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The spontaneous recruitment and suppression of degrees of freedom in rhythmic hand movements

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Abstract

In most studies examining pattern switching in biological coordination, emphasis is placed on identifying the mechanisms underlying bifurcations in an already active set of components. Less well understood are the processes by which quiescent degrees of freedom (*df*) are recruited and active *df* suppressed. To examine such behavior, we studied four bimanual and two unimanual coordination patterns. Subjects produced the patterns in time with an auditory metronome whose frequency increased from 1.5 to 4.25 Hz in 0.25 Hz steps. Interlimb transitions from asymmetric to symmetric patterns in a motion plane occurred at critical cycling frequencies, f_1 . Spatial transitions, characterized by recruitment of y -(vertical) and suppression of x -(horizontal) motion, also occurred at critical cycling frequencies, f_2 . This recruitment–suppression process was either abrupt (2–3 cycles) or gradual (1 to 6 plateaus) where the finger-tips traversed an elliptical orbit in x, y space. Similar spatial transitions were observed in unimanual conditions. The results are discussed in reference to the problem of how task-specific coordination patterns are modified. The Hopf bifurcation is presented as a generic mechanism underlying the recruitment and suppression of *df*. Similarities between the four component bimanual pattern dynamics and the coordination dynamics of four limb patterns (e.g., in quadrupeds) are discussed.

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1. Introduction

A ubiquitous feature of human and animal coordination is the ability to assemble task-specific coordinative patterns in the form of phase and frequency mode-locked states among participating components. In many circumstances, the task-defined goal may remain constant while environmental conditions undergo change. How is task-specific behavior flexibly modified under such conditions? In many experimental model systems, it has been demonstrated that the modification of task-specific coordinative patterns can take one of three archetypal forms (Kelso, 1994, for review): (1) pattern switching among states of absolute coordination; (2) the onset of relative coordination; and (3) spontaneous recruitment of previously quiescent *df* and suppression of active *df*. Theoretically, such coordinative changes have been linked to specific dynamical mechanisms in nonlinear dynamical systems: for example, pattern switching has been modeled as an inverted pitchfork bifurcation (Haken et al., 1985) and relative coordination has been linked to intermittency and saddle-node bifurcations (DeGuzman and Kelso, 1991; Kelso et al., 1990). The *recruitment* and *suppression* of *df*, however, has received relatively less attention, even though it has been documented, e.g., the recruitment of vertical flexion–extension of the back during the gallop in the horse and cheetah (Grillner, 1975, 1981). It has also recently been observed in the coordination among the upperarm, forearm and trunk in a reaching and grasping task (see e.g., Kelso et al., 1994). However, this form of flexible modification of a coordinative pattern is not well understood. The present experiment is specifically designed to study the coordination dynamics underlying the recruitment and suppression of *df* in biological coordination. A preliminary report is provided in Kelso et al. (1993).¹

An extensive amount of experimental and theoretical work has shown that the synergetic concepts of *order parameter*, *multistability* and *loss of stability*, as well as the tools of nonlinear dynamical systems provide a plausible basis for understanding biological coordination (see e.g., Haken, 1983; Kelso and Schöner, 1987; Schöner and Kelso, 1988; Turvey, 1990). The experimental strategy of scaling the system to a critical value of some non-specific *control parameter* has proven valuable in identifying the underlying mechanisms of pattern stabil-

¹ A brief description of the observed transitions in this experiment may be found in Kelso et al. (1993). In that manuscript, emphasis was placed on developing a Hopf bifurcation model of the observed spatial transitions. Here, we present a detailed quantitative analysis of the transitions studying the stability of the patterns before and after qualitative change. A brief discussion of the Hopf bifurcation model is presented for the sake of completion.

ity, switching and relative coordination. This experimental strategy provides an opportunity to identify critical points in task-specific coordination where pattern switching occurs or slips or jumps in coordination arise. It is near these points of pattern change that a system's relevant coordination variables or *order parameters* and their *dynamics* (equations of motion) may be identified (e.g., Haken et al., 1985; Kelso and Schöner, 1987). In a variety of experiments, the relative phasing ϕ between active components has been shown to undergo abrupt jumps when a change in pattern occurs. For example, transitions from anti-phase to in-phase patterns in bimanual coordination tasks (Kelso, 1981, 1984), perception-action coordination (Kelso et al., 1990; Wimmers et al., 1992), and single limb multijoint movements (Buchanan and Kelso, 1993; Kelso et al., 1991a) are all characterized by an abrupt shift in the relative phase between the active components from $\phi \approx 180^\circ$ to $\phi \approx 0^\circ$. Subsequent modeling of these transitions has shown that relative phase acts as an *order parameter* governing the formation and change of coordinative patterns in these experimental systems (see e.g., Haken et al., 1985; Kelso et al., 1990; Schöner et al., 1986). The observation of *critical phenomena*, e.g., critical fluctuations (Buchanan and Kelso, 1993; Carson et al., 1995; Kelso and Scholz, 1985; Kelso et al., 1986; Schmidt et al., 1990) and critical slowing down (Buchanan and Kelso, 1993; Scholz and Kelso, 1989; Scholz et al., 1987), in the order parameter relative phase ϕ before the transition indicates that *loss of stability* is the mechanism underlying pattern switching. When pattern switching results from loss of stability, the behavior is said to be self-organized.

Stability and loss of stability also play an essential role in relative coordination. Loss of entrainment in periodically driven single limb movements (Kelso et al., 1990) and switching from higher order (5:3, 4:3) to low order (1:1, 1:2) frequency ratios in bimanual coordination (e.g., DeGuzman and Kelso, 1991; Kelso and DeGuzman, 1988; Peper et al., 1995; Treffner and Turvey, 1993) are both governed by the tendency of the components to synchronize in either in-phase or anti-phase (absolute) coordinative states. The tendency to synchronize and the conflict between sustaining a specific frequency ratio or pacing with an external source (whose frequency changes) in these tasks leads to jumps between frequency ratios and phase slippage, both characteristic of relative coordination. In these situations, depending on the value of the control parameter, movement frequency, the attraction may be toward in-phase or anti-phase (low frequencies), in-phase only (intermediate frequencies), or neither (very fast frequencies) (see e.g., Byblow et al., 1994; DeGuzman and Kelso, 1991; Kelso et al., 1991b, 1990). This results from the differential stability of the patterns as a function of cycling frequency, as evident in the bimanual transition experi-

ments of Kelso (1981, 1984) and Kelso and Scholz (1985) (see also, Kelso et al., 1986; Schöner et al., 1986).

Another important feature of the pattern switching and relative coordination work is the connection between these flexible forms of coordinative modification and generic bifurcations of dynamical systems (Kelso, 1994). Switching between coordinative patterns takes the form of inverted pitchfork bifurcations. This type of bifurcation is characteristic of a jump from an unstable to stable *fixed point* attractor as a control parameter is systematically varied. Provided certain time scale assumptions are met, systems undergoing this type of bifurcation are characterized by loss of stability and increases in local relaxation time near the transition point (Schöner et al., 1986). The onset of relative coordination takes the form of a tangent bifurcation in the region of a destabilized saddle-node which contains both a stable and unstable direction. Systems undergoing this type of bifurcation tend to spend some time in the vicinity of the stable fixed point (phase- and frequency-entrained states) and then escape (phase slippage, jumps etc.) along the unstable direction. The underlying mechanism of this type of behavior in nonlinear dynamical systems near tangent bifurcations is intermittency. As a mechanism of coordinative change, intermittency provides biological systems with the ability to switch in and out of nearly mode-locked states (Kelso et al., 1990).

The functional features of multistability, pattern switching and relative coordination arise from the nonlinear interactions among the system's many individual components. The essential feature of the experimental and theoretical work reviewed above is the demonstration that the behavior of biological systems can be described in a low-dimensional space. By viewing biological coordination as a pattern formation process and focusing on the properties of multistability and pattern switching, we believe that very similar self-organizing processes may underlie the recruitment and suppression of *df*.

