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Facilitation of Nonpreferred Coordination Patterns During the Transition from Discrete to Continuous Movements

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This study investigates how motor coordination undergoes the passage from a discrete to a continuous movement régime. Participants repeated concatenated discrete movements with each hand such that one hand was lagging the other by a quarter of a cycle (i.e., with a 90° phase difference). As movement frequency increased, the tendency to persist in this relative phase competed with a progressive effect of the interlimb coupling favoring 0° and 180°. In 61% of the participants, a switch from a discrete to a continuous motion régime was accompanied by a shift toward the 0° or 180°. The 0° was more often favored than 180°. The remaining participants sustained a relative phase close to 90° even at the highest movement frequency and proved to be more accurate at the initial lowest frequency. These findings indicate that a priming effect may circumvent the tendency to produce preferred patterns and favor the production of nonpreferred patterns and that initial individual differences affect how motor coordination evolves with changing constraints.

Keywords: bimanual coordination, relative phase, individual differences, coordination dynamics, priming effect

In rhythmic bimanual tasks, the motor repertoire has been shown to exhibit only two preferred, spontaneously stable coordination patterns, in-phase and antiphase (Kelso, 1984). Operationally, these patterns can be captured by the relative phase between the moving limbs, in-phase being defined by 0° and antiphase by 180° phase relationship. The high stability of the 0° and 180° patterns is reflected by the small variability of relative phase and by systematic deviations toward either of the two stable patterns when different relative phases values are to be produced (Wenderoth, & Bock, 2001; Zanone & Kelso, 1992). These deviations signal that the motor system tends to attract the produced pattern toward the 0° and 180° patterns, confining the possibilities of the motor system to a small set of preferred patterns.

Breaking away from these few preferred patterns is a goal of learning (Atchy-Dalama, Peper, Zanone, & Beek, 2005; Delignières, Nourrit, Sioud, Leroyer, Zattara, & Micaleff, 1998; Fontaine, Lee, & Swinnen, 1997; Hodges, & Franks, 2002; Wenderoth, Bock, & Krohn, 2002; Zanone & Kelso, 1992, 1997). Numer-

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ous studies showed that after fairly long practice, often involving as much as 200 practice trials (Hodges, & Franks, 2002; Hurley, & Lee, 2006, Lee, Swinnen, & Verschueren, 1995; Smethurst, & Carson, 2001), novel, spontaneously unstable coordination patterns can eventually be stabilized (Zanone, & Kelso, 1992, 1997). Another way to modify how nonpreferred patterns are acquired is to study different coordination systems characterized by various coupling strength. Coupling strength is the force that synchronize the limb with each other, thereby restricting the motor output to these only two 0° and 180° stable patterns (Amazeen, 2002; Walter, & Swinnen, 1992). Recently, Levin and colleagues (2004) showed that learning a novel, nonpreferred pattern is easier for joint combinations characterized by a weak coupling, such as the shoulders, than for joint combinations characterized by a strong coupling, such as the fingers. Thus, we shall build on the idea that when the interlimb coupling strength is weakened by the experimental settings, new, nonpreferred patterns may arise easier or faster.

To manipulate the coupling strength, it is important to start defining what coupling is and how it appears and disappears. Broadly speaking, coupling refers to the influence of one limb on the other (Cincotta, & Ziemann, 2008). In healthy adults performing unimanual tasks, in which one limb should be at rest while the other is moving, the coupling effect is inhibited (Daffertshofer, Van den Berg, & Beek, 1999). Kelso, Southard, and Goodman (1979; Tayler, & Davids, 1997) showed that in a unimanual task limbs velocities appears independent: there is no observable effect of coupling. An effect of coupling appears in bimanual tasks, in which both limbs should move simultaneously: limb positions and velocities become interdependent as the inhibition is released (Franz and Ramachandran, 1998; Schöner, 1990; Ridderikhoff, Peper, & Beek, 2006). Thus, as soon as but only when the two limbs move simultaneously, a coupling effect manifests itself, constraining the bimanual movements to the two stable coordination patterns, 0° and 180°.

A contribution of the current study is to present a novel experimental paradigm that arguably allows manipulating the coupling strength gradually as well as promoting the production of nonpreferred coordination patterns. In order induce a progressive increase in coupling strength, participants started performing a sequence of concatenated unimanual movements, for which the coupling has no expected effect on movement trajectories. In this task, half-cycles of flexion/extension periodic movements must be produced by the left and by the right hand consecutively and concatenated in such a way that each half-cycle of one hand attains a full stop at its reversal point before the other hand starts moving (see Figure 1, top row, left panel). Because in such a move-stop-move-stop sequence, the velocity and acceleration of each half-cycle reaches zero at reversals and each novel half-cycle must be initiated by a novel impulse, these movements may be coined as discrete (Buchanan, Park, & Shea, 2006; Guiard, 1997). Due to the lack of a better term, we shall henceforth refer to such a concatenation of half-cycles in a discrete movement régime as a concatenated sequence.

When participant are instructed to repeat a concatenated sequence while speeding up its execution gradually, the dwell time during which each limb is at rest progressively wanes (de Poel, Peper, & Beek, 2007; Huys, Studenka, Rheaume, Zelaznik, & Jirsa, 2008). As a result, limbs will come to move more and more continuously, that is, restoring the mechanical energy from one half-cycle to another and driving acceleration away from zero at reversals (Buchanan, Park, & Shea,

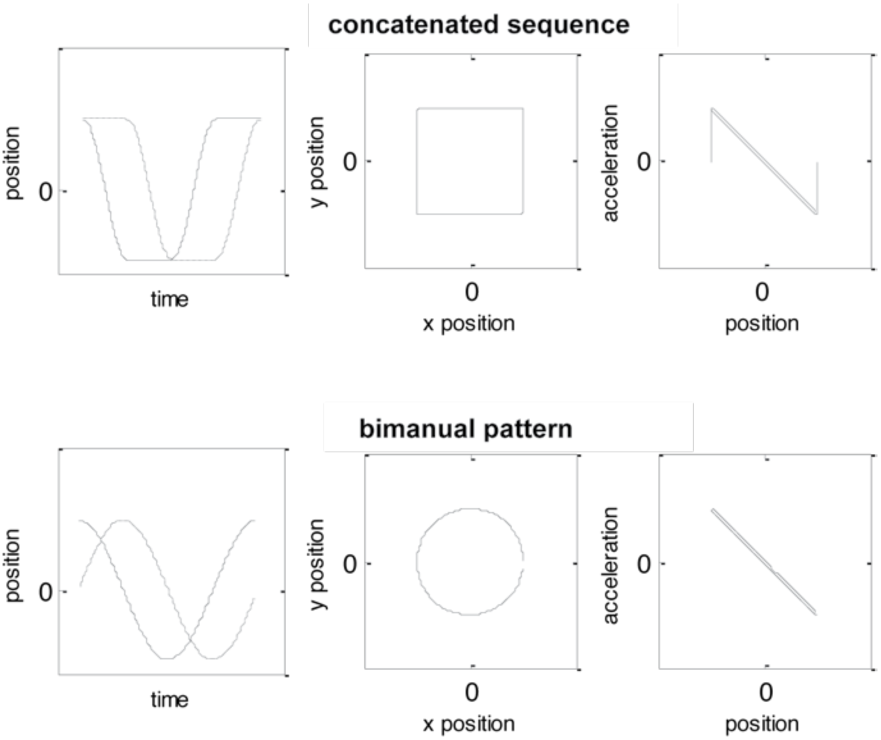

Figure 1 — Simulated trajectories of two limbs, x and y (left panels, solid and dashed line, respectively), realizing a 90° relative phase pattern as a concatenated sequence (left panel in top row) and as bimanual pattern (left panel in bottom row). The corresponding Lissajous figure is a square for concatenated sequence (middle panel in top row) and a circle for bimanual pattern (middle panel in bottom row). The corresponding Hooke portrait of a single limb is an N for concatenated sequence (right panel in top row) and a straight line for bimanual pattern (right panel in bottom row). Arrows indicate how relative phase is calculated using a peack-picking procedure: the duration represented by the solid horizontal line is divided by the duration represented by the dotted horizontal line, multiplied by 360°. Both the concatenated sequence and the bimanual pattern display the same 90° relative phase.

2006; Guiard, 1997). Along with the conversion from a discrete to a continuous movement régime, the concatenated unimanual sequence becomes a bimanual movement. Hence, the coupling strength increases, effectively constraining the two-limb movements to the preferred, 0° and 180° phase relationships.

