

Posturally induced transitions in rhythmic multijoint limb movements

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Abstract. The coordination dynamics (e.g., stability, loss of stability, switching) of multijoint arm movements are studied as a function of forearm rotation. Rhythmical coordination of flexion and extension of the right elbow and wrist was examined under the following conditions: (1) forearm supine (forearm angle 0°), simultaneous coordination of wrist flexion/elbow flexion and wrist extension/elbow extension (termed in-phase); and (2) forearm prone (forearm angle 160°), simultaneous coordination of wrist flexion/elbow extension and wrist extension/elbow flexion (termed anti-phase). Starting in either pattern, subjects rotated the forearm in nine 20° steps, producing 15 cycles of motion per step at a frequency of 1.25 Hz. Spontaneous transitions from pattern 1 to pattern 2 and from pattern 2 to pattern 1 were observed at a critical forearm angle. The critical angle depended on the *direction* of forearm rotational change, thus revealing the *hysteretic* nature of the switching process. En route to the transition, regardless of direction of forearm rotation, *enhancement of phase fluctuations* and an increase in perturbation response times (*critical slowing down*) were observed in the relative phasing between the joints. Such observations support loss of stability as a central, self-organizing process underlying coordinative change. Neurophysiological mechanisms supporting multijoint coordinative dynamics are discussed.

Key words: Spatial orientation – Transition – Hysteresis – Single limb multijoint movements – Self-organization

Introduction

How does the central nervous system (CNS) assemble its many subsystems into coordinated patterns of behavior? What algorithms or rules are used by the CNS to control and coordinate multi-degree-of-freedom movements?

And how is flexibility, as observed, for example, by the ability of the system to switch spontaneously from one action to another according to task demands, to be understood? One entry point into these questions has been to identify properties of the end-effector trajectory (e.g., the path of a human hand or the hindlimb of a frog) that remain invariant across experimental manipulations such as distance, speed, and load. Examples include the constrained relation between curvature and velocity of hand trajectories (e.g., Viviani and Schneider 1991) and unimodal velocity time profiles in discrete, two-joint (e.g., Abend et al. 1982; Flash and Hogan 1985) or two-handed movements (Kelso et al. 1979). In such formulations, trajectory planning takes place in terms of end-effector motions in external space (e.g., Flash and Hogan 1985) or in terms of direct low-level coupling between muscle activation and equilibrium positions (e.g., Bizzi et al. 1991; see also Berkenblit et al. 1986). Possible coordinative constraints among the joints themselves are usually not considered.

On the other hand, Soechting and colleagues have observed fixed phase relations between the orientation angles of the arm (upper arm and forearm) during drawing and pointing movements (Soechting et al. 1986; Soechting and Terzuolo 1987a, b). Via such phasing constraints it has been possible to generate an algorithm that maps joint angle space (intrinsic coordinates) into Cartesian space (extrinsic coordinates, cf. Soechting and Terzuolo 1986). Relatedly, a so-called *direction-dependent* constraint on multijoint coordination has been found in three independent studies (Baldissera et al. 1982; Kelso and Jeka 1992; Kelso et al. 1991). The basic result is that it is much easier to coordinate joints of the same (Kelso et al. 1991) or different (Baldissera et al. 1982; Kelso and Jeka 1992) limbs when these joints are rotated in the same direction, especially as the rate of movement increases. Such findings suggest that the algorithms used by the brain place a higher priority on direction of movement than any particular muscle groupings, a notion that seems consistent with correlations be-

tween neuronal ensemble activity in motor cortex and direction of hand movement (Georgopoulos 1990, for review).