As a springboard into the recruitment–suppression problem, we explore in more detail a serendipitous finding first reported by Kelso and Scholz (1985). In the original bimanual experiments of Kelso (1981, 1984), the finger or wrists were free to move only on the horizontal plane (x), i.e., only one kinematic degree of freedom was active. However, Kelso and Scholz (1985) observed that through the removal of this constraint, i.e., subjects were allowed to move on both the horizontal (x) and vertical (y) planes (two kinematic *df*), some very interesting things may occur in a simple bimanual coordination task. For example, with the forearms prone and index fingers parallel to the floor (horizontal plane), Kelso and Scholz observed transitions from asymmetric (simultaneous activation of non-homologous muscles) to symmetric (simulta-

neous activation of homologous muscles) coordination patterns at a critical cycling frequency (around 2.0 to 2.5 Hz). Following this transition, the fingers lifted off the x -plane by recruiting motion in the y -direction at the highest frequencies in their experiment (3.25 and 3.5 Hz). This recruitment of y -motion occurred in both initial patterns of coordination, symmetric and asymmetric. In some cases, the trajectories of the fingers became rotary and in other cases an abrupt jump from the horizontal (suppress x -motion) to vertical (recruit y -motion) plane of motion occurred. The observation of this second unexpected transition raises several issues not investigated by Kelso and Scholz. What are the underlying dynamics (e.g., stability, loss of stability, bifurcation mechanism) of these recruitment–suppression processes? What influence does recruiting and suppressing df have on the ongoing coordinative pattern's dynamics? How flexible is this recruitment and suppression process? To answer these questions, we extended the Kelso and Scholz (1985) experiment in three ways: (1) subjects initiated coordinative patterns at a higher frequency (1.5 Hz compared to a preferred pace < 1.5 Hz); (2) we scaled subjects to higher movement frequencies (4.25 Hz compared to 3.5 Hz); and (3) we studied both horizontal and vertical symmetric and asymmetric patterns. Here we show through an appropriate coordinate transform one-way to qualitatively characterize recruitment–suppression processes and quantitatively measure the dynamics (multistability, loss of stability, pattern switching) of such processes in this four component (x , y motion of two fingers) system.

2. Methods

2.1. Subjects

Six adults, 21 to 45 years of age, volunteered for this experiment. All subjects were graduate or undergraduate students attending Florida Atlantic University and were naive to the purpose of the experiment.

2.2. Apparatus

Abduction–adduction (horizontal plane) and flexion–extension (vertical plane) motions of the index fingers were recorded with the WATSMART™ 3D motion analysis system. Light weight infra-red light emitting diodes (IREDs) were attached to the tips of the index fingers and head of the 2nd metacarpophalangeal joint. The calibration error across sessions ($n = 6$) was 1.79 mm

($sd = 0.17$). The finger apparatus consisted of a pair of plastiform molds and a horizontal bar mounted on a small table positioned at the subject's waist. The forearms were secured in a prone position in the plastiform molds with velcro straps to eliminate extraneous movement of the wrists and elbows. The fingers of each hand extended over the horizontal bar with the index fingers parallel to the floor and digits III through V secured in a flexion position. The thumbs extended under the horizontal bar to form a grip. An auditory metronome was simulated by a series of 50 ms square wave pulses output through an RS232 port (Mac II) connected to an external speaker. An IBM PC/AT was used for data acquisition and storage.

2.3. Procedures and conditions

Subjects produced six rhythmic coordination patterns in time with an auditory metronome whose frequency increased. Four of these were bimanual patterns: two abduction–adduction patterns, horizontal symmetric (HS) (simultaneous activation of homologous muscle groups) and asymmetric (HAS) (simultaneous activation of non-homologous muscle groups), ten trials each; and two flexion–extension patterns, vertical symmetric (VS) and asymmetric (VAS), five trials each. The other two patterns required unimanual abduction–adduction of the left (LF) and right (RF) index fingers in the horizontal plane, five trials each. The ten trials for the horizontal conditions were split into blocks of five trials and each subject performed 40 trials in eight experimental blocks, six bimanual and two unimanual. The trial blocks were randomized across subjects. The required pacing frequency, f_r , increased from 1.5 Hz to 4.25 Hz in 0.25 Hz steps with 12 cycles of motion per step.² Each trial was 56 sec in length and the experiment lasted approximately 1 hour with subjects receiving approximately a 2 min rest between trial blocks. The main task was to produce the required coordination pattern while maintaining a 1:1 frequency synchronization with the auditory metronome. Subjects were instructed to maintain the initial pattern of coordination for as long as possible, but if they should feel the pattern begin to change '*not to intervene*', but to adopt whatever pattern of coordination felt most

² Plateau length was set to a constant number of cycles in this experiment for two reasons. First, our longest plateau was 8 sec for 1.5 Hz. Twelve plateaus at this length correspond to a 96 sec trial. Trials of this length with frequencies above 4 Hz may produce considerable fatigue. Based on subject reports, fatigue did not seem a problem with trials of 1 minute in length. Second, trials could have been kept to around 1 minute with only 3 to 4 cycles in our slower plateaus, 1.5 to 2.0 Hz. The issue at this end, is whether or not a reliable measure of stability is achievable with so few cycles. To circumvent the fatigue issue and accurately measure stability, plateau length was held constant as a function of cycle number and not plateau length.

comfortable. The subjects were familiarized with each pattern before starting the experimental trials.

2.4. Data analysis

The IREDs were sampled at 200 Hz and the raw data were transformed into 3 dimensional coordinates using a direct linear transformation. There were a total of 144 cycles of motion per trial and approximately 5760 cycles of data were analyzed for each subject. Based on a previous convention, wherein the relative phase ϕ between the fingers was treated as an order parameter (e.g., Haken et al., 1985), the symmetric and asymmetric patterns, whether horizontal or vertical, may be characterized by relative phase values of $\phi \approx 0^\circ$ and $\phi \approx 180^\circ$, respectively. With this definition we note that the symmetry of the patterns does not depend on the plane of motion. However, distinguishing between patterns with the same symmetry in different motion planes requires the explicit specification of the plane of motion, i.e., horizontal (x) or vertical (y). Relative phase, as defined previously, cannot uniquely characterize the four bimanual patterns. To achieve a unified description of the patterns, a coordinate transformation was performed such that the x and y amplitudes of the fingers were approximately constant. The purpose of the transformation was to derive a relative phase vector, $\vec{\phi}$, that uniquely described the four initial patterns and transitions.

First, we assume that the x and y projections of each component can be represented by a sinusoidal waveform with a fixed amplitude and a constant time varying argument, phase ϕ . This allows each initial bimanual pattern to be described with four individual component phases at any time t , or if one phase is fixed, then only three relative phases between the components are needed. Due to the transitions between planes, the four amplitudes of motion can change drastically in time. Projections onto the horizontal (or vertical) axis are appreciable only if the motion is predominantly horizontal (or vertical). To circumvent this difficulty, the coordinate axes are rotated so that at any time t there are comparable amplitudes in both directions. Let (x, y) and (x', y') be the coordinates of a component finger in the original and rotated coordinate system, respectively. Then,

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = A \begin{pmatrix} x \\ y \end{pmatrix}, \quad (1)$$

where

$$A = C_i \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix},$$

and

$$C_i = \begin{cases} -1, & i = l, \\ 1, & i = r, \end{cases} \quad (3)$$

where $\theta = \pi/4$ and the indices 'l' and 'r' refer to the left and right fingers, respectively. The x' and y' time series from the left finger in the horizontal conditions are multiplied by -1 to accommodate the symmetry feature of the physiological coordinate system, i.e., signals peaking in the same direction are really asymmetric based on the contraction of the underlying muscle groups (e.g., Kelso, 1984; Kelso and Scholz, 1985). To remain consistent, the vertical left finger signals are also multiplied by -1 . Within this new frame of reference, component amplitude has been eliminated from the description of the patterns and each pattern can now be characterized by a relative phase vector, $\vec{\phi} = (\phi_1, \phi_2, \phi_3)$, where

$$\begin{aligned} \phi_1 &= (y'_r, y'_l) \\ \phi_2 &= (y'_r, x'_l) \\ \phi_3 &= (y'_r, x'_r) \end{aligned} \quad (4)$$

and (a, b) is the relative phase (ϕ_i) of $b(y'_l, x'_l, x'_r)$ with respect to $a(y'_r)$. The relative phases ϕ_1 and ϕ_2 capture the between component phasing. The relative phase ϕ_3 , referred to as the within component phase, provides a measure of horizontal and vertical motion of the right finger. The expected relative phase vectors for the four initial patterns are shown in the first four columns of Table 1. The coordinate transformation also allows the individual finger trial data to be characterized by a single within component phase, right finger = ϕ_3 (see above) and left finger = $\phi_4(y'_l, x'_l)$.

The transformed time series were smoothed (with a moving window covering 11 points or 55 msec of data) and used to derive point estimates of relative phase for each ϕ_i in $\vec{\phi}$. Plateau means and standard deviations for each ϕ_i were

Table 1

Expected values of $\vec{\phi}$ for the four initial bimanual patterns and rotary motion based on the coordinate transformation

	HS	HAS	VS	VAS	ROT
ϕ_1	0°	180°	180°	0°	90°
ϕ_2	0°	180°	0°	180°	0°
ϕ_3	0°	0°	180°	180°	90°

computed for all plateaus within each trial for each subject separately. The relative phase means were averaged and used to test the robustness of the coordinate transformation. To examine the stability of the initial patterns before and after pattern switching, we computed a global measure of variability, ϕ_{sd} , (see Kelso and Jeka, 1992). This was done by taking the square of the summed plateau standard deviations of ϕ_1 , ϕ_2 , ϕ_3 :

$$\phi_{sd} = \sqrt{\phi_{1sd} + \phi_{2sd} + \phi_{3sd}}. \quad (5)$$

Cycle durations (cynd) for the left and right fingers were computed from the transformed time series, y'_t and y'_l , with an automatic peak-picking routine. The cycle durations were computed by taking the time t_{n+1} for a peak and subtracting the time t_n for the previous peak. The observed cycle frequency, f_o , is then, $f_o = 1/\text{cynd}$. The individual cycle frequencies were averaged within a plateau for each trial.