Another feature of our paradigm is that it aims to facilitate the production of a novel, nonpreferred phase relationship in the continuous movement régime due to a priming effect. Priming is a well-established and robust effect in behavioral studies: if two responses are somewhat related, the production of one of these facilitates the later production of the other (Schacter, Chiu, & Ochsner, 1993; Tulving, & Schacter, 1990). For instance, Helbig, Steinwender, Graf and Kiefer, (2010) reported that watching a movie showing hands performing an action in interaction with an unseen object (i.e., stapling with an unseen stapler) facilitates the subsequent labeling of another manipulable object (e.g., scissors), because it typically involves a comparable action (i.e., closing the hand to compress the handles). Taking inspiration from these findings, we hypothesized that if the initial concatenated sequence is somewhat akin to a novel, nonpreferred phase relationship, the motor system might exhibit such a nonpreferred pattern despite the growing effect of the coupling strength with increasing frequency that tend to install the preferred 0° and 180° phase relationships. Specifically, the concatenated sequence primes the nonpreferred 90° phase relationship by construction. When both limbs move continuously, the 90° coordination bimanual pattern implies the dominant hand leads the nondominant hand by a quarter of cycle (see Figure 1, left panel in bottom row). However, if each limb comes to a full stop at the reversal points and remains at this point until the other hand reaches the corresponding reversal, the bimanual pattern is transformed into the concatenated sequence (see Figure 1, left panel in top row). Both concatenated sequence and bimanual pattern are then characterized by 90° point-estimated relative phase, as assessed by a traditional peak-picking procedure (Rosenblum, Pikovsky, Kurths, Schafer, & Tass, 2001; Zanone & Kelso, 1992): they set a time delay corresponding to a quarter of a cycle between, say, reversal points (see Figure 1, left panel in top and bottom row). Taking inspiration from the studies on priming effect, we hypothesize that the 90° phase relationship initially produced through the concatenated sequence facilitates the emergence and the performance of the nonpreferred 90° phase relationship when continuous bimanual motion is installed.

Whether the produced movement is more akin to a concatenated discrete sequence or to a bimanual 90° continuous pattern can be asserted by looking at a so-called Lissajous plot, where, typically, the right limb position is plotted versus left limb position. An ideal realization of the concatenated sequence would lead to a squared shape (see Figure 1, middle panel in top row), whereas an ideal realization of bimanual 90° pattern would lead to a circle (see Figure 1, middle panel in bottom row). The extent to which limb movement is continuous is manifested in a so-called Hooke portrait, plotting limb acceleration as a function of position. An ideal concatenated sequence, in which limbs move one by one, would produce an N-shaped Hooke portrait (see Figure 1, right panel in top row), whereas an ideal bimanual continuous motion the Hooke portrait is a straight line (see Figure 1, right panel in bottom row; see also, Mottet & Bootsma, 1999; 2001).

To quantify the degree of discreteness versus continuousness of the limb motion, various kinematic measures can be used (see Hogan & Sternad, 2007, for a review). We shall adopt that proposed by Guiard (1993, 1997): the harmonicity index, HR, which ranges from 0 for an ideally discrete motion to 1 for an ideally harmonic motion. In unimanual tasks (Buchanan, Park, & Shea, 2006; Guiard, 1993; Mottet, & Bootsma, 1999; Mottet, Giuard, Ferrand, & Bootsma, 2001), the increase of HR when movement switches from discrete to continuous follows a S-shaped function (Guiard, 1997). The evolution of HR is accompanied by an abrupt rise and fall of HR variability (Buchanan, Park, & Shea, 2006). These experimental features are hallmarks of abrupt changes, or nonlinear transitions, between different motion regimes so that continuous and discrete motion may be conceived of as distinct classes of movement (Friedman, Zatsiorsky, Latash, 2009; Schaal, Sternad, Osu, & Kawato, 2004).

With a clear, kinematically-based distinction between discrete and continuous motion regimes at hand, the rationale of the present experiment is as follows. Participants are instructed to produce the concatenated sequence such as those presented in Figure 1 (top panel), with a gradually higher frequency. With increasing frequency, the movements lose their discreteness and start moving continuously and simultaneously. Along with the increase in harmonicity, the interlimb coupling enters into play, constraining the bimanual system to produce only 0° or 180° bimanual coordination patterns. Of critical interest here is what happens at high movement frequency, when both limbs start moving continuously. If a priming effect overwrites the impact of the raising interlimb coupling, the 90° coordination pattern should be sustained after the switch to continuous movement. In contrast, if the interlimb coupling wins over the priming effect, either the 0° or the 180° pattern should arise, resulting in a trend toward 180° or a trend toward 0° of the produced relative phase.

Now, if as predicted different participants follow distinct paths, converging either toward the preferred 0° and 180° patterns, or remain close to the nonpreferred 90° one, we shall seek for an effect of the initial individual differences by comparing the performance of both groups at the low frequencies. Previous studies on learning bimanual coordination patterns (Zanone & Kelso, 1997) showed that small initial differences in the kinematics of movements and in coordination preferences across participants may have substantial effects on how the learning process itself unfolds in the long run.

Method

By rotating two handles in coincidence with a visual metronome at low frequency, participants had first to produce a concatenated sequence of four concatenated unimanual half-cycles exhibiting 90° of point-estimated relative phase. Movement frequency was then progressively increased.

Subjects

Eighteen unpaid participants, 3 male and 15 female, aged between 18 and 46 and enlisted at Paul Sabatier University or at the Institute of Motor Therapy of Toulouse, volunteered to participate in the experiment. All participants reported normal or corrected-to normal visual acuity and had no physical impairment impeding the required pattern production. The study was approved by the local ethical committee of Paul Sabatier University and participants provided a written informed consent in accordance with the Helsinki Declaration.

Apparatus

Two customized rotating handles, separated 60 cm. were mounted on a vertical support secured to a table. Participants sat 70 cm in front of this device, in an adjustable armchair with their elbows flexed at about 90° and their forearm laying on the armrest, so that they could comfortably grasp the handles. The rotatory motion of the handles was restricted to the frontal plane, allowing wrist pronation–supination movements only. Each handle position was recorded by a linear potentiometer (20-K resistance and .25% linearity), one complete revolution of which provided values in the [-5V, 5V] interval. The outputs of two potentiometers were digitized at 200 Hz using an AtoD system (Data Translation, DT BNC BOX USB 9800 Series) controlled by Vee Pro (Agilent Technologies) program and stored for further processing.

A 17” monitor displaying a visual metronome composed of 1-cm^2 yellow squares flicking on a black screen was located 80 cm in front of the participant. Each blink lasted less than 0.02 s. For probe trials, in which various relative phases were required, two squares positioned on a horizontal line were used to pace the left and right hand oscillations, respectively, at 1 Hz. The interstimulus intervals (ISI) between the right and left squares were controlled via a custom program. Increasing ISI from zero to the largest interval specified various relative phases ranging from 0° to 180. For experimental trials, only one square set in the middle of the screen was displayed at various frequencies, as it had to specify only movement frequency by blinking once per cycle.

Procedure

To familiarize participants with the experimental device, participants were instructed to produce 0° and 180° patterns for 20 s two times. Immediately after familiarization, they had to produce a 180° pattern for 20 s at the frequency they felt most comfortable four times, the fourth occurrence being used to define the individual’s spontaneous frequency. Then, the existing motor repertoire was probed with the help of the visual metronome. In the probe trials, participants were required to produce a 0°, 180° and 90° relative phase by trying to synchronize the left and right wrist pronation with the onset of the left and right square, respectively. Each probe trial lasted 20 s. Eighteen, so-called bistable participants, who failed in producing the 90° pattern with satisfactory accuracy (90° ± 30°) and variability (< 20°) were selected to pursue the experiment.

In the experiment proper, participants were instructed to repeat the concatenated sequence, composed of four, successive, unimanual half-cycles: dominant hand wrist pronation, nondominant hand wrist pronation, dominant hand wrist supination, nondominant wrist hand supination (cf. Figure 1). Each concatenated sequence should be initiated in coincidence with the visual signal provided by the visual metronome. An experimental trial involved nine frequency levels presented in increasing order, with no pause and no separating stimulus between them. The individual spontaneous frequency was set as being the fourth frequency level, serving as a base for defining the other frequencies. Three slower and four faster frequency levels were defined by successively decreasing and increasing the base frequency in as many steps of 30%. For instance, for a participant exhibiting a 1 Hz spontaneous frequency, the nine frequency levels were 0.29, 0.44, 0.66, 1, 1.33, 1.77, 2.24, 3.13, and 4.16 Hz. In an experimental session, four experimental trials were administered. A plateau at each frequency level lasted 20 s, and the whole experimental session took about 45 min.

Data Reduction

Six variables were taken under scrutiny: (1) the number of produced motion cycles, (2) dwell times, (3) harmonicity index, (4) interlimb relative phase, (5) interlimb relative position, and (6) the thickness of phase plane trajectories.

Dwell times were computed using the method proposed by Buchanan, Park and Shea (2006). For mean-centered data, movement onsets were identified with reference to peak velocity values. From the point of peak velocity for each half-cycle, a backward search was performed to find the first point in the velocity trace that reached 10% of the peak velocity value following a reversal. Movement offset was localized by a forward search from each half-cycle peak velocity value to find the last point that was 15% of the peak velocity value before the movement reversal. Dwell time was defined as movement onset at n+1-movement offset at n. Dwell time amounts to this difference multiplied by the sampling frequency (200Hz).

The harmonicity index was computed using the method by Mottet and Bootsma, (1999; 2001; Nourrit, Delignières, Caillou, Deschamps, & Lauriot, 2003). For an ideally harmonic motion, the coefficient of determination (r^2) of the linear regression of position onto acceleration equals 1. For discrete motion, r^2 is smaller and the residuals of this regression reveal the departure from harmonicity. The quantity HR provides thus an index of harmonicity, HR index, (Mottet, & Bootsma, 1999; 2001; Nourrit, Delignières, Caillou, Deschamps, & Lauriot, 2003), amounting to HR = 1 in case of an ideally harmonic movement. A decrease from 1 informs on the departure from an ideally harmonic movement in the direction of a more unharmonic motion. To compute HR cycle by cycle, each limb's position time series was detrended, mean-centered and normalized, rescaling the data between +1 and −1. Then, for every movement cycle, a time window was defined between two adjacent zero-crossings from a negative to a positive value, so that a time window contained two movement direction reversals. For each time window, the dataset was differentiated twice for producing the Hooke portrait (position vs acceleration), and the corresponding HR index computed.