Whereas partial answers, especially to the algorithm issue raised at the beginning of this article, are emerging, answers to the first (the assembly problem) and third (the flexibility problem) are less clear. Insights into how patterns of multijoint arm movement are assembled by the CNS might be obtained by studying *switches* in coordination which necessarily require *reassembly* among the components involved. Such reassembly processes have been studied in paradigms that investigate spontaneous transitions from one coordination pattern to another as movement rate or frequency of motion is increased (e.g., Hoyt and Taylor 1981; Kelso 1984; Kelso et al. 1991; Schmidt et al. 1990; Wimmers et al. 1992). A novel aspect of the present research is that a *spatial* parameter, the rotation of the forearm, is systematically varied and the coordination between elbow and wrist joints evaluated using kinematic measures. Calculations of relative phase variability between the joints as well as the system's response to perturbations are used to evaluate the *stability* of coordination patterns as forearm orientation is changed. If spontaneous transitions are observed from one multijoint coordination pattern to another, as our previous research suggests (e.g., Kelso et al. 1991), and if such transitions are accompanied by loss of stability (seen, for example, through an increase in relative phase fluctuations and a slower response of the system to perturbations as it approaches a transition point), then it seems likely that coordinative changes are due to *self-organizing* processes in the nervous system (Haken 1983; Haken and Wunderlin 1991; Haken et al. 1985; Kelso 1984; Schöner and Kelso 1988). "Self-organization", the creation of new or different patterns, involves cooperation among the components involved and is always produced by an instability mechanism. Because of the complexity of the nervous system, self-organization is likely to be observed at several different levels, e.g., in firing patterns of interneurons in the spinal cord controlling wrist and elbow muscles, as well as in higher structures and behavior itself (Katchalsky et al. 1974; Kelso et al. 1992).

Because self-organization is an essentially nonlinear process, a further feature we might expect to find is *hysteresis*, i.e., the locus of transitions should depend on the direction of parameter change. Thus, rotating the forearm from supine to prone in the present experiment may induce a transition in coordination at angles different from the reverse, prone to supine operation. Such hysteresis means that multiple (here, two) patterns of multijoint coordination are stable and coexist for the *same* value of the manipulated parameter (forearm angle): which one is observed depends on the direction of parameter change. In the quest for a deeper understanding of principles of coordination, hysteresis plays an important role, because it demonstrates the multifunctional nature of the neural control system and provides hints about the underlying coordination dynamics.

Materials and methods

Subjects

Six right-handed volunteers (18–40 years of age), naive to the purpose of the experiment, rhythmically coordinated the flexion/extension of the wrist and elbow joint of the right arm in the sagittal plane of motion, while voluntarily changing forearm angle (rotation from supine to prone and vice versa) in nine prespecified steps.

Experimental apparatus

Kinematic measures of wrist abduction/adduction and flexion/extension, elbow flexion/extension, and forearm rotation (Fig. 1A) were derived from signals generated by a forearm rotation and positioning device and wrist goniometer (Fig. 1B, C). A linear potentiometer (10 k Ω) attached to the (hinge) joint of two coupled aluminum bars provided an analog measure of elbow flexion/extension in the sagittal plane. The subject's elbow was placed in the apparatus so that the elbow joint and hinge joint of the aluminum bars were colinear. The subject's forearm was secured to one of the aluminum bars with the use of an adjustable forearm brace constructed of moldable plastic (see Fig. 1B). A forearm rotation and positioning device (FRPD frame) controlled the rotation of the forearm and consisted of a potentiometer (50 k Ω) which registered forearm angle (i.e., supine to prone), a flange-mounted brake (torque 26.69 N, weight 90.7 g, 24 Volts d.c.) which allowed for control of forearm position (rotation in degrees), and a rotation gear and belt which provided the link between the subject's wrist, potentiometer, and brake. The belt was secured to the rotation gear and attached to a velcro band wrapped around the wrist (see Fig. 1C). When the brake was engaged the forearm was constrained to a specific forearm angle, and when disengaged the forearm rotated freely. A DEC PC was used to control the engagement of the brake (precalibrated change in forearm potentiometer voltage) and the time of brake release (preset interval in seconds). Two light-emitting diodes (LEDs) mounted directly in front of the subject signaled the start (green LED) and stop (red LED) of forearm rotation.

The wrist goniometer was mounted on the medial side of the wrist and hand when the forearm was supine (see Fig. 1C). The wrist goniometer consisted of four pieces of plexiglass connected via two hinge joints and one rotary joint. Two linear potentiometers (10 k Ω) registered the angular displacement about the wrist, allowing independent monitoring of wrist flexion/extension and abduction/adduction. The rotary joint allowed simultaneous monitoring of wrist flexion/extension and abduction/adduction.

An analog-digital (A/D) conversion unit (WATSCOPE) was used to collect and store the elbow, wrist, and forearm potentiometer signals. A three-dimensional (3-D) optoelectronic motion analysis system (2 camera; WATSMART) was used to monitor three infrared-emitting diodes (IREDS) placed on the subject's arm, as follows: (1) the lateral surface of the second metacarpal, thereby allowing for the monitoring of the hand trajectory; (2) the lateral epicondyle, in order to monitor the lateral movement of the elbow; and (3) the acromion process, in order to monitor the lateral and vertical movement of the shoulder. The elbow and shoulder IREDS provided a check on any major postural adjustments during a trial. Both the WATSCOPE and WATSMART data were stored on an IBM PC/AT for later off-line analysis. A MAC II was used to generate the metronome signal and controlled all the data collection procedures for the entire experiment.