3. Results

3.1. Accuracy of tracking

To check metronome tracking accuracy, we performed a regression of observed frequency, f_o , on required frequency, f_r , as a function of frequency plateau for each trial in a subject's data set. The individual trial r^2 values were averaged across trials within a condition for each subject. The mean r^2 values ranged from a maximum of 0.97 (sd = 0.02) for the right finger in the vertical symmetric pattern, to a minimum of 0.91 (sd = 0.07) for the left finger in the vertical asymmetric pattern. The high mean r^2 values indicate that subjects paced quite well with the metronome for all required frequencies.

3.2. Pattern classification: Relative phase $\vec{\phi}$

The mean values of $\vec{\phi}$ for the four initial bimanual patterns before any pattern switching are presented in Table 2. Overall, there was very good agreement between the expected values of $\vec{\phi}$ and the observed (compare Tables

Table 2

Pre-transition values of $\vec{\phi}$ for the four initial bimanual patterns and rotary motion as a function of the coordinate transformation

	HS	HAS	VS	VAS	ROT
ϕ_1	9°	183°	195°	28°	104°
ϕ_2	10°	171°	8°	177°	13°
ϕ_3	10°	9°	185°	190°	84°

1 and 2 columns 1 to 4). The relative phase $\vec{\phi}$ s of the four initial bimanual patterns were analyzed in a one-way MANOVA (4 patterns, 3 relative phase values). A significant pattern effect was found, $F(9,45) = 124.5$, $p < 0.01$. Univariate tests of the ϕ s ($p < 0.01$) revealed the expected differences between patterns based on the values reported in Table 1. For example, the horizontal symmetric pattern was significantly different from the horizontal asymmetric pattern for $\phi_{1,2}$. Based on these results, the relative phase $\vec{\phi}$ uniquely characterizes each bimanual pattern and removes any reference to component amplitude.

3.3. Bimanual coordination: Transitions and the recruitment–suppression of df

We observed two types of transitions in the bimanual conditions: (1) transitions from asymmetric to symmetric patterns within a motion plane; and (2) transitions from horizontal to vertical motion. The first transition we classified as an *interlimb* transition and the second as a *spatial* transition.

3.3.1. Interlimb transitions

The asymmetric to symmetric transitions within a motion plane are characterized by an abrupt reordering of the *same* df , i.e., abduction–adduction and flexion–extension. A total of 80 interlimb transitions occurred: horizontal plane 50/60; vertical plane 30/30. Over 73% (37, horizontal; 21 vertical) of these occurred within a narrow range of cycling frequencies, 1.75 Hz to 2.25 Hz. In Fig. 1, transformed time series sets and corresponding relative phase plots showing a horizontal interlimb transition are plotted. The transition from horizontal symmetric to asymmetric occurred at 2.5 Hz. The between component phase measures ϕ_1 (Fig. 1A) and ϕ_2 (Fig. 1B) capture the abrupt reordering of components from the asymmetric to symmetric pattern. The phase measure ϕ_3 shows the motion of the right finger remained predominantly horizontal (Fig. 1C) during the transition. In general, interlimb transitions spanned 1–3 cycles of motion.

3.3.2. Spatial transitions

Whereas the interlimb transitions are characterized by a reordering of already active df , spatial transitions involve the recruitment of previously quiescent (vertical, y) and suppression of active (horizontal, x) df . The recruitment and suppression of df took two qualitatively different forms. On some trials a rapid exchange in the amplitudes of x - and y -motion occurred, whereas on other

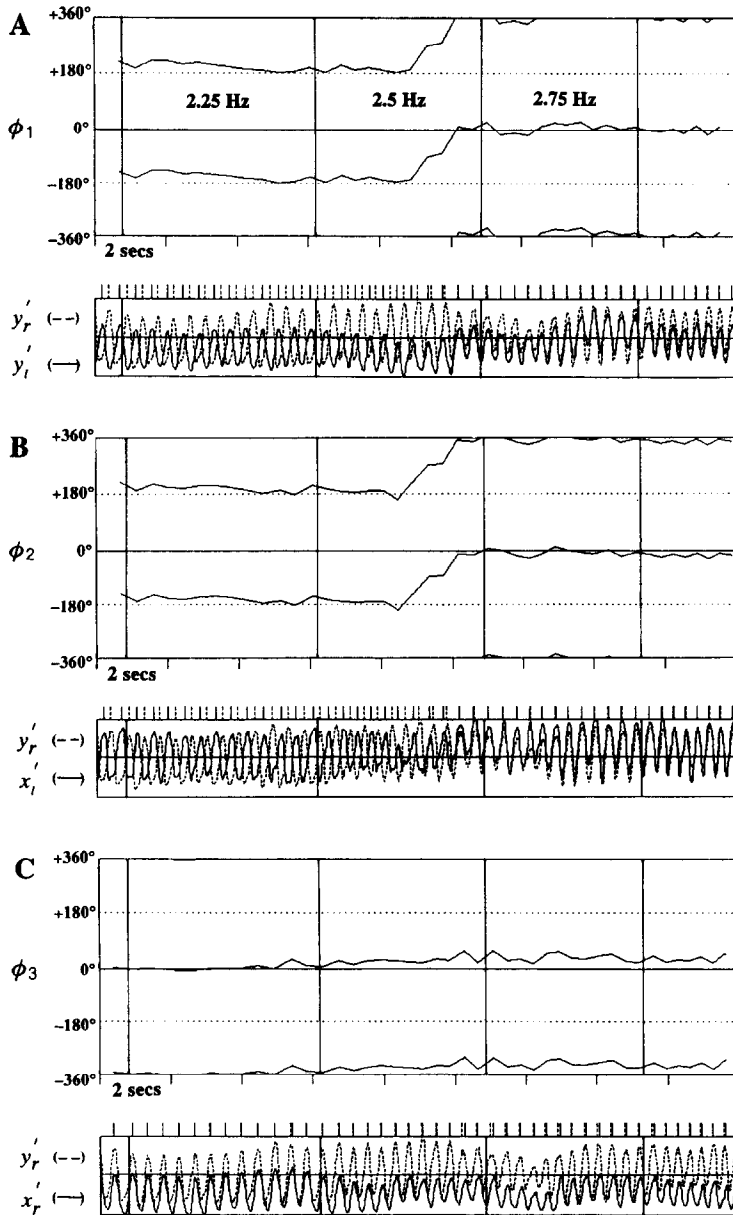


Fig. 1. The transformed time series (bottom frames) and corresponding relative phase plots (top frames) for a horizontal interlimb transition are plotted. Frequency plateaus are demarcated by the vertical lines in all three plots. The reference signal y_r' is plotted as the dashed line. The between component phase measures, ϕ_1 and ϕ_2 , are plotted in (A) and (B). The within component phase measure ϕ_3 is plotted in (C).

Table 3

Number of spatial transitions as a function of subject, condition and type

Subject	Bimanual		Unimanual			
	Abrupt	Rotary	Abrupt		Rotary	
			LF	RF	LF	RF
S1	20	—	5	5	—	—
S2	—	20	3	3	—	2
S3	13	4	1	—	4	5
S4	13	—	3	2	—	—
S5	3	9	2	2	3	1
S6	4	13	4	—	1	4

trials, vertical motion was gradually recruited and horizontal motion gradually suppressed.

In five subjects, we characterized fifty-three spatial transitions as abrupt in nature (see Table 3). These abrupt transitions occurred at ten different cycling frequencies (2.0 to 4.0 Hz) with an average transition frequency of 2.75 Hz (sd = 0.5 Hz). A set of transformed time series and corresponding relative phase plots around the transition region for an abrupt spatial transition are plotted in Fig. 2. Below the transition, motion is predominantly in the x -direction, as indicated by the value of $\phi_3 \approx 0^\circ$ (Fig. 2A). At a cycling frequency of 3.5 Hz, the abrupt shift in the within component phase measure ϕ_3 from 0° to 180° captures the suppression of x -motion and recruitment of y -motion in the right finger. The same shift in the between component phase measure ϕ_1 indicates the left finger switched motion planes simultaneously with the right finger (Fig. 2C). The between component phase measure ϕ_2 (Fig. 2B) stays near 0° indicating that the fingers remain phase entrained throughout the transition. The short transient (1–3 cycles) characteristic of these abrupt spatial shifts is seen clearly in ϕ_3 and ϕ_1 (Fig. 2A, C).