To examine the interlimb coordination, two measures were computed. First, a classic peak-picking algorithm was used to assess interlimb relative position with regard to reversal points (see left panels of Figure 1). A point-estimated relative phase was then calculated as the time difference between the consecutive maximal pronation of the right and left hands, divided by the period of the corresponding right-leading hand cycle, multiplied by 360°. We refer below to this measure as to interlimb *relative phase*. Since relative phase captures the interlimb coordination at only one event per movement cycle, a second measure assessing the average coordination between the limbs over the whole cycle was provided using Lissajous figures. This method was based on the classic geometric interpretation of the linear coefficient of correlation of Lissajous figures (Ferguson, & Takane, 1989), and is presented in the next paragraph in greater detail.

For any two standardized sets of data x and y represented on a scatter plot (i.e., in the xy-plane), the coefficient of correlation r between x and y is equivalent to the cosine of the angle α between two regression lines: the linear regression of x on y and the linear regression of y on ×. It is thus possible to compute the angle α from the value of r. Practically, if the scatter plot forms an ideal circle so that the two regression lines are orthogonal (see regression lines inside the circular plot in the 4th panel of Figure 2), the corresponding coefficient of correlation r amounts to 0°. Arccosine of 0 is 1.57 radians, that is, 90°, which corresponds to the angle α between the two regression lines. If the two regression lines superpose exactly, $r = 1$ and *arcos* (1) = 0° for positive slope, whereas $r = -1$ and *arcos* (−1) = 3.14 radians, that is,180° for negative slope of the regression lines. Due to the lack of a

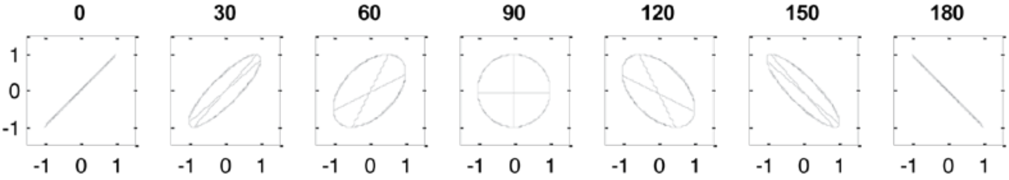

Figure 2 — Interlimb relative position calculated for simulated data, representing ideally harmonic and stable trajectories. In the Lissajous figures, a sinusoid was delayed from the other by a relative phase value, RP, ranging from 0° to 180° by step of 30°. The two lines inside each Lissajous figures represent two regression lines. The value displayed above each of the figures refer to the angle α between the two regression lines. The angle α was calculated as the arcosinus of the coefficient of correlation r between the two simulated datasets in each Lissajous plot. These values of α are exactly matching with the values of corresponding to relative phases.

better term, we shall coin this measure interlimb *relative position*. For simulated datasets, representing ideally harmonic and stable timeseries, the values of relative position and relative phase are matching exactly (see the values of α displayed above each panel in Figure 2).

In the present experiment, to compute cycle by cycle relative positions, the time window was defined with respect to the position time series of the dominant hand, and applied to the dominant and nondominant hand time series. Then, a Lissajous plot was produced, and the corresponding arccosine of the coefficient of correlation between the two time series computed.

The thickness of the phase plane trajectories was examined at four points in the cycle, the two extreme velocities and two extreme positions, using a method borrowed from Temprado, Zanone, Monno, and Laurent (1999). The limb position timeseries was filtered with a second order dual pass Butterworth filter with a cutoff frequency of 10 Hz. For the 3rd and last frequency levels, position and velocity data were normalized within a ± 1 interval. Then, the Cartesian coordinates of each point in the phase plane were converted into their polar equivalents (viz. radial coordinate and angular coordinate). For each point, the standard deviation of the radial coordinates was calculated, providing thus an index of the thickness of the phase trajectories: the points characterized by the lowest radial standard deviation indicate the narrowing of the phase trajectories.

Statistical Analysis

For each Hand (dominant vs. nondominant) and for each Frequency Level (1–9), the number of cycles, the mean HR and the corresponding standard deviation (*SD*) of HR were computed. Next, for each Hand, each Frequency Level and each Direction of excursion (supination vs. pronation), mean dwell times were calculated. Finally, for each Frequency Level, mean interlimb relative phase, mean interlimb relative position and the corresponding measures of variability were provided. Given that interlimb relative phase and relative position are circular variables, we used circular statistics for these two variables. Note that circular measure of variability, R, decreases from 1 to 0 when data variability increases (Batschelet, 1981).

This analysis was completed by calculating a measure for accuracy, that is, the absolute error (AE) between the mean of the produced and required relative phase (i.e., 90°) and between the mean of produced and required relative position (i.e., 90°). Then, the thickness of the phase trajectories at the Extreme Positions (minimum vs maximum) for the two Variable (positions vs velocity) was analyzed at two Frequency Levels (3 vs 9) for the dominant and the non dominant hand separately.

For all variables data from the four trials were collapsed. In all analyses, the whole set of experimental factors were treated as repeated measures factors, except for Group (2) treated as a group factor. The ANOVAs were followed by an estimation of the effect size (η^2) and, if necessary, by a trend analysis using polynomial contrasts. Linear polynomial contrasts test whether the distribution of data presents a statistically reliable trend. Quadratic contrasts reveal the presence of one statistically reliable trend reversal, that is, of an U-shaped distribution. Cubic contrast indicates the presence of two, statistically reliable trend reversals, that is, of an S-shaped distribution.

The distributions of all the dependent variables were normal (those of harmonicity indexes, $Z = .590$, $p > .877$, and of their SDs, $Z = .535$, $p > .937$). If the data did not satisfy the sphericity of variances assumption with regard to Geisser-Greenhouse's index, the required adjustments were applied. For all results, only significant effects at $p < .05$ are reported.

Results

Overall Inspection of Individual Data

Visual inspection of the individual Lissajous figures (see Figure 3) as a function of Frequency Level revealed three types of evolution: toward the 0° pattern (left-slanted line, top row in Figure 3), toward 90° (an almost circular pattern, middle row in Figure 3), or a mix of 0° and 180° patterns (left-slanted and right-slanted lines, bottom row in Figure 3). On the basis of the Lissajous plots, the 18 participants were assigned to three different groups: 50% of participants ($N = 9$) were classified in the 0° Group, 39% ($N = 7$) in the 90° Group and only 11% ($N = 2$) in the 180° Group. This classification was supported by a hierarchical cluster analysis carried out on relative position and on relative phase, using squared Euclidian distance. We coin the group of participants who sustained a pattern close to 90° as the Steady Group. Participants belonging to 0° and 180° Group were then collapsed into a single Evolving group, to compare their accuracy and variability to those of the Steady group.

Mean interlimb relative phase and mean interlimb relative position is displayed as a function of Frequency Level in the top and the bottom panel of Figure 4, respectively. For interlimb relative phase, there was an uptrend toward 146.3° or a downtrend toward 13.8° for the Evolving Group (empty symbols). No such trend was observed for the Steady Group (solid symbols), as relative phase remained about 60.32°. Similar patterns of results arise for interlimb relative position. There was an uptrend toward 126.6° or a downtrend toward 27.7° for the Evolving Group (empty symbols), and no trend was observed for the Steady Group (solid symbols): relative position remained about 77.46°.

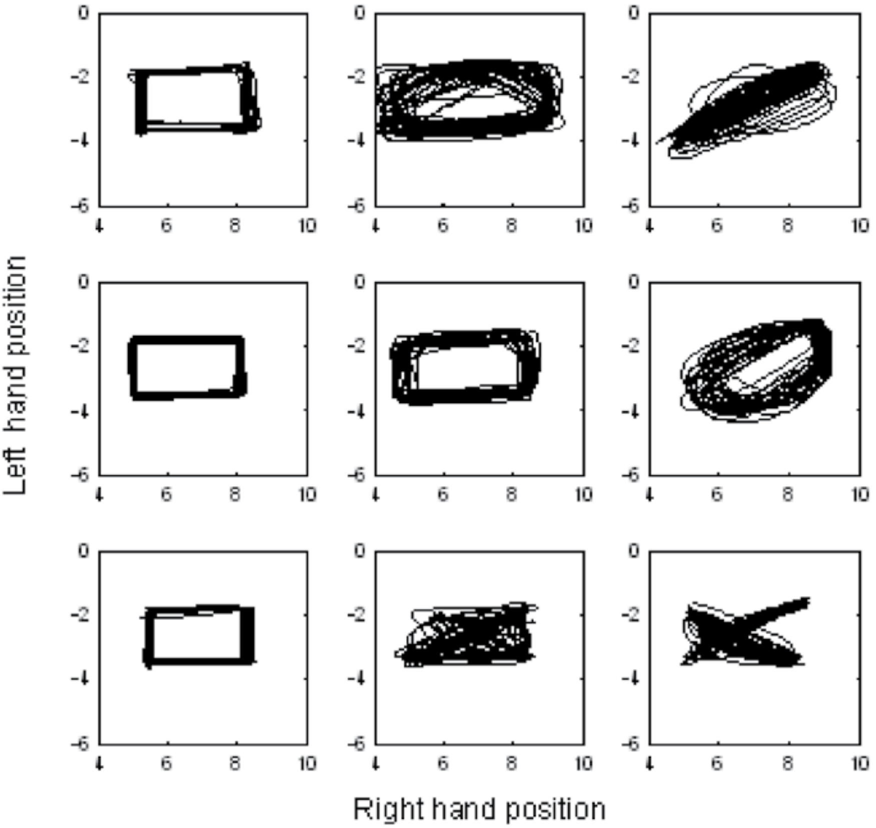

Figure 3 — Evolution of individual Lissajous figures (in arbitrary units) with increasing frequency. Each column represents the starting, median, and ending frequency levels for three different participants (first, second, and third row, respectively). See text for details.