Experimental conditions

The range of angular displacement of the forearm explored was 160°. Starting with the forearm supine, referred to as 0° of forearm angle, subjects rotated the forearm to a prone position, 160° of forearm angle, in the following ascending order: 0°, 20°, 40°, 60°,

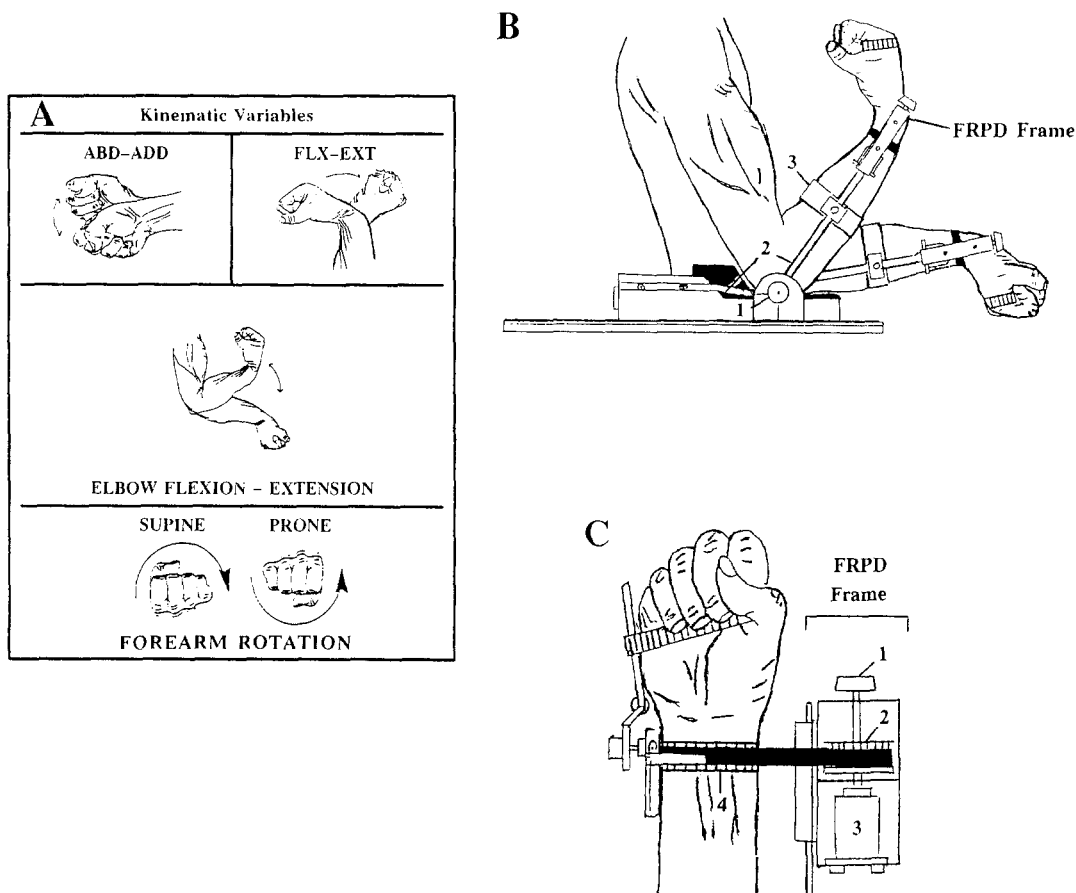


Fig. 1. A The kinematic variables measured: wrist abduction/adduction and flexion/extension (*ABD-ADD* and *FLX-EXT*), elbow flexion/extension and forearm rotation (supine to prone). **B** The positioning of a subject in the apparatus. The potentiometer (1), aluminum bars (2), and forearm brace (3) provided a measure of

elbow flexion/extension in the sagittal plane. **C** The attachment of the wrist goniometer and the forearm rotation and positioning device (FRPD frame). The potentiometer (1), rotation gear and belt (2), brake (3), and velcro strap (4) controlled forearm rotation

80°, 100°, 120°, 140°, and 160°. Starting with the forearm prone, subjects rotated the forearm through the same steps in a descending order. A single trial consisted of moving through all nine forearm angles in one direction (ascending or descending). Paired with an initial forearm angle was a specific coordinative pattern: (1) starting with the forearm supine, subjects coordinated wrist flexion/extension with elbow flexion/extension (supine in-phase); and (2) starting with the forearm prone, subjects coordinated wrist extension/flexion with elbow flexion/extension (prone anti-phase).