Gradual spatial transitions from horizontal to vertical motion, characterized by the rotary motion of the finger tips, were observed in the data of four subjects. Plotted in Fig. 3 are Lissajous representations of the raw x , y times series of the fingers from a trial in which a gradual transition from horizontal to vertical motion occurred. The rotary motion of the fingers is striking in this example and represents one frequency plateau (2.25 Hz) or 12 cycles of motion. Transformed time series and corresponding relative phase plots for a complete trial exhibiting a gradual spatial transition from horizontal to vertical symmetric motion are plotted in Fig. 4. In this trial, the gradual transition covered 8 frequency plateaus, from 2.0 to 3.75 Hz. We used two criteria based on the

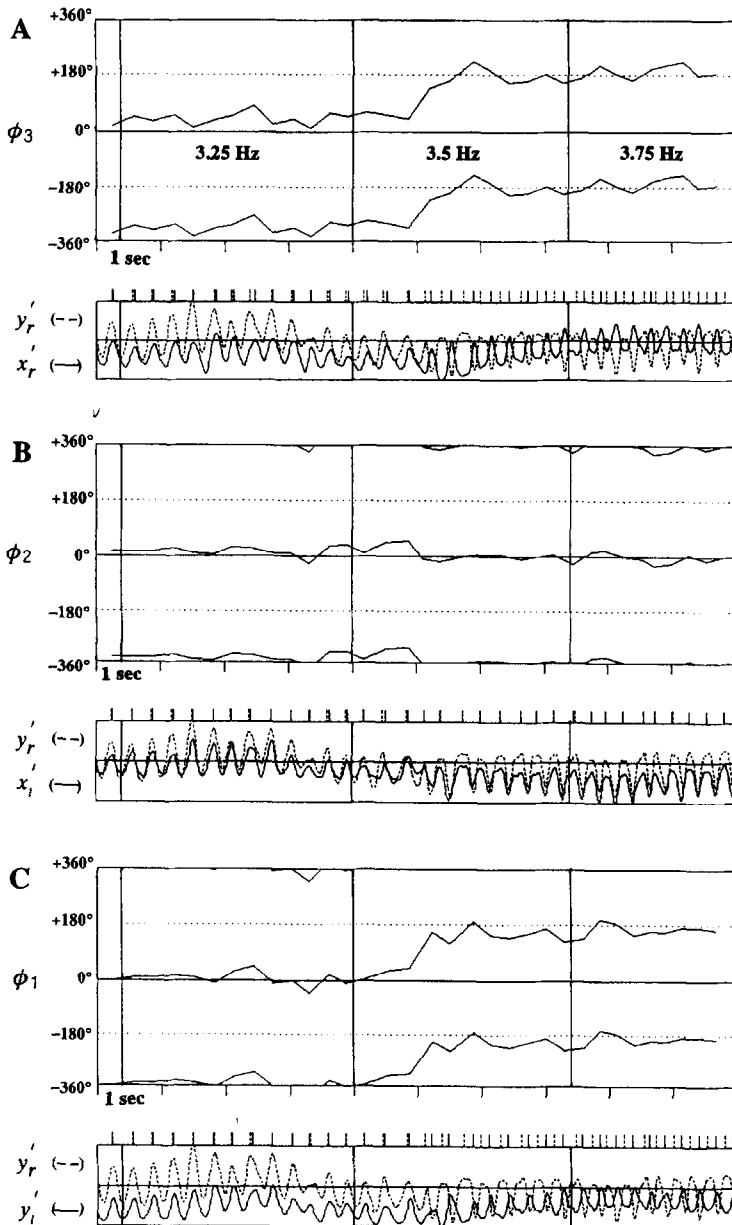


Fig. 2. A set of transformed time series and corresponding relative phase plots for an abrupt spatial transition are plotted: (A) within component phase ϕ_3 ; (B) between component phase ϕ_2 ; and (C) between component phase ϕ_1 . The plateau boundaries are indicated by the vertical lines and the transition frequency is 3.5 Hz. The reference signal y_r' is plotted as the dashed line.

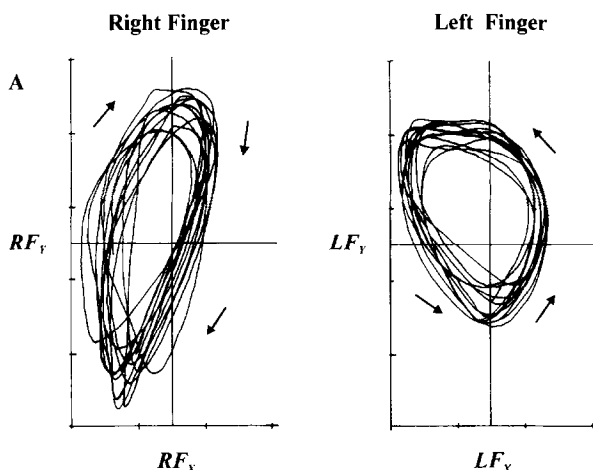


Fig. 3. Plotted is a single plateau of the raw x - and y -trajectories of the fingers from a trial starting in the horizontal symmetric pattern. The superposition of the original x - and y -dynamics clearly show rotary motion with the left finger moving counterclockwise and the right finger clockwise.

value of $\vec{\phi}$ to classify a spatial transition as gradual with rotary motion of the fingers. First, the value of the within component phase ϕ_3 must range between 45° and 135° . This indicates that the motion of the right finger is rotary, producing an elliptical trajectory. The value of the between component phase measure ϕ_1 should be within the same range as ϕ_3 if the left and right finger trajectories are similar in shape and orientation. Dissimilar trajectories between the fingers will produce values of ϕ_1 outside the range of ϕ_3 . However, if the right finger is predominantly rotary the coordination between fingers is classified as such. The gradual transition from horizontal symmetric to rotary motion is evident in the drift in the phase values of both ϕ_3 (Fig. 4A) and ϕ_1 (Fig. 4C) from around 15° to 70° across plateaus 3 (2.0 Hz) and 4 (2.25 Hz). Throughout rotary motion in this trial (spanning 6 plateaus, 2.25 to 3.5 Hz), the values of ϕ_3 ranged from 70° (2.25 Hz) to 105° (3.5 Hz) and those of ϕ_1 from 76° (2.25 Hz) to 133° (3.5 Hz). The fingers remained phase-entrained near 0° on this trial as seen in the plot of the within component phase measure ϕ_2 (Fig. 4B). The transition from rotary to vertical motion occurred in plateau 10 (3.75 Hz), the mean values of ϕ_3 and ϕ_1 shift to near 150° and 201° , respectively.

Based on the above criteria, we classified 46 spatial transitions as gradual transitions characterized by rotary motion of the finger tips (see Table 3). Gradual spatial transitions started on 10 of the 12 frequency plateaus with an average onset frequency of 2.25 Hz (sd = 0.5 Hz). Rotary motion was identified