At the last Frequency Level, the performance of the Steady Group appears thus closer to the 90° pattern than that of Evolving Group. Mean AE of interlimb relative phase and of relative position are displayed as a function of Frequency Level in Figure 5 (top and bottom panels, respectively). For interlimb relative phase, the individual values of AE ranged from 54° to 89° (M = 63.93, *SD* = 29.07) for the Evolving Group, and from 5° to 45° (M = 33.96, *SD* = 26.30) for the Steady Group. For interlimb relative position, the individual values of AE ranged from 38° to 75° (M = 57.66, *SD* = 14.28) for the Evolving Group, and from 5° to 25° (M = 14.54, *SD* = 10.34) for the Steady Group.

Evolving vs. Steady Group at the Highest Frequency Level

A 2 (Group) ANOVA on both AEs was carried out to ensure us that, as suggested by the visual inspection of the data, the Evolving Group was less accurate than the

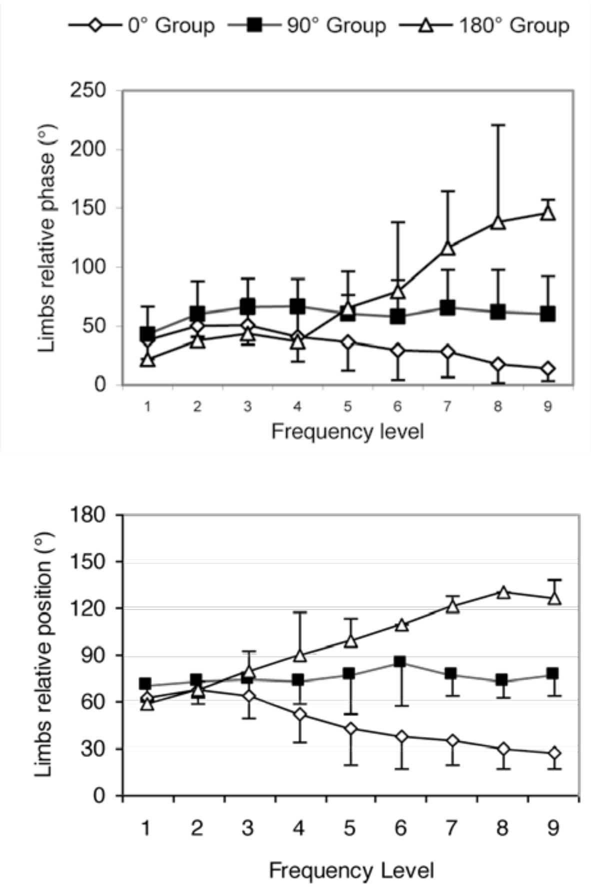

Figure 4 — Mean relative phase (top panel) and relative position (bottom panel) as a function of Frequency Level, for the 90° Group (solid symbols), 0° and 180° Groups (empty diamonds and triangles, respectively). Vertical bars represent the intersubject standard deviation.

Steady Group at the last Frequency Level. For AE of relative phase, the analysis revealed that AE was reliably higher for the Evolving Group than for the Steady Group, $F(1, 16) = 71.924$, $p < 000$, $\eta^2 = .818$. For AE of interlimb relative position, the analysis indicated that AE was higher for the Evolving Group than for the Steady Group, $F(1, 16) = 46.345$, $p < 000$, $\eta^2 = .743$. The results indicate that at the last Frequency Level, the performance of the Steady Group was closer to the required 90° pattern than that of the Evolving Group.

Number of Cycles

The average number of cycles is displayed in Figure 6 (top panel), as a function of Frequency Level. A 9 (Frequency Level) × 2 (Hand) ANOVA revealed a main

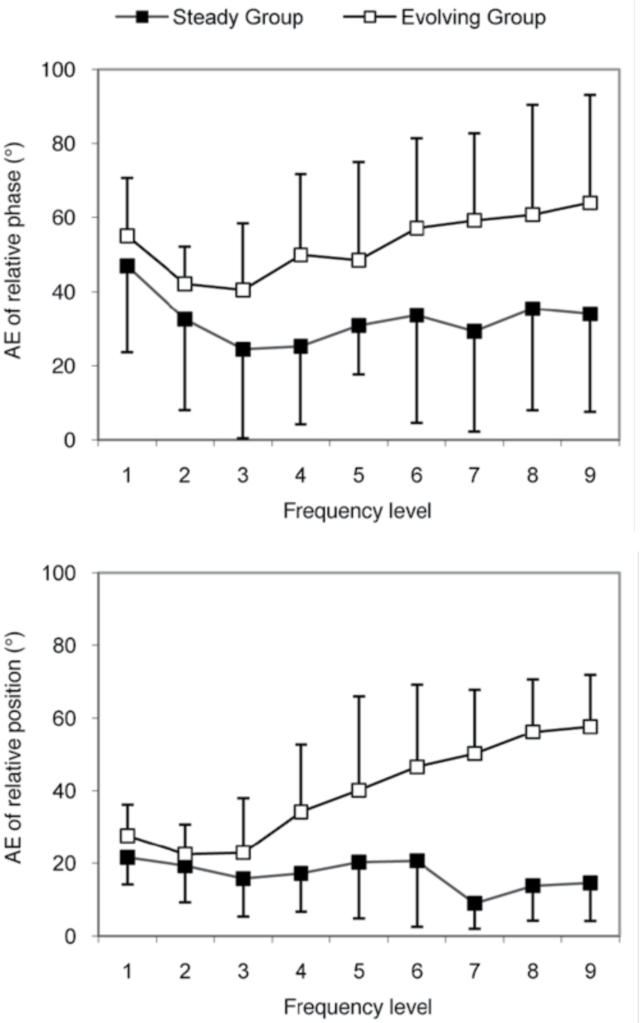

Figure 5 — Absolute error of relative phase (top panel) and relative position (bottom panel) as a function of Frequency Level for the Evolving Group (solid symbols) and the Steady Group (empty symbols). Vertical bars represent intersubject standard deviation. From the very beginning, AE of the Evolving Group is higher than that of Steady group.

significant effect of Frequency Level, $F(8,136) = 73.566$, $p < .000$, $\eta^2 = .814$. Participants increased movement frequency in response to the growing rate of the visual metronome. A significant quadratic polynomial contrast, $F(1,17) = 33.593$, $p < .000$, $\eta^2 = .664$, captured the trend reversal about 8th frequency level, describing the drop in number of cycles at the highest frequency level. These results suggest that the participants fulfilled the frequency requirements imposed by the task.

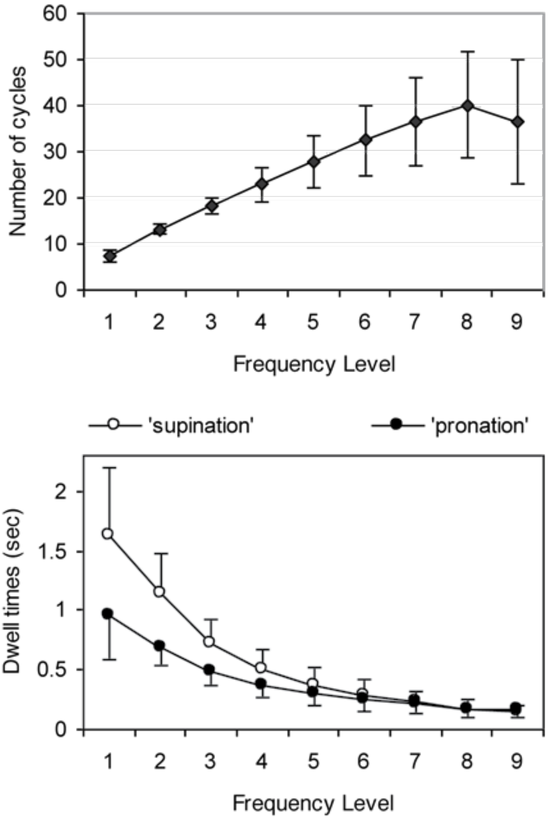

Figure 6 — Top Panel: number of cycles as a function of Frequency Level. Bottom Panel: dwell times as a function of Frequency Level for supination and pronation movements. Vertical bars represent intersubject standard deviation. The number of cycles increased and dwell times decreased with increasing movement frequency.

Dwell Times

Mean dwell times are displayed in Figure 6 (bottom panel), as a function of Frequency Level and Direction. A 9 (Frequency Level) × 2 (Hand) × 2 (Direction) ANOVA revealed main significant effects of Frequency Level, $F(8, 136) = 63.566$ $p < .000$, $\eta^2 = 0.789$, Direction ($F(1, 17) = 18.462$, $p < .000$, $\eta^2 = 0.521$, and a reliable Direction × Frequency Level interaction, $F(1.236, 21.012) = 9.342$, $p < .004$, $\eta^2 = 0.355$. Dwell times decreased with the increasing frequency of the visual metronome, a trend captured by a significant quadratic polynomial contrast, $F(1,17) = 32.699$, $p < .000$, $\eta^2 = .658$. Dwell times were longer in supination than in pronation, but this difference decreased with movement frequency. On the whole, these results indicate that dwell time progressively waned as movement frequency increased.