Ten experimental trials per initial condition (1 and 2) were performed in two separate sessions, with 1 day between sessions. The trials were blocked in groups of 5, with one block of each initial condition performed on each day. On the 1st day, three subjects performed the supine block first and three performed the prone block first. On day 2, the order of block presentation was reversed. Each trial consisted of 135 cycles of motion (15 cycles for each forearm angle) and lasted 108 s (12 s for each forearm angle). Thus, approximately 2700 cycles were analyzed per subject. The required frequency of motion was 1.25 Hz and paced by an auditory metronome. Previous research (Kelso et al. 1991) has shown that the required coordination patterns are stably performed at this frequency, thereby allowing a thorough examination of the coordinative patterns as a function of forearm angle, while reducing the influence of cycling frequency. The start of every trial was signaled by a flash from the green LED. Following this signal, a 2-s delay occurred before the first beat of the metronome. The flash and delay were preparatory events to help insure a smooth initial entrainment to the metronome. After 15 metronome beats, the brake was released and the green LED flashed, cueing the subject to rotate the

forearm. Following a voltage change of ± 0.99 V (equivalent to 20°, with a resolution of $\pm 0.5^\circ$), the brake reengaged and the red LED flashed, cueing the subject to stop rotating the forearm. The end of a trial was signaled by the red LED. Only a set voltage change in the required direction, ascending or descending, could engage the brake, thus ensuring that the subject did not accidentally rotate to a wrong position.

Before the experiment began, two forearm control trials and four practice trials were used to familiarize the subjects with the rotation of the forearm and the coordinative patterns. In the forearm control trials, subjects held their elbow at roughly a 45° angle to the horizontal plane and rotated the forearm through the nine forearm angles (ascending and descending) without flexing/extending the elbow and wrist. In the practice trials, subjects produced the required patterns (at a frequency of 1.0 Hz) while rotating their forearm through the nine forearm angles. Following the control trials, subjects were told that their main task was to maintain the initial coordination pattern for as long as possible. Further, subjects were instructed that if the pattern began to change, not to intervene, but rather adopt the pattern that was most comfortable under the current conditions. Emphasis was placed on maintaining the required frequency of motion and keeping the elbow and wrist moving smoothly throughout the entire trial.

Data analysis

The potentiometer and IRED data were sampled at 100 Hz and stored for later off-line analysis. The following dependent measures

were calculated: frequency of motion and angular displacement of elbow and wrist flexion/extension; relative phasing between elbow and wrist flexion/extension; perturbation response times (which we call *settling times*); and perturbation-induced switching times.

Relative phase was calculated as a point estimate based on the position in time of peak wrist flexion or extension with respect to the local peak-to-peak cycle of elbow flexion or extension. Coordination of wrist flexion/extension with elbow flexion/extension (pattern 1) was defined as a relative phase of $\Phi = 0^\circ$ (in-phase) for all forearm angles; coordination of wrist flexion/extension with elbow extension/flexion (pattern 2) was defined as a relative phase of $\Phi = 180^\circ$ (anti-phase). The standard deviation around the mean relative phase was used to measure phase fluctuations before and after the transition from one pattern to another.

Every change in forearm angle, due to the mechanical locking of the brake, can be viewed as a perturbation of the coordinative pattern. This effect provided an opportunity to derive estimates of settling time, i.e., the time it takes to return to a stable pattern following an external perturbation (e.g., Scholz et al. 1987; Scholz and Kelso 1989; Schöner et al. 1986). Settling times were computed using the following criteria (cf. Scholz et al. 1987; Scholz and Kelso 1989): first, for the coordinative pattern to be considered stable, relative phase variability before the change in forearm angle (brake release) was required to be less than $\pm 15^\circ$; second, after the brake reengaged, the relative phase of the following cycle had to be $\pm 15^\circ$ greater than the previous two cycles in order for it to be considered a perturbation of the pattern; third, the pattern was considered to have settled when relative phase returned to the preperturbation relative phase value for two cycles and phase variability was less than $\pm 15^\circ$. Settling times were computed by subtracting the time at which the brake engaged from the time at which the pattern had stabilized. On other occasions, the engagement or locking of the brake "kicked" the system (or induced transitions) from one coordinative pattern to another. This provided an opportunity to derive estimates of perturbation-induced switching time, i.e., the time it takes to switch from one coordination pattern to another (e.g., Scholz and Kelso 1989; Schöner et al. 1986). Perturbation-induced switching times were calculated by taking the time at which the new pattern was first established minus the time at which the brake was engaged. The new pattern was considered stable when relative phase attained a significantly new value (never returning to the preperturbation value) and the phase variability over the next two cycles of motion was less than $\pm 15^\circ$.