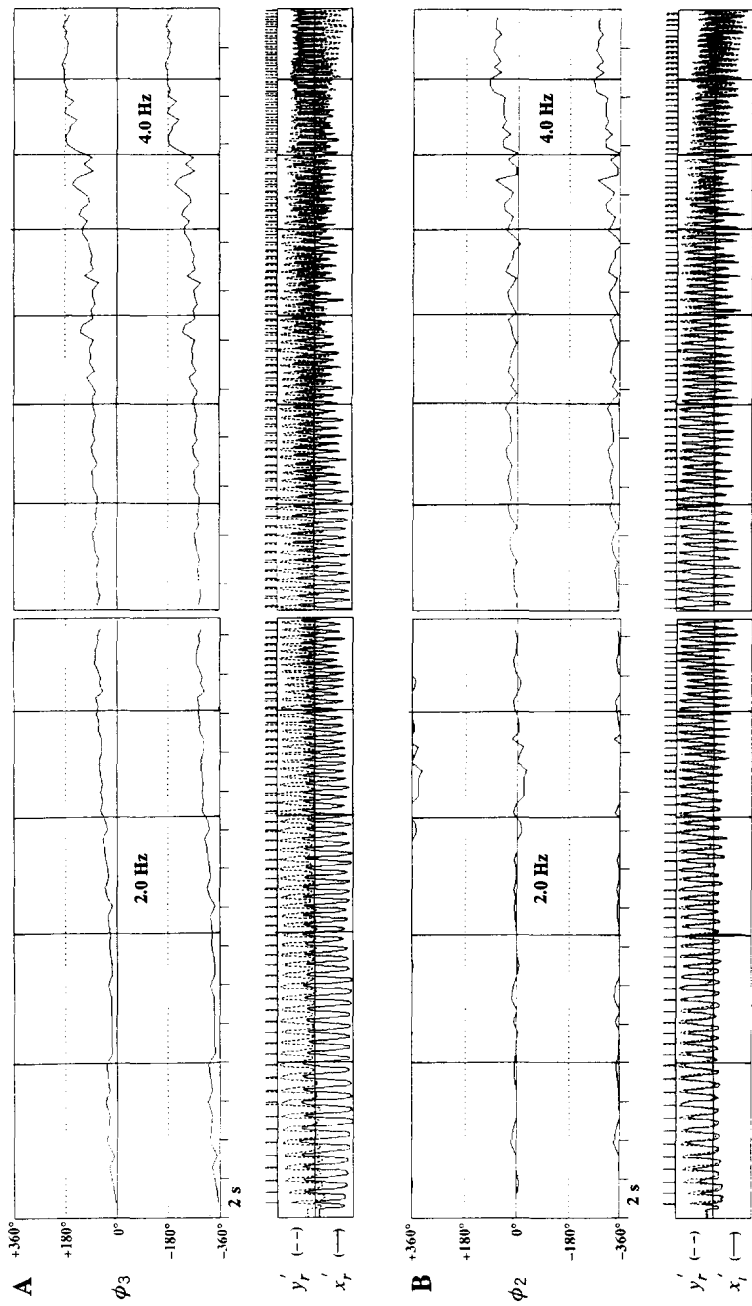


Fig. 4. A set of transformed time series (bottom frames) and corresponding relative phase plots for a complete trial starting in the horizontal symmetric pattern are shown: (A) within component phase ϕ_3 ; (B) between component phase ϕ_2 ; and (C) between component phase ϕ_1 . The vertical bars demarcate the 12 frequency plateaus and y' is plotted as the dashed line.

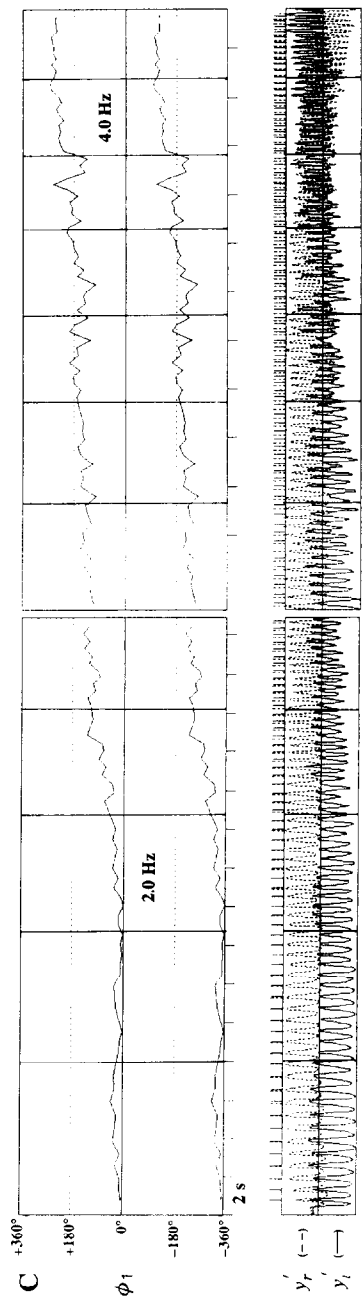


Fig. 4 (continued).

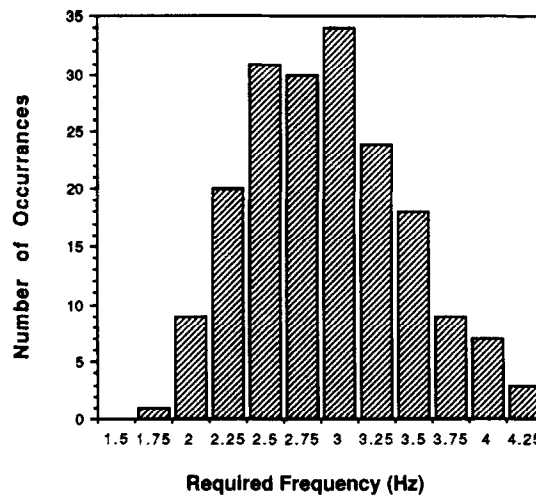


Fig. 5. The histogram portrays the number of occurrences of rotary motion as a function of required cycling frequency.

on 11 of the 12 (1.75 to 4.0 Hz) frequency plateaus (Fig. 5), the behavior lasting anywhere from one to eight plateaus, with an average length of 4.1 ($sd = 1.8$) frequency plateaus (Table 4). The mean values of $\vec{\phi}$ for all observed rotary motion are shown in Table 2 column 5. There is good agreement between the expected values for rotary motion (Table 1 column 5) and the observed values. The relative phase $\vec{\phi}$ for rotary motion was compared individually to all four initial bimanual patterns in one-way pattern MANOVAs with 2 levels of pattern and 3 phase measures. This analysis revealed that the relative phase $\vec{\phi}$ for rotary motion was significantly different from the other four initial bimanual patterns, $F_s > 221.0$ ($ps < 0.01$) (compare column 5 to columns 1–4 in Table 2).

Table 4
Length of rotary motion as a function of subject and condition

Subject	Bimanual		Unimanual			
			LF		RF	
	M	sd	M	sd	M	sd
S2	4.5	1.2	—	—	2	1
S3	3	2	1.8	0.4	6.4	1.5
S5	2.8	1.5	2.6	0.9	1	—
S6	4.5	2.3	2.0	—	9.5	0.5

3.4. Bimanual coordination: Pattern switching and phase variability

In experiments demonstrating phase transitions between coordinative patterns (see Section 1), the transition is characterized by a reordering of the same biomechanical df within a single motion plane. This is also the case for the interlimb transitions reported here. With the observation of spatial transitions, we have the opportunity to compare patterns with the same symmetry that are performed in different motion planes. Furthermore, the spatial transitions involve a reordering of already active df and previously quiescent df . How will the recruitment and suppression of df influence the stability of the coordinative patterns? To study this issue, we examined the changes in ϕ_{sd} as a function of the initial coordination pattern and type of transition, interlimb and spatial.

3.4.1. Initial condition variability

To examine the initial variability of the four patterns, the pre-transition values of ϕ_{sd} for the four bimanual patterns were analyzed in a one-way ANOVA with pattern as the only factor. A significant pattern effect was observed, $F(3,15) = 26.3$, $p < 0.01$, post hoc tests ($p < 0.01$) revealing that the symmetric patterns (vertical, $\phi_{sd} = 6.6$; horizontal, $\phi_{sd} = 6.7$) were less variable than the asymmetric patterns (horizontal, $\phi_{sd} = 7.4$; vertical, $\phi_{sd} = 7.9$). Even though the difference between the asymmetric patterns was small, the horizontal asymmetric pattern was less variable than the vertical asymmetric pattern. The most important aspect of these results is the differential stability of the patterns as a function of pattern symmetry more so than the plane of motion.

3.4.2. Interlimb transition variability

Are interlimb transitions from asymmetric to symmetric patterns accompanied by enhancement of fluctuations regardless of the motion plane? To test for fluctuation enhancement in the interlimb transitions, we aligned the pre-transition variability data (ϕ_{sd}) of the asymmetric patterns to the transition plateau and averaged backwards from this point. These values are compared to the respective symmetric patterns in two-way Pattern \times Position ANOVAs. For horizontal motion, the aligned asymmetric data are compared to the first four frequency plateaus of the symmetric data (1.5–2.25 Hz); and for the vertical patterns, the asymmetric data are compared to the symmetric pattern across the first five frequency plateaus (1.5–2.5 Hz). The analysis of the horizontal patterns revealed no significant difference in the variability of the asymmetric and symmetric patterns, $F(1,5) = 2.7$, $p > 0.1$. However, variability increased as a function of pre-transition position in the asymmetric pattern and frequency

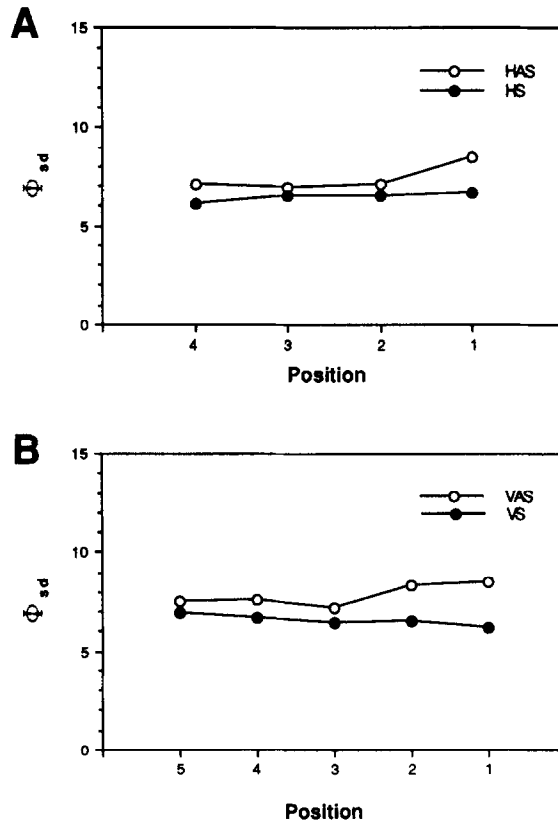


Fig. 6. Plotted in (A) are the pre-transition mean values of ϕ_{sd} for the horizontal asymmetric (\circ) and symmetric (\bullet) patterns. Plotted in (B) are the pre-transition mean values of ϕ_{sd} for the vertical asymmetric (\circ) and symmetric (\bullet) patterns. The numbers on the abscissa (both graphs) correspond to the normalized pre-transition positions for the asymmetric patterns. The values of the symmetric patterns are plotted as a function of cycling frequency starting at 1.5 Hz (position 4 in (A) and position 5 in (B)) and going to 2.25 Hz for the horizontal and 2.5 Hz for the vertical symmetric pattern (position 1).