Harmonicity Index

Mean harmonicity index for the dominant and nondominant Hand is displayed in Figure 7 (top panel), as a function of Frequency Level. A 9 (Frequency Level) × 2 (Hand) ANOVA revealed a main significant effect of Hand, $F(1,17) = 5.672$, $p < .029$, $\eta^2 = .250$, and of Frequency Level, $F(8,136) = 294.523$, $p < .000$, $\eta^2 = .945$. Harmonicity was consistently higher for the dominant than for the nondominant hand ($M = 0.558$, $SD = 0.18$ vs $M = 0.529$, $SD = 0.17$, respectively), and increased with movement frequency. For both the dominant and nondominant hands, there was a significant polynomial cubic contrasts, $F(1,17) = 79.430$, $p < .000$, $\eta^2 = .824$ and $F(1,17) = 54.373$, $p < .000$, $\eta^2 = .762$, respectively, indicative of two reliable trend reversals. These results suggest that harmonicity increased following a nonlinear S-shaped evolution.

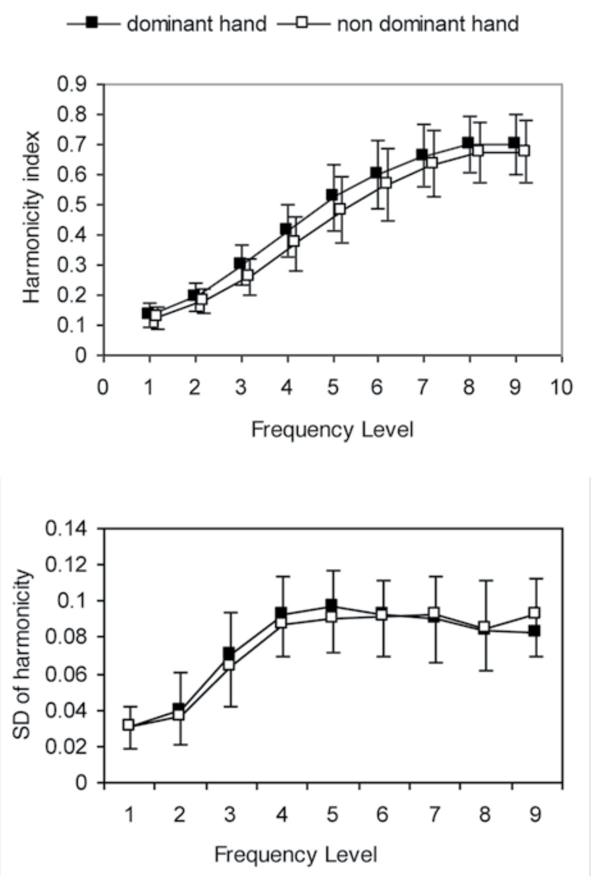

Figure 7 — Mean harmonicity index (top panel) and its *SD* (bottom panel) as a function of Frequency Level for the dominant (black square) and nondominant (white square) Hand. Vertical bars represent intersubject standard deviation. Mean harmonicity index and *SD* increased as a function of movement frequency.

SD of harmonicity index is displayed as a function of Frequency Level, in the bottom panel of Figure 7 for the dominant and nondominant hand, respectively. A 9 (Frequency Level) × 2 (Hand) ANOVA revealed a main significant effect of Frequency Level, $F(8,136) = 43.549, p < .000, \eta^2 = .719$, and a significant Hand × Frequency Level interaction, $F(8.136) = 2.183, p < .032, \eta^2 = .114$. For the dominant and the nondominant hands, there was a significant polynomial quadratic contrast, $F(1,17) = 108.723, p < .000, \eta^2 = .865$, and $F(1,17) = 71.018, p < .000, \eta^2 = .807$, respectively, reflecting a single trend reversal. These results suggest that the variability of harmonicity increased up to 4–5th frequency level and then remained stationary and that this difference is slightly different between the hands.

Interlimb Relative Phase

Mean absolute error of interlimb relative phase is displayed as a function of Frequency Level in the top panel of Figure 5. AE allows differentiating the Evolving Group whose performance tended toward 0° or 180° (empty symbols) from the Steady Group that remained closer to 90° (solid symbols).

For AE of relative phase, a 2 (Group) × 9 (Frequency Level) ANOVA revealed a main significant Group effect, $F(1, 16) = 9.315, p < .008, \eta^2 = .368$ and a significant Frequency Level × Group interaction, $F(8, 128) = 2.11, p < .039, \eta^2 = .314$. These results indicate that the accuracy of the Steady Groups was higher than that of the Evolving Group, and that this difference increased with Frequency Level. Linear Polynomial contrasts revealed that there was a reliable linear uptrend for the Evolving Group, $F(1, 10) = 6.142, p < .047, \eta^2 = .275$, and no reliable linear trend for the Steady Group, $\mathrm{F}(1,6) = .052, p = .828$, ns, $\eta^2 = .009$.

Variability (R) of interlimb relative phase is displayed as a function of Frequency Level in the top panel of Figure 8 for the Evolving (empty symbols) and the Steady Group (solid symbols). A 2 (Group) × 9 (Frequency Level) ANOVA revealed main significant effects of Frequency Level, $F(8,128) = 7.322, p < .000, \eta^2 = .314$ and of Group, $F(1.16) = 4.945, p < .041, \eta^2 = .211$. These results indicated that R decreased, that is, relative phase variability increased with movement frequency and that was larger for participants whose relative phase remained steady. These results suggest that the Evolving and the Steady Groups differed in accuracy as well as in variability.

Interlimb Relative Position

Mean AE of interlimb relative position is displayed as a function of Frequency Level in the bottom panel of Figure 5, illustrating the evolution of performance for the Evolving (empty squares) and the Steady Groups (solid squares). A 2 (Group) × 9 (Frequency Level) ANOVA carried out on AE revealed a main significant effect of Frequency Level, $F(8, 128) = 6.467, p < .000, \eta^2 = .288$, and of Group, $F(1, 16) = 15.875, p < .001, \eta^2 = 498$, as well as a significant Frequency Level × Group interaction, $F(8, 128) = 7.830, p < .000, \eta^2 = .498$. These results indicate that the accuracy of the Steady Groups was higher than that of the Evolving Group, and that this difference increased with Frequency Level. Linear Polynomial contrasts revealed that there was a reliable linear uptrend for the Evolving Group,

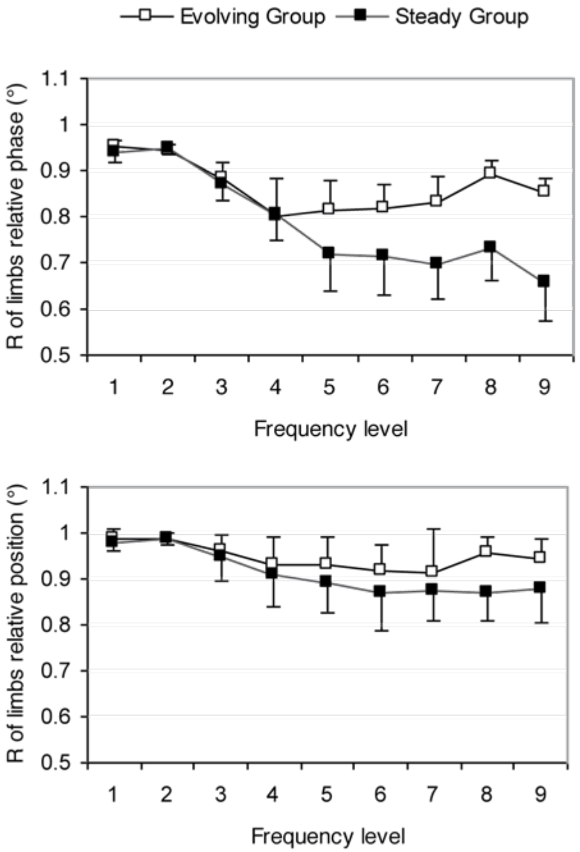

Figure 8 — Variability of relative phase (top panel) and relative position (bottom panel) as a function of Frequency Level, for the Steady and the Evolving Group (solid and empty symbols, respectively). Vertical bars represent intersubject standard deviation The lower R is, the larger variability. Variability increased with movement frequency..

$F(1, 10) = 53.428$, $p < 000$, $\eta^2 = .842$, but no reliable trend for the Steady Group, $F(1,6) = .173$, $p = .692$, ns, $\eta^2 = .028$.

Variability (R) of interlimb relative phase is displayed as a function of Frequency Level in the bottom panel of Figure 8 for the Evolving (empty symbols) and the Steady Group (solid symbols). A 2 (Group) × 9 (Frequency Level) ANOVA carried out on R revealed a main significant Frequency Level effect, $F(8,120) = 13.369$, $p < .0005$, $\eta^2 = .455$, and a significant Frequency Level × Group interaction, $F(8.128) = 2.091$, $p < .041$, $\eta^2 = .116$. These results indicated that R decreased, that is, limbs relative position variability increased with movement frequency and that this increase was larger for the participants whose relative position remained steady. These results revealed that the Evolving and the Steady Groups evolved in a different fashion in accuracy and in variability.