Results

Accuracy of tracking

To check the accuracy of tracking the metronome, the elbow and wrist cycle durations were analyzed in an ANOVA with condition (supine in-phase vs prone anti-phase), component (elbow vs wrist), and forearm position (nine angular positions) as factors. For this analysis, the initial forearm angle of 0° in the supine condition and 160° in the prone condition were taken as position 1. There were no significant ($p > 0.2$) differences between conditions (supine in-phase: mean 799 ms, SD 28 ms; prone anti-phase: mean 798 ms, SD 29 ms) or components (wrist: mean 798 ms, SD = 34 ms; elbow: mean 799 ms, SD 22 ms). The only significant effect was for forearm position [$F(8,2115) = 1.35$, $p < 0.05$]. Post hoc tests ($p < 0.05$) revealed that the mean cycle duration for forearm positions three (mean 802 ms, SD 21 ms) and four (mean 803 ms, SD 17 ms) was slightly larger than forearm position 1 (mean 792 ms, SD 23 ms). However,

the mean cycle times did not depart significantly from the requirement (800 ms) for any of the three positions. These results indicate that subjects tracked the metronome consistently across all forearm positions.

Transitions and hysteresis: mean relative phase

Representative data from two complete trials for a single subject (BM) are displayed in Fig. 2. The eight vertical lines in the top traces demarcate the nine forearm positions. In Fig. 2A, a transition from the in-phase to anti-phase pattern occurred following the step change from position 7 (120°) to position 8 (140°). In Fig. 2B, a transition from the anti-phase to in-phase pattern occurred following the step change from position 6 (60°) to position 7 (40°). The switching portrayed in these examples was quite abrupt, occurring within a cycle or two, quite typical of transitions observed throughout the experiment. Table 1 shows the number of transitions for each subject that occurred within a given range of forearm angles. Usually, switching occurred over a fairly restricted range, two or three steps of forearm angle change. One subject (MK) was inconsistent in where she switched going in the supine to prone direction, but not vice versa. Another subject (VC) did not switch at all as she rotated the forearm from supine to prone, but very high variability was observed in the relative phasing between the elbow and wrist joints.

The example waveforms in Fig. 2 reveal that switching occurred with the forearm in position 8 (forearm angle 140°) as the forearm was rotated from supine to prone, and after the sixth position (forearm angle 60°) in the prone to supine direction. Thus the absolute forearm angle for switching from one coordination pattern to another differed by 80° and depended on the *direction* of forearm rotation. As shown in Table 1, five of the six subjects showed this hysteresis effect quite strongly. Figure 3 shows that transitions occurred on a total of 90 out of a possible 120 trials across all six subjects: 34 transitions from the in-phase to anti-phase pattern (Fig. 3B); and 56 transitions from the anti-phase to in-phase pattern (Fig. 3B). Across all six subjects, 62% of the transitions from the in-phase to anti-phase pattern occurred within a 40° range (120° – 160° ; see Fig. 3A) and 61% of the transitions from the anti-phase to in-phase pattern occurred within a 40° range (100° – 60° ; see Fig. 3B).

In Fig. 4A, each point represents the group mean relative phase of either the in-phase or anti-phase pattern as a function of forearm angle and initial condition (prone or supine), quantitatively confirming the transition and hysteresis effects. Statistical analysis bears this picture out: between 0 and 40° and between 120 and 160° of forearm angle no meaningful differences existed between the patterns. Note in Fig. 4A that the relative phasing between the joints remains "invariant" as forearm rotation is changed, but jumps qualitatively at a critical point. The locus of qualitative change closely depends, on average, on the direction of forearm angle change, i.e., a clear hysteresis effect.