in the symmetric pattern, $F(3,15) = 4.2$, $p < 0.01$. As shown in Fig. 6A, the largest increase in the asymmetric pattern variability occurs just before the transition plateau, while the symmetric pattern remains more or less constant across the first four frequency plateaus with a small increase from plateau 1 to 4. The analysis of the vertical patterns revealed a significant difference in the overall variability of the patterns, $F(1,5) = 5.6$, $p < 0.05$, with the variability of the symmetric pattern less than the asymmetric pattern. More importantly, a significant pattern \times position interaction effect occurred in the vertical pattern data, $F(4,16) = 3.3$, $p < 0.05$. Simple main effects tests ($p < 0.05$) of this

interaction revealed a significant increase in the vertical asymmetric pattern variability before the transition, while the variability of the symmetric pattern decreased slightly as frequency increased (Fig. 6B). The increase in the vertical asymmetric pattern variability is evidence of *enhancement of fluctuations* before the transition, a signature of dynamic instability.

3.4.3. Spatial transition variability

Is fluctuation enhancement observed in horizontal motion before the recruitment of *y*-motion in the abrupt and gradual spatial transitions? To test for fluctuation enhancement before the spatial transitions, we aligned the pre-spatial transition variability data (ϕ_{sd}) from the horizontal motion trials and averaged backwards across five plateaus. These normalized averages were compared to vertical symmetric motion across the first five frequency plateaus (1.5 to 2.5 Hz) in a two-way Pattern \times Position ANOVA. Overall, vertical symmetric motion was less variable than horizontal motion before the spatial transition, $F(1,5) = 12.81$, $p < 0.01$. A significant pattern \times position interaction was found, $F(4,20) = 6.5$, $p < 0.01$. Simple main effect tests ($p < 0.05$) revealed no difference in the patterns for the first three pre-spatial transition positions. However, for pre-transition positions 2 and 1, the variability of horizontal motion was significantly larger than vertical motion (Fig. 7). Based on these results, we conclude that enhancement of fluctuations occur in horizontal motion before the recruitment of *y*-motion.

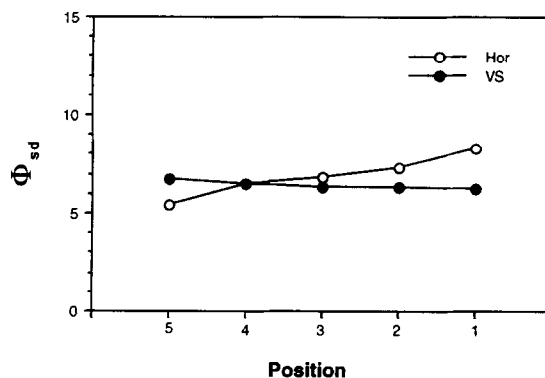


Fig. 7. The pre-transition mean values of ϕ_{sd} for horizontal motion (\circ) before the spatial transition are plotted. The numbers on the abscissa correspond to the normalized position of these values. The mean values of ϕ_{sd} corresponding to vertical symmetric motion (\bullet) for cycling frequencies of 1.5 Hz (position 5) to 2.5 Hz (position 1) are also plotted.

3.4.4. Variability of rotary motion

Is rotary motion a stable coordinative pattern? Are enhancement of fluctuations observed in rotary motion before the complete suppression of x -motion? To answer this question, we compared ϕ_{sd} of rotary motion and vertical symmetric motion across plateaus 3 (2.25 Hz) through 11 (4.0 Hz) in a two-way Pattern \times Plateau ANOVA. Overall, rotary motion ($\phi_{sd} = 7.8$) was more variable than vertical symmetric motion ($\phi_{sd} = 6.5$), $F(1,3) = 73.9$, $p < 0.01$, and there was no significant change in the variability of rotary motion as a function of frequency plateau ($p > 0.1$). Although rotary motion was more variable, its variability remained fairly constant across a large range of cycling frequencies. To test for fluctuation enhancement, we aligned rotary motion ϕ_{sd} to the transition plateau and averaged backwards across four pre-transition positions. These four pre-transition positions were analyzed in a one-way ANOVA with plateau as the factor. A significant increase in the variability of ϕ_{sd} as a function of pre-transition plateau was found, $F(3,9) = 6.6$, $p < 0.05$. Post hoc tests ($p < 0.05$) revealed that the mean value of ϕ_{sd} on the plateau before the transition ($\phi_{sd} = 8.5$) was significantly larger than 3 ($\phi_{sd} = 7.6$) and 4 ($\phi_{sd} = 7.4$) plateaus away from the transition. The above results demonstrate that rotary motion is a stable coordinative pattern in this system with suppression of x -motion again accompanied by enhancement of fluctuations.

3.4.5. Post transition behavior

The post spatial transition mean values of $\vec{\phi}$ for the two initial horizontal patterns (now vertical) and the post-transition mean values of the vertical asymmetric pattern (now symmetric) are shown in the first three columns of Table 5. The values for the vertical symmetric pattern are shown in column four for comparison. A one-way MANOVA with 4 levels of pattern revealed no significant difference between the values shown in Table 5, $F(9,39) = 1.14$, $p > 0.3$. This clearly shows that after the spatial transition, motion is predominantly vertical symmetric. The post-transition variability of the patterns was

Table 5
Post-transition values of $\vec{\phi}$ for the two initial horizontal patterns and the vertical asymmetric pattern

	HS	HAS	VAS	VS
ϕ_1	203°	203°	196°	195°
ϕ_2	23°	28°	16°	8°
ϕ_3	180°	177°	187°	185°

compared in a one-way ANOVA with initial pattern as the factor. The analysis of ϕ_{sd} revealed a significant pattern effect, $F(3,15) = 7.63$, $p < 0.01$. Post hoc tests ($p < 0.05$) show that the initial vertical symmetric pattern ($\phi_{sd} = 6.6$) is less variable than the post-transition horizontal (asymmetric, $\phi_{sd} = 6.9$; symmetric, $\phi_{sd} = 7.0$) and vertical asymmetric ($\phi_{sd} = 6.9$) patterns.

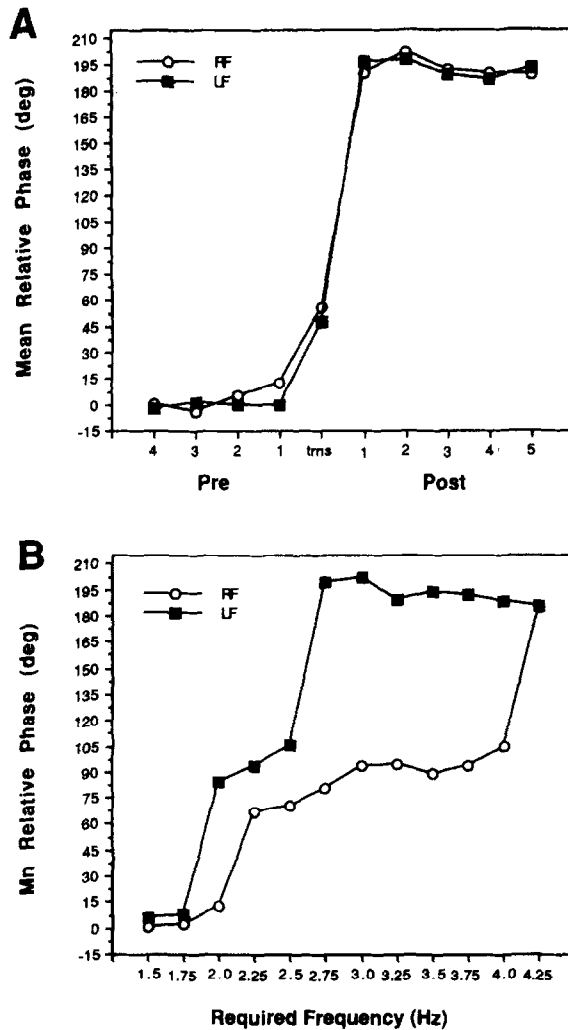


Fig. 8. Plotted in (A) are the pre- and post-transition means of ϕ_3 (RF) and ϕ_4 (LF) for the abrupt spatial transition trials. Plotted in (B) are the means for ϕ_3 (RF) and ϕ_4 (LF) for the gradual transition trials.