Limb Relative Position and Relative Phase

For each participant, individual correlation coefficients (*r*) between the 36 mean relative positions and 36 mean relative phases were computed, to assess the extent to which the two measures convey similar information. For all participants, there was a significant correlation between means, with *r* ranging from 0.72 to 0.96 ($p < .05$). There was also a significant correlation between R ($p < .05$),, which ranged from 0.74 to 0.91.

At first sight, these results suggest that relative position and relative phase provides congruent information. A closer look into the data revealed that 84% of mean relative positions were higher than the corresponding mean relative phases. Paired sample *t* test indicated that mean relative position was significantly larger than the corresponding mean relative phase ($t(17) = 10.146, p < .042$). This indicates that relative position provides slightly distinct information than relative phase: as it takes into account all sample data, it is quite sensitive to clustering at the reversal points due to the dwelling of the limbs.

Evolving vs. Steady Group Comparison at the Lowest Frequency Level

A 2 (Group) ANOVA on absolute error was performed to compare the Evolving and Steady Groups at the first Frequency Level. For interlimb relative phase, the analysis revealed that AE was higher for the Evolving than for the Steady Group, $F\,(1, 16) = 4.939, p < .04, \eta^2 = .236$). For interlimb relative position, the analysis indicated that AE was higher for the Evolving than for the Steady Group, $F\,(1, 16) = 5.052, p < .039, \eta^2 = .240$). These findings indicate that the Steady Group was more accurate than the Evolving Group at the first Frequency Level.

Thickness of Phase Space Trajectories

The thickness of phase plane trajectories is displayed as a function of the Extreme Position (minimum vs. maximum), the Variable (position vs velocity) and the two Frequency Levels (3rd vs. 9th) on Figure 9 for the Dominant Hand (bottom panel) of two individuals. For Dominant Hand, 2 (Extreme Position) × 2 (Frequency Level) × 2 (Variable) ANOVA revealed a significant Variable × Frequency Level, $F(1,17) = 32.754, p < .000, \eta^2 = .658$, and Extreme Point × Variable interactions, $F(1,17) = 24.324, p < .000, \eta^2 = .589$. In particular, at the third frequency level, the thickness of phase plane was larger for the extreme velocity than the extreme position, $F(1, 17) = 58.483, p < .000, \eta^2 = .775$. At the highest frequency level, there was no reliable difference between these variables, $\mathrm{F}(1, 17) = 3.129, p < .095$, ns, $\eta^2 = .155$. For the Non Dominant Hand, the same analysis indicated a main effect of Frequency Level, $F(1,17) = 5.084, p < .039, \eta^2 = .241$, and significant Variable × Frequency Level, $F(1,17) = 11.929, p < .003, \eta^2 = .427$, and Extreme Point × Variable interactions, $F(1,17) = 19.806, p < .000, \eta^2 = .553$. In particular, at the third frequency level, the thickness of phase plane was larger for the extreme velocity than the extreme position, $F(1, 17) = 8.837, p < .009, \eta^2 = .342$. At the highest frequency level, there was a reliable difference between these variables, $\mathrm{F}(1, 17) = 8.088, p < .012, \eta^2 = .336$.

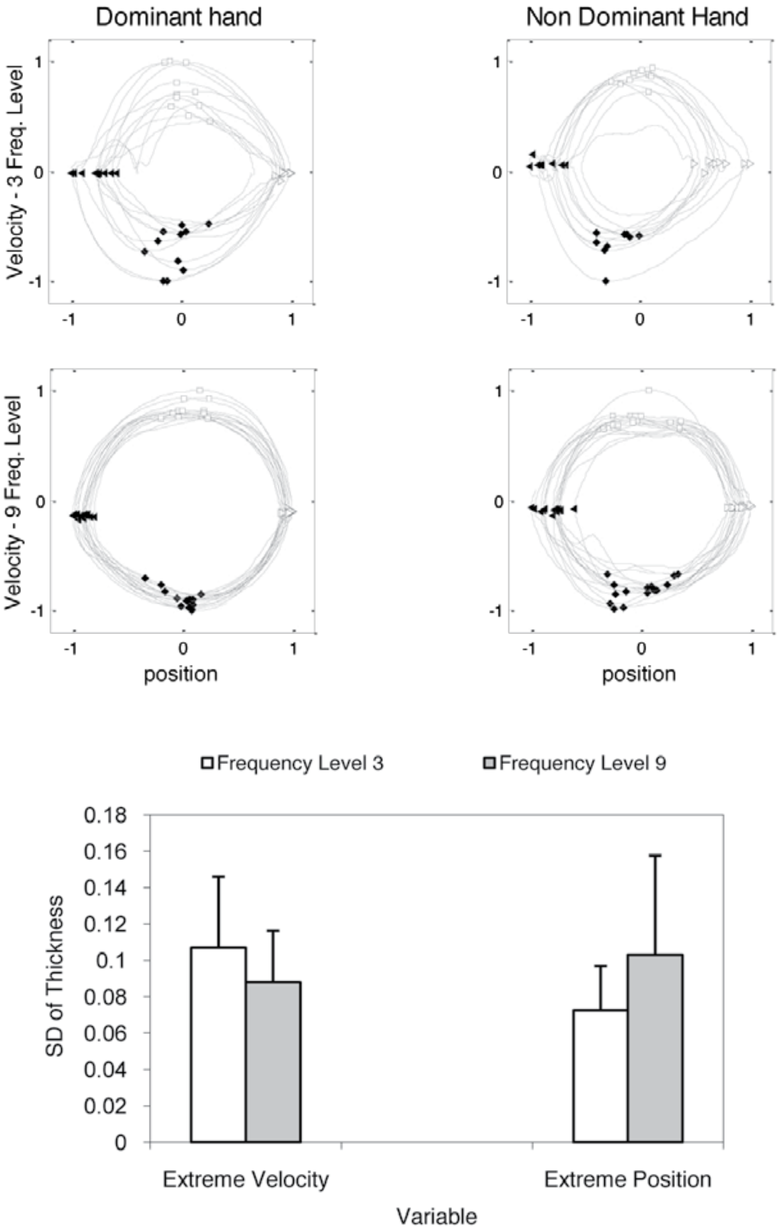

Figure 9 — Individual phase plots (top panels) for the Dominant and Non-Dominant Hand (left and right columns, respectively) and average thickness of the trajectories in phase space at remarkable points (bottom panel) for the Dominant Hand. In the individual phase plots (top panels), black and white triangles indicate reversal points, white and black diamonds peak velocity. In the bottom panel, vertical bars represent intersubject standard deviation.

Discussion

The twofold goal of the current study was to investigate the switch between a discrete and a continuous régime of bimanual motion, while some priming induces a nonpreferred 90° relative phase pattern. Accordingly, participants were initially required to produce a concatenated sequence yielding a 90° point-estimated relative phase. As movement frequency increased, dwell times decreased and harmonicity (HR) augmented, accompanied by a rise in the HR index variability. These findings suggest a passage from fairly discrete to continuous motion régime. Simultaneously, interlimb relative phase and relative position exhibited an uptrend or a downtrend in 61% of participants: The emerging coupling did its job at pulling—attracting—both limb movements toward the two preferred, 0° and 180° bimanual coordination patterns. But, there is more to it: 39% participants were able to sustain a nonpreferred pattern, in spite of the expected effect of coupling favoring 0° and 180°. Priming effect was able to circumvent the coordinative constraint imposed by rising coupling strength.

One can wonder how these few participants were able to remain close to the 90° pattern. An answer might be gleaned by examining the lowest, initial frequency level. Notably, these participants proved to be slightly more accurate than the other participants, who evolved toward either 0° or 180° patterns: they were closer to the required 90° by an amount of 8°. These results suggest that the slight initial difference in accuracy had large effects as frequency increased. These findings provide a novel instance of the impact that initial individual differences may have on the evolution of coordination patterns. Previous studies reported that initial individual differences affected the learning and memorization of nonpreferred patterns (Tallet, Kostrubiec, & Zanone, 2008; Zanone & Kelso, 1992). The experimental evidence provided here suggests that initial individual differences can also impact the emergence of nonpreferred patterns without any learning. A speculative answer to this trend toward increasing differences over time was suggested by Sherry & Schacter (1987). In case of incompatible task constraints (here, priming effect and coupling strength), what makes an individual behavior compatible with one constraint makes it incompatible with the other. As a result, an individual performance initially close to 90° will tend to get even closer, whereas an initial performance away from 90° will tend to depart further: So will individual differences increase, ultimately leading to distinct behaviors.

Our experimental work raises several issues. In the introduction, we grounded our expectations on the priming effect, that is, the facilitation of a required response due to the earlier production of another response, somewhat related to the required one. How the priming effect works in our situation, that is, what information and how it can be transferred from the discrete to the continuous motion régime remains an unanswered question. By construction, the concatenated sequence sets a time delay corresponding to a quarter of a cycle (i.e., 90° relative phase) between any equivalent positions of the two limbs, say, between reversal points or peak velocities. It has been suggested that essential information for coordination can be confined in essential local points of the movement cycle, often coined as anchors (Byblow, Carson, & Goodman, 1994) and that the effect of this local information could expand over the whole cycle (de Poel, Peper, & Beek, 2007; Fink, Foo, Jirsa, & Kelso, 2000; Kelso, & Jeka, 1992; Kelso, Fink, DeLapain, &

Carlson, 2001; Lagarde, & Kelso, 2006; Maslovat, Chua, Lee, & Franks, 2006). In our case, if a pattern close to 90° was produced at the anchor points in the discrete motion régime, it might well be that this essential information, that is, something specifying the 90° phase relationship,transfers to the continuous motion régime and extends then to the entire cycle.

