419.
- Smethurst, C. J., & Carson, R. G. (2001). The acquisition of movement skills: Practice enhances the dynamic stability of bimanual coordination. *Human Movement Science*, 20, 499–529.
- Sternad, D., Amazeen, E. L., & Turvey, M. T. (1996). Diffusive, synaptic, and synergetic coupling: An evaluation through in-phase and antiphase rhythmic movements. *Journal of Motor Behavior*, 28, 255–269.
- Swinnen, S. P., Lee, T. D., Verschueren, S., Serrien, D. J., & Bogaerds, H. (1997). Interlimb coordination: Learning and transfer under different feedback conditions. *Human Movement Science*, 16, 749–785.
- Temprado, J. J. (2004). A dynamical approach to the interplay of attention and bimanual coordination. In V. K. Jirsa & J. A. S. Kelso (Eds.), *Coordination dynamics: Issues and trends* (pp. 21–39). New York: Springer Verlag.
- Tong, C., Wolpert, D. M., & Flanagan, J. R. (2002). Kinematics and dynamics are not represented independently in motor working memory: Evidence from an interference study. *The Journal of Neuroscience*, 22, 1108–1113.
- Tuller, B., & Kelso, J. A. S. (1989). Environmentally specified patterns of movement coordination in normal and split brain subjects. *Experimental Brain Research*, 75, 306–316.
- Wenderoth, N., Bock, O., & Krohn, R. (2002). Learning a new bimanual coordination pattern is influenced by existing attractors. *Motor Control*, 6, 166–182.
- Winter, D. A. (1990). *Biomechanics and motor control of human movement* (2nd ed.). New York: Wiley.
- Wright, D. L., & Shea, C. H. (2001). Manipulating generalized motor program difficulty during blocked and random practice does not affect parameter learning. *Research Quarterly for Exercise and Sport*, 72, 32–38.
- Wulf, G., McNevin, N. H., & Shea, C. H. (2001). The automaticity of complex motor skill learning as a function of attentional focus. *The Quarterly Journal of Experimental Psychology*, 54A, 1143–1154.
- Wulf, G., & Prinz, W. (2001). Directing attention to movement effects enhances learning: A review. *Psychonomic Bulletin & Review*, 8, 648–660.
- Wulf, G., & Schmidt, R. A. (1989). The learning of generalized motor programs: Reducing the relative frequency of knowledge of results enhances memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 15, 748–757.
- Wulf, G., Schmidt, R. A., & Deubel, H. (1993). Reduced feedback frequency enhances generalized motor program learning but not parameterization learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 19, 1134–1150.
- Yamanishi, J., Kawato, M., & Suzuki, R. (1980). Two coupled oscillators as a model for the coordinated finger tapping by 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: Theoretical structure and experimental agenda. In S. Swinnen, H. Heuer, J. Massion, & P. Casaer (Eds.), *Interlimb coordination: Neural, dynamical, and cognitive constraints* (pp. 461–490). San Diego, CA: Academic Press.
- Zanone, P. G., & Kelso, J. A. S. (1997). Coordination dynamics of learning and transfer. Collective and component variables. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 1454–1480.

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