3.5. Unimanual coordination: Spatial transitions and the recruitment–suppression of df

Abrupt spatial transitions from horizontal to vertical motion occurred in 30 individual finger trials for the six subjects: 12 in the RF and 18 in the LF trials (see Table 3). These transitions spanned a large range of cycling frequencies (1.75 to 4.0 Hz) with most LF transitions (12) occurring at cycling frequencies ≤ 2.25 Hz and all RF transitions occurring at frequencies ≥ 2.25 Hz. On the average, these transitions spanned 2–3 cycles of motion. The pre-transition data from the abrupt individual finger trials were aligned to the transition plateau and back averaged across four pre-transitions plateaus and forward averaged across five post-transition plateaus. The resultant mean values are plotted in Fig. 8A. The shift from $\phi_{3,4} \approx 0^\circ$ (horizontal motion) to 180° (vertical motion) is clearly seen in the pre- and post-transition portions of the graph.

Gradual spatial transitions from horizontal to vertical motion occurred on 20 of the individual finger trials: 12 in the RF and 8 in the LF trials (see Table 3). As in the bimanual conditions, gradual transitions and rotary motion of the individual fingers were also observed in the data of Ss 2,3,5 and 6. On the average, the start of the gradual transition occurred at a frequency of 2.0 Hz in the LF and 2.25 Hz in the RF. The difference in average length of rotary motion between the individual fingers was quite large, LF 2 plateaus and RF 6 plateaus, and was the result of the lengthy segments of rotary motion produced by S3 and S6 (Table 4). Both subjects produced longer segments of rotary motion in the individual RF than in the bimanual conditions. The plateau mean values of ϕ_3 and ϕ_4 from the gradual transition trials were aligned as a function of dominant behavior within a frequency plateau. The resultant means are plotted in Fig. 8B. The shift from $\phi_{3,4} \approx 0^\circ$ to 90° at cycling frequencies of 2.0 Hz in the LF and 2.25 Hz in the RF clearly show that the motion of the fingers became rotary. The shift from $\phi_{3,4} \approx 90^\circ$ to 180° at cycling frequencies of 2.75 Hz in the LF and 4.25 Hz in the RF show the transition from rotary to predominantly vertical motion.

3.6. Perception-action patterns and spatial transition pathways

The data presented up to this point indicate that loss of stability is an essential mechanism underlying the observed interlimb and spatial transitions. Instabilities, then, appear to be essential to the way in which df are recruited and suppressed. Can instabilities account for the two different types of spatial transitions, abrupt and gradual? Or, is some other aspect of the coordination

more important in determining when recruitment and suppression of df will be abrupt or gradual? One possibility is that the perception-action pattern formed between the metronome and fingers, itself a dynamic pattern, may interact with the intrinsic coordination dynamics (e.g., Byblow et al., 1994) and play a role in the type of spatial transition observed. We explored this issue by examining the finger-metronome perception-action pattern in the horizontal conditions. A visual inspection of the data revealed that subjects synchronized either peak adduction or abduction to the metronome in many trials. Out of the 53 abrupt bimanual spatial transitions, adduction of one or both fingers was synchronized with the metronome on 29 (55%) trials, abduction on 9 (17%) trials, and no specific relationship on 15 (28%) trials. Of the 46 gradual bimanual transitions, abduction of the fingers was synchronized with the metronome on 32 (70%) trials, adduction on 2 (4%) trials, and no specific relationship on 12 (26%) trials. These results suggest that the perception-action dynamics may be quite influential in the recruitment-suppression of df , and warrant further study. Interestingly, such a strong relationship was not observed in the individual fingers.

3.7. Hopf bifurcation and the recruitment and suppression of df

In this section, we develop a model of the gradual spatial transition in a single finger leading to rotary motion and then vertical motion and compare it to the experimental results (see also Kelso et al., 1993). Previous work has shown that the dynamics of one-dimensional planar movements can be modeled by nonlinear oscillators where the appropriate phase space is (x, \dot{x}) for each component (Haken et al., 1985; Kay et al., 1987). In the present situation, the appropriate phase space of the end effector is two dimensional (x, \dot{x}, y, \dot{y}) for each component. To capture the basic phenomenon of recruitment and suppression of df , the behavior of an individual finger was modeled using the following pair of nonlinear oscillators,

$$\dot{r}_i = r_i(a_i(f) - r_i^2), \quad (6)$$

$$\dot{\theta}_i = 2\pi f, \quad (7)$$

where r_i and θ_i are the polar coordinates of oscillator i ($i = x, y$ for motion in the x - and y -directions respectively) and $a_i(f)$ are parameters corresponding to the frequency of motion f .

Three essential features of the dynamics render equations (6) and (7) appropriate for the present case. First, when $a_i(f) \leq 0$, a stable fixed point exists at the origin ($r_i = 0$) that attracts all initial conditions in the (r_i, θ_i) plane. Second,

when $a_i(f)$ increases above 0, the fixed point at the origin becomes unstable and gradual oscillations appear and a stable limit cycle forms with amplitude $r_i = \sqrt{a_i(f)}$. The annihilation of the fixed point and gradual increase in oscillations are typical of systems that undergo *supercritical* Hopf bifurcations. Third, decreasing $a_i(f)$ from above 0 damps out the oscillations in the x -direction and a stable fixed point at the origin emerges. In this case, the annihilation of the limit cycle and stabilization of the fixed point is an inverted Hopf bifurcation.

Since recruitment and suppression resulted from increasing frequency, the parameters $a_i(f)$ were set to depend on cycling frequency f in the following manner:

$$a_x(f) = k_x(f_2 - f), \quad (8)$$

$$a_y(f) = k_y(f - f_1), \quad (9)$$

with k_x and k_y having a constant value of unity. For numerical computations, the values chosen were $f_1 = 2.0$ Hz and $f_2 = 4.0$ Hz. Both of these values are in good agreement with the experimental frequencies at which elliptical motion first appeared and finally disappeared. The value of f in the model increased over the experimental frequency range from 1.5 Hz to 4.25 Hz. The solutions to equations 6 and 7 can be written as,

$$\theta_i(t) = \theta_i(0) + 2\pi ft, \quad (10)$$

where $\theta_i(0)$ are the initial phases at $t = 0$. In this form, the relative phase between the x - and y -oscillators is then

$$\phi = \theta_x(t) - \theta_y(t) = \theta_x(0) - \theta_y(0). \quad (11)$$

For the numerical simulations, the phase ϕ was set to 90° when oscillations

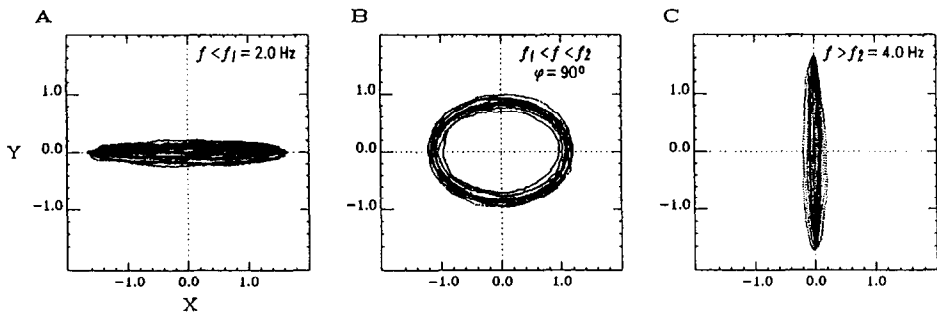


Fig. 9. Plotted are the end-effector trajectories computed from the Hopf bifurcation model of the recruitment and suppression process (see text for details) using non-linear oscillators with added noise.

were present in both the x - and y -directions. This value is consistent with the values of ϕ_3 and ϕ_4 observed during rotary motion in both the unimanual and bimanual horizontal conditions.

When $f = 1.50 \text{ Hz} < f_1$, motion in the x -direction is that of a stable limit cycle and motion in the y -direction a stable fixed point (Fig. 9A). Setting $f = 2.75 \text{ Hz} > f_1$, produces a bifurcation from a fixed point to limit cycle in the y -direction and the trajectory forms an ellipse with $\phi = 90^\circ$ between the x - and y -oscillators (Fig. 9B). This conforms exactly to a supercritical Hopf bifurcation in the y -direction. At $f = 4.5 \text{ Hz} > f_2$, oscillations in the x -direction are annihilated and only the stable limit cycle in y remains (Fig. 9C). This corresponds to an inverted Hopf bifurcation in the x -direction. Obviously, if f_1 is close to f_2 , one may see an *abrupt* transition from horizontal to vertical motion which, as we have observed experimentally, occurs on approximately half of the trials. It is quite clear that damping of horizontal motion and growth of vertical motion occurs simultaneously, exactly as the Hopf model predicts.