In previous studies, anchors points were identified by the convergence of trajectories in phase space, that is, thinner parts in the phase plots. In our data, thickness was smaller for extreme positions (viz. reversal points) than for extreme velocities at the third frequency level, qualifying the former as anchors. With increasing movement frequency, however, the location of the point of minimal thickness changed in the direction of maximal velocity. This evolution in anchoring points makes it unclear how the priming effect is actually conveyed through the change in the movement régime.

Regarding our finding of nonpreferred pattern being sustained, all things considered, the persistence in the initial pattern is quite surprising. In previous studies investigating similar phenomenon, namely hysteresis, (Abernethy, Hanna & Plooy, 2002; Diedrich & Warren, 1995, 1998; Haken, Kelso, & Bunz 1985; Hoyt, & Taylor, 1981), participants persisted in the most preferred pattern despite a change in movement frequency allowing the emergence of less preferred ones. Our experiment indicate that the opposite effect is possible: A nonpreferred pattern was sustained despite the change in movement frequency favoring the preferred 0° and 180° patterns. To our knowledge, the only comparable findings reported in the literature are those by Siegel and Rachlin (1995) using behaviorist schedules. When pigeons were initially induced to adopt nonpreferred choices, they persisted in this nonpreferred choice despite the evolution of the reinforcement schedule toward conditions allowing the preferred one. The authors argued that this effect may pertain to some “cost” associated with behavioral change: Once a behavioral pattern begins, it would become more ”costly” to interrupt than to sustain it, even if it is a nonpreferred one (Rachlin, 1995). These findings suggest that the tendency to produce preferred patterns may be circumvented, because the motor system tends to avoid some cost associated with behavioral pattern change. The work by Temprado, Monno, Zanone and Kelso (2002) on the attentional cost associated to changing bimanual patterns lends some support to this assumption. The authors showed that attentional cost increases in the vicinity of the switch between 180° and 0° patterns.

Overall, these two abovementioned issues pertain to a broader and basic issue as to understanding the relationship between the discrete and the continuous motion régime. Buchanan, Park, and Shea (2006) reported typical hallmarks of nonlinear transitions from a discrete to a continuous movement (see Introduction) and claimed that these movements belong indeed to two distinct regimes of motion (Huys, et al., 2008; Jirsa, & Kelso, 2005) or two distinct units of action (Buchanan, Park, Ryu, & Shea, 2003; van Mourik & Beek, 2004). Additional support for a qualitative difference between discrete and continuous motion is that they may involve different neural underpinnings (Schaall, Sternad, Osu, & Kawato, 2004): Patients with cerebellar lesions exhibit deficits in discontinuous movements only (Spencer, Zelaznick, Diedrichsen, & Ivry, 2003). In our data, the S-shaped evolution of harmonicity and its increase in variability is quite in line with such a conceptualization.

Yet, the distinction between discrete and continuous motion régime calls for further investigation. The issue can be cast in terms of a trade-off between the advantages and disadvantages offered by continuous vs. discrete motion. Harmonic movements are known to be less "effortful" than discrete movements, because mechanical energy can be stored in an elastic form before movement reversals and be released back to the benefit of moving in the other direction. In contrast, in the discrete movement, all the kinetic energy available at reversals is dissipated, since the movement stops, so that the initial impulse of the next half-cycle should be created anew (Adam, & Paas, 1996; Adam, Paas, & Eyssen, 1995). One can wonder what advantages offered by the discrete motion régime induce the motor system to adopt such biomechanically suboptimal configuration.

A first explanation comes from an information processing approach. In a unimanual Fitts task, in which one limb must continuously travel between two targets, discrete motion spontaneously appears in conditions with a high index of difficulty (Mottet, & Bootsma, 1999). Decreasing the velocity close to the reversals favors motor control by increasing the time available for visual feedbacks to operate and for movement to be monitored at these points (Adam, & Paas, 1996).

A second explanation comes from a dynamical system approach. Our intuition is that the apparently disadvantageous strategy of losing harmonicity allows the motor system to rapidly stabilize the required motor outcome, because it offers an escape from the preferred patterns defined by coupling strength. Several findings lend support to this proposal. In a task akin to ski slalom, in which periodic sideways movements should be made on a simulator, learners first performed discrete lateral movements, to rapidly put up with a motor outcome consistent with the device. Numerous additional practice trials were then required to initiate a slow progress toward a harmonic régime (Nourrit, Delignières, Caillou, Deschamps, & Lauriot, 2003; Teulier, Nourrit, & Delignières, 2006). The authors suggested that stopping at reversals allowed the motor system to weaken the coupling constraints and to master the task rapidly. It is only once this first suboptimal outcome is learned that the motor system would slowly converge to the less effortful, biomechanically more optimal, continuous movement.

A third explanation is suggested by the work of Zanone and Kelso (1997; Kelso, 2008), in which participants had to learn a nonpreferred bimanual pattern. A closer look at the reported data reveals that after a successful learning of 90° (or 270°), movement trajectory departed from continuous harmonic motion régime. Short epochs of congruent performance with the required relative phase alternated with longer periods of relative phase wrapping, these being interspersed with short periods where relative phase remained close to 0° or 180°. This spontaneous change in limbs kinematics had the advantage to allow the coordination system to comply with opposing demands: to simultaneously produce the nonpreferred pattern required by the task and the preferred patterns required by coupling strength. Thanks to such a compromise, the coordination system may go beyond a simple fixed phase-locking, thus avoiding to be trapped into a unique, if coherent coordination state (Kelso, 2008). If the suggestion might be right, it would attests to the truly adaptive nature of the coordination system, which is capable of subtle and flexible compliance with multiple, even competing demands—quite a critical strategy in the face of a complex and conflicting environment.

A final comment concerns hand dominance. In our experiment, the increase in harmonicity and increase in HR variability was slightly larger for the dominant than for the nondominant hand. The dominant hand appears to lead the nondominant hand in the switch from a discrete to a continuous régime. This asymmetry in discreteness may introduce an asymmetry in the arising coupling strength. To date, asymmetries in coupling strength were reported as pertaining to handedness (de Poel, et al., 2007; Treffner, & Turvey, 1996) and to different amplitudes in the hand movement (Peper, Boer, de Poel, & Beek, 2008).

To sum up, in the current study, we set two effects in conflict: the priming effect, which entailed the persistence in nonpreferred pattern, close to 90°, and the interlimb coupling strength, which favored the 0° and 180° patterns. A minority of the participants profited from the priming effect, allowing them to sustain the nonpreferred pattern at high movement frequencies, while the majority evolved, sort of naturally, toward 0° or 180° pattern. A first lesson here is that the tendency to produce spontaneously stable patterns may be circumvented by the priming effect, favoring the rise of nonpreferred patterns. A second lesson is that initial differences between individual participants have a critical impact on the future evolution of motor coordination and performance. However small initially, interindividual differences may eventually give rise to large differences in the longer run.

References

Abernethy, B., Hanna, A., & Plooy, A. (2002). The attentional demands of preferred and non-preferred gait patterns. *Gait & Posture, 15,* 256–265.

Adam, J.J., & Paas, F.G.W.C. (1996). Dwell time in reciprocal aiming tasks. *Human Movement Science, 15,* 1–24.

Adam, J.J., Paas, F.G.W.C., Eyssen, I.C.J.M., Slingerland, H., Bekkering, H., & Drost, M.R. (1995). The control of two-element, reciprocal aiming movements: Evidence for chunking. *Human Movement Science, 14,* 1–11.

Amazeen, P.G. (2002). Is dynamics the content of a generalized motor program for rhythmic interlimb coordination? *Journal of Motor Behavior, 34,* 233–251.

Atchy-Dalama, P., Peper, C.E., Zanone, P.G., & Beek, P.G. (2005). Movement-related sensory feedback mediates the learning of a new bimanual relative phase pattern. *Journal of Motor Behavior, 37,* 186–196.

Batschelet, E. (1981). *Circular statistics in biology*. London: Academic Press.

Buchanan, J.J., Park, J.H., & Shea, C.H. (2006). Target width scaling in a repetitive aiming task: switching between cyclical and discrete units of action. *Experimental Brain Research, 175,* 710–725.

Buchanan, J.J., Park, J.H., Ryu, Y.U., & Shea, C.H. (2003). Discrete and cyclical units of action in a mixed target pair aiming task. *Experimental Brain Research, 150,* 473–489.

Byblow, W.D., Carson, R.G., & Goodman, D. (1994). Expressions of asymmetries and anchoring in bimanual coordination. *Human Movement Science, 13,* 3–28.

Cincotta, M., & Ziemann, U. (2008). Neurophysiology of unimanual motor control and mirror movements. *Clinical Neurophysiology, 119,* 744–762.

Daffertshofer, A., van den Berg, C., & Beek, P.G. (1999). A dynamical model for mirror movements. *Physica D. Nonlinear Phenomena, 132,* 243–266.

Delignières, D., Nourrit, D., Sioud, R., Leroyer, P., Zattara, M., & Micaleff, J.P. (1998). Preferred coordination modes in the first steps of the learning of a complex gymnastics skill. *Human Movement Science, 17,* 221–241.