4. Discussion

Even though biological systems have a tendency to produce simple phase and frequency synchronized patterns, the processes of pattern switching, relative coordination and the recruitment and suppression of df allow for the flexible modification of these patterns under varying environmental conditions. These three forms of coordinative change are ubiquitous and are essential in humans' and animals' ability to adjust behavior in a task-specific fashion.

One of the main similarities between pattern switching and recruitment and suppression arises in the role of pattern symmetry in constraining the way in which coordination can change. Analysis of interlimb and spatial transitions show that symmetry constraints dictate the direction of pattern switching within and across motion planes. Interlimb switching is always from asymmetric to symmetric coordination patterns. The spatial transitions are also constrained by pattern symmetry. Pattern switching from horizontal symmetric motion are always in the direction of vertical or rotary symmetric motion. When spatial transitions were from horizontal asymmetric to vertical motion, symmetry constraints still dictated the direction of pattern change. Transitions were always from horizontal asymmetric to vertical symmetric (3 trials) or rotary symmetric (4 trials). Transitions from horizontal motion to rotary or vertical asymmetric motion were not observed.

The present analysis of phase variability (ϕ_{sd}) demonstrates that stability and

loss of stability are key processes in both pattern switching and recruitment–suppression. Enhancement of fluctuations occurred in the vertical asymmetric pattern before the transition to the vertical symmetric pattern. This finding is consistent with previous transition phenomena observed in earlier bimanual (e.g., Kelso and Scholz, 1985; Kelso et al., 1986), perception-action (Kelso et al., 1990; Schmidt et al., 1990; Wimmers et al., 1992), single limb multijoint movement (Buchanan and Kelso, 1993; Kelso et al., 1991a,b) and multilimb studies (Carson et al., 1995; Jeka and Kelso, 1995). Horizontal interlimb transitions did not exhibit fluctuation enhancement before pattern switching from asymmetric to symmetric patterns. There are several reasons why fluctuations did not arise in this case, and they appear to be related to stability processes. First, the initial variability of both horizontal bimanual patterns in this experiment may be enhanced already since we started subjects at higher frequencies compared to earlier work (e.g., Kelso, 1984; Kelso and Scholz, 1985). Second, most of the horizontal asymmetric to symmetric transitions occurred within the second and third frequency plateaus. Thus, the anti-phase pattern was maintained only for a very short time following its initiation. These two factors lead to the conclusion that the asymmetric horizontal pattern was already in the vicinity of a critical point or unstable region of parameter space. Furthermore, the significant position effect indicates that the symmetric pattern was also undergoing a change in variability associated with the transition from horizontal to vertical motion. The latter conclusion derives from the fact that enhancement of fluctuations *did* occur in horizontal motion before the recruitment of vertical motion. As a package, these results demonstrate that stability plays a key role in pattern switching and recruitment–suppression processes, both of which are essential aspects of flexibility in biological coordination. Regardless of the motion plane or underlying muscle groups, pattern formation within and across motion planes in this experiment is governed by very similar self-organizing principles.

Another feature of both abrupt and spatial transitions that ties directly into pattern stability, is the length of the transient between patterns. In each case, the length of the transient is only about 2–3 cycles of motion. This suggests that the mean first passage time associated with pattern change and recruitment–suppression processes may be on an equivalent time scale. Theoretical and experimental work has shown that time scales associated with pattern stability, parameter rate increases and relaxation time following a perturbation are essential in demonstrating that pattern switching results from loss of stability (Scholz and Kelso, 1989, 1990; Scholz et al., 1987; Schöner et al., 1986; for review see Kelso et al., 1987). The design of this experiment did not allow us to test

directly the time scale relations associated with the recruitment and suppression of df . However, experiments exploring the switching time from horizontal to vertical motion, horizontal to rotary motion and vice-versa would provide evidence to further establish the link between these processes. The stability analysis leads to several predictions that may help identify the time scale relations underlying recruitment and suppression. First, switching from vertical to horizontal motion should take longer than the reverse. Second, switching from horizontal to rotary should take longer than the switch from horizontal to vertical. Third, relaxation times following a perturbation should be predictable based on the variability of the patterns as a function of cycling frequency. Substantiation of these hypotheses may help to further elucidate the role of stability mechanisms in the recruitment and suppression of df .

Recent work studying bimanual coordination in a circle drawing task (Semjen et al., 1995) and a line-circle drawing task (Franz et al., 1991) have produced results similar to those we report here. Semjen et al. required subjects to draw circles with both hands in four different patterns of coordination: symmetric, toward and away from the body midline, and asymmetric, one hand moving toward and the other away from the midline. Results of their experiment are consistent with those presented here. First, symmetric patterns are more stable than asymmetric patterns at both self-paced and faster frequencies. Second, transitions from asymmetric to symmetric patterns occur at faster frequencies, even when more df are already active than in the case of our interlimb asymmetric to symmetric transitions. Third, in many instances, the transition from asymmetric to symmetric patterns involved the production of linear trajectories in one hand. That is, possible suppression of a df followed by recruitment of the same df may have promoted a switch from asymmetric to symmetric coordination. And fourth, both the symmetric and asymmetric patterns were more stable when the dominant hand moved in an outward clockwise direction from the subject's perspective. In our experiment, most rotary motion occurred when the right hand (all six subjects were right handed) synchronized abduction (outward motion) to the metronome. Such results from two diverse experiments hint that spatially defined constraints may play a very prominent role in how df are recruited and suppressed.

While the work of Semjen et al. (1995) did not demonstrate as clearly the recruitment and suppression of df , the work of Franz et al. (1991), we believe, most assuredly did. In this experiment, one task required subjects to draw a vertical line with one hand and a circle with the other hand. The main finding was that the hand drawing the line became more 'circle-like' (recruitment) and the hand drawing the circle became more 'line-like' (suppression). Interestingly,

when the hands both drew circles or lines no change in the trajectories was observed. The results of this experiment were interpreted with respect to von Holst's magnet effect von Holst (1939/1973). Temporally, the magnet effect describes the tendency of two components with different natural frequencies to draw or attract one another to a common frequency. Franz et al. interpreted the altering of the hand trajectories as a spatial magnet effect, i.e., the differing spatial trajectories drew one another to more similar trajectories. Based on the results, the authors suggest that some form of single minimization principle (i.e., minimum torque or minimum jerk) governs the so called spatial magnet effect. Another plausible interpretation, based on our results, is that under the condition of different spatial trajectories, the central nervous system recruited and suppressed df to stabilize the global coordinative pattern both spatially and temporally. Whether such processes lead to or arise from such biomechanical constraints as minimum joint torque change or trajectory jerk is an open question.

Both of the above experiments are open to analysis with respect to the coordinate transformation we introduced here. Whether or not the transformation we utilize provides a more succinct description compared to the description other authors provide is open to investigation. However, experiments studying recruitment and suppression under such varying conditions may shed light on the combined role of spatial and temporal constraints in coordination in general. Most illuminating may be experiments similar to those of Franz et al. (1991) and Semjen et al. (1995) under conditions of frequency scaling and spatial orientation scaling. The form that transitions take and the role of recruitment–suppression processes in the transitions may help clarify how stability mechanisms and biomechanical constraints interact to constrain the production of multi degree of freedom movements.

The coexistence of four stable bimanual patterns, two symmetric and two asymmetric, clearly shows that the system is multistable in time and space. Abrupt interlimb transitions within a single motion plane have previously been modeled along a single dimension with relative phase as the order parameter (e.g., Haken et al., 1985; Schöner et al., 1986). Simultaneous movement of the fingers in the x – y plane leads to more complicated dynamics. Previous theoretical modeling of gait patterns and transitions in quadrupeds (Collins and Stewart, 1993; Schöner et al., 1990) and humans (Jeka et al., 1993a,b) has shown that the dynamics of a four component system can be understood in terms of the relative phases between four oscillators. In Schöner et al. (1990), a set of relative phases (3) is treated as the collective variable and is used to classify gaits based on their symmetry properties. Different stable gaits are shown to correspond to attractors

of the relative phase dynamics and transitions between gaits are hypothesized to take the form of non-equilibrium phase transitions resulting from loss of stability. Explicitly modeled are the features of hysteresis, critical slowing down and critical fluctuations, all predicted features of such transitions. A further feature of such research is that transitions between gaits may be gradual or abrupt. At the level of coordination patterns and their dynamics, a highly suggestive parallel exists between gradual and abrupt transitions in a four component ('quadruped gait') system and the abrupt and gradual spatial transitions we report here. Even though we have offered the Hopf bifurcation as a model-independent mechanism for the recruitment and suppression of df , further theoretical modeling addressing the coupling between components and the different forms of spatial transitions is needed. Specifically, the model should incorporate both supercritical and subcritical Hopf bifurcations as generic mechanisms underlying the gradual and abrupt spatial transitions. The theoretical treatment of gait and gait transitions in quadrupeds by Schöner et al. (1990) offers a possible starting point for developing such a model and designing future experiments.

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