De Poel, H.J., Peper, C.L., & Beek, P.G. (2007). Handness-related assymetry in coupling strength in bimanual coordination: furthering theory and evidence. *Acta Psychologica, 124,* 209–237.

Diedrich, F.J., & Warren, W.H. (1995). Why change gaits? Dynamics of the walk-run transition. *Journal of Experimental Psychology. Human Perception and Performance, 21,* 183–202.

Diedrich, F.J., & Warren, W.H. (1998). The dynamics of gait transitions: Effects of grade and load. *Journal of Motor Behavior, 30,* 60–78.

Ferguson, G.A., & Takane, Y. (1989). *Statistical analysis in psychology and education.* New York: McGraw-Hill.

Fink, P., Foo, P., Jirsa, V.K., & Kelso, J.A.S. (2000). Local and global stabilization of coordination by sensory information. *Experimental Brain Research, 134,* 9–20.

Fontaine, R.J., Lee, T.D., & Swinnen, S.P. (1997). Learning a new bimanual coordination pattern: reciprocal influencies of intrinsic and to-be-learned patterns. *Canadian Journal of Experimental Psychology, 51,* 1–9.

Friedman J, SKM V, Zatsiorsky VM, Latash ML. (2009). The sources of two components of variance: An example of multifinger cyclic force production tasks at different frequencies. *Experimental Brain Research, 196,* 263–277.

Franz, E.A., & Ramachandran, V.S. (1998). Bimanual coupling in amputees with phantom limbs. *Nature Neuroscience, 6,* 443–444.

Guiard, Y. (1993). On Fitts' and Hooke's laws: simple harmonic movement in upper-limb cyclical aiming. *Acta Psychologica, 82,* 139–159.

Guiard, Y. (1997). Fitts' law in the discrete vs. continuous paradigm. *Human Movement Science, 16,* 97–131.

Haken, H., Kelso, J.A.S., & Bunz, H. (1985). A theoretical model of phase transitions in human movements. *Biological Cybernetics, 51,* 347–356.

Helbig, H.B., Steinwender, J., Graf, M., & Kiefer, M. (2010). Action observation can prime visual object recognition. *Experimental Brain Research, 200,* 251–258.

Hodges, N.J., & Franks, I.M. (2002). Learning as a function of coordination bias: building upon pre-practice behaviours. *Human Movement Science, 21,* 231–258.

Hogan, N., & Sternad, D. (2007). On rhythmic and discrete movement: Reflections, definitions and implications for motor control. *Experimental Brain Research, 181,* 13–30.

Hoyt, D.F., & Taylor, C.R. (1981). Gait and the energetics of locomotion in horses. *Nature, 292,* 239–240.

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.

Huys, R., Studenka, B.E., Rheaume, N.L., Zelaznik, H.N., & Jirsa, V.K. (2008). Distinct timing mechanisms produce discrete and continuous movements. *PLoS Computational Biology, 4,* e100061.

Jirsa, V.K., & Kelso, J.A.S. (2005). The excitator as a minimal model for the coordination dynamics of discrete and rhythmic movements. *Journal of Motor Behavior, 37,* 35–51.

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. (2008). An essay to understanding the mind. *Ecological Psychology, 20,* 180–208.

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., Fink, P., DeLaplain, C.R., & Carson, R.G. (2001). Haptic information stabilizes and destabilizes coordination dynamics. *Proceedings. Biological Sciences, 268,* 1207–1213.

Kelso, J.A.S., Southard, D., & Goodman, D. (1979). On the nature of human interlimb coordination. *Science, 203,* 1029–1031.

Lagarde, J., & Kelso, J.A.S. (2006). Binding of movement, sound and touch: multimodal coordination dynamics. *Experimental Brain Research, 173,* 673–688.

Lee, T.D., Swinnen, S.P., & Verschueren, S. (1995). Relative phase alterations during bimanual skill acquisition. *Journal of Motor Behavior, 27,* 263–274.

Levin, O., Suy, E., Huybrechts, J., Vangheluwe, S., & Swinnen, S.P. (2004). Bimanual coordination involving homologous and heterologous joint combinations: when lower stability is associated with higher flexibility. *Behavioural Brain Research, 152,* 437–445.

Maslovat, D., Chua, R., Lee, T.D., & Franks, I.M. (2006). Anchoring strategies for learning a bimanual coordination pattern. *Journal of Motor Behavior, 38,* 101–117.

Mottet, D., & Bootsma, R. J. (2001). The dynamics of rhythmical aiming in 2D task space: relation between geometry and kinematics under examination. *Human Movement Science*, 213-241.

Mottet, D., Guiard, Y., Ferrand, T., & Bootsma, R.J. (2001). Two-handed performance of a rhythmical fitts task by individuals and dyads. *Journal of Experimental Psychology. Human Perception and Performance, 27,* 1275–1286.

Mottet, D., & Bootsma, R.J. (1999). The dynamics of goal-directed rhythmical aiming. *Biological Cybernetics, 80,* 235–245.

van Mourik, A.M., & Beek, P.G. (2004). Discrete and cyclical movements: unified dynamics or separate control? *Acta Psychologica, 117,* 121–138.

Nourrit, D., Delignières, D., Caillou, N., Deschamps, T., & Lauriot, B. (2003). On discontinuities in motor learning: A longitudinal study of complex skill acquisition on a ski-simulator. *Journal of Motor Behavior, 35,* 151–170.

Peper, C.E., Boer, B.J., de Poel, H.J., & Beek, P.G. (2008). Interlimb coupling strength scales with movement amplitude. *Neuroscience Letters, 437,* 10–14.

Rachlin, H. (1995). Self-control: Beyond commitment. *The Behavioral and Brain Sciences, 18*(1), 109–159.

Ridderikhoff, A., Peper, L.E., & Beek, P.G. (2006). Bilateral phase entrainment by movement-elicited afference contributes equally to the stability of in-phase and antiphase coordination. *Neuroscience Letters, 399,* 71–75.

Rosenblum, M., Pikovsky, A., Kurths, J., Schaefer, C., & Tass, P. (2001). Phase synchronization: from theory to data analysis. In F. Moss & S. Gielen (Eds.), *Handbook of Biological Physics, vol. 4, Neuro-Informatics*, (pp. 279-321), Amsterdam: Elsevier Science.

Schaal1, S., Sternad, D., Osu, R. & Kawato, M. (2004). Rhythmic arm movement is not discrete. *Nature Neuroscience, 7*, 1136-1143.

Schacter, D.L., Chiu, C.Y.P., & Ochsner, K.N. (1993). Implicit Memory: A Selective Review. *Annual Review of Neuroscience, 16,* 159–182.

Schöner, G. (1990). A dynamic theory of coordination of discrete movement. *Biological Cybernetics, 63,* 257–270.

Sherry, D.F., & Schacter, D.L. (1987). The Evolution of Multiple Memory Systems. *Psychological Review, 94,* 439–454.

Siegel, E., & Rachlin, H. (1995). Soft commitment: self-control achieved by response persistence. *Journal of the Experimental Analysis of Behavior, 64,* 117–128.

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.

Spencer, R., Zelaznick, H., Diedrichsen, J., & Ivry, R.B. (2003). Disrupted timing in discontinuous but not continuous movements by cerebellar lesions. *Science, 300,* 1437–1439.

Tallet, J., Kostrubiec, V., & Zanone, P.G. (2008). Role of stability in the dynamics of learning, memorizing and forgetting coordination patterns. *Journal of Motor Behavior, 40,* 103–116.

Tayler, M.A., & Davids, K. (1997). Catching with both hands: An evaluation of neural cross-talk and coordinative structure models of bimanual coordination. *Journal of Motor Behavior, 29,* 254–262.

Temprado, J.J., Monno, A., Zanone, P.G., & Kelso, J.A.S. (2002). Attentional demands reflect learning-induced alterations of bimanual coordination dynamics. *The European Journal of Neuroscience, 16,* 1390–1394.

Temprado, J. J., Zanone, P.G., Monno, A., & Laurent, M. (1999). Attentional load associated with performing and stabilizing perferred bimanuals patterns, *Journal of Experimental Psychology: Human Perception and Performance, 25*, 1579-1594.

Teulier, C., Nourrit, D., & Delignières, D. (2006). The evolution of oscillatory behavior during learning on a ski-simulator. *Research Quarterly for Exercise and Sport, 77,* 464–475.

Treffner, P.G., & Turver, M.T. (1996). Symmetry, broken symmetry, and handedness in bimanual coordination dynamics. *Experimental Brain Research, 107*, 463 478.

Tulving, E., & Schacter, D.L. (1990). Priming and human memory systems. *Science, 247,* 301–306.

Walter, C.B., & Swinnen, S.P. (1992). Adaptative tuning of interlimb attraction to facilitate bimanual decoupling. *Journal of Motor Behavior, 24,* 95–104.

Wenderoth, N., & Bock, O. (2001). Learning of a new bimanual coordination pattern is governed by three distinct processes. *Motor Control, 5,* 23–35.

Wenderoth, N., Bock, O., & Krohn, R. (2002). Learning a new bimanual coordination pattern is influentiated by existing attractors. *Motor Control, 6,* 166–182.

Zanone, P.G., & Kelso, J.A.S. (1992). Learning and transfer as dynamical paradigms for behavioral change. G.E. Stelmach & J. Requin (Eds.), *Tutorials in Motor Behavior II*, 563-582. Amsterdam: North Holland.

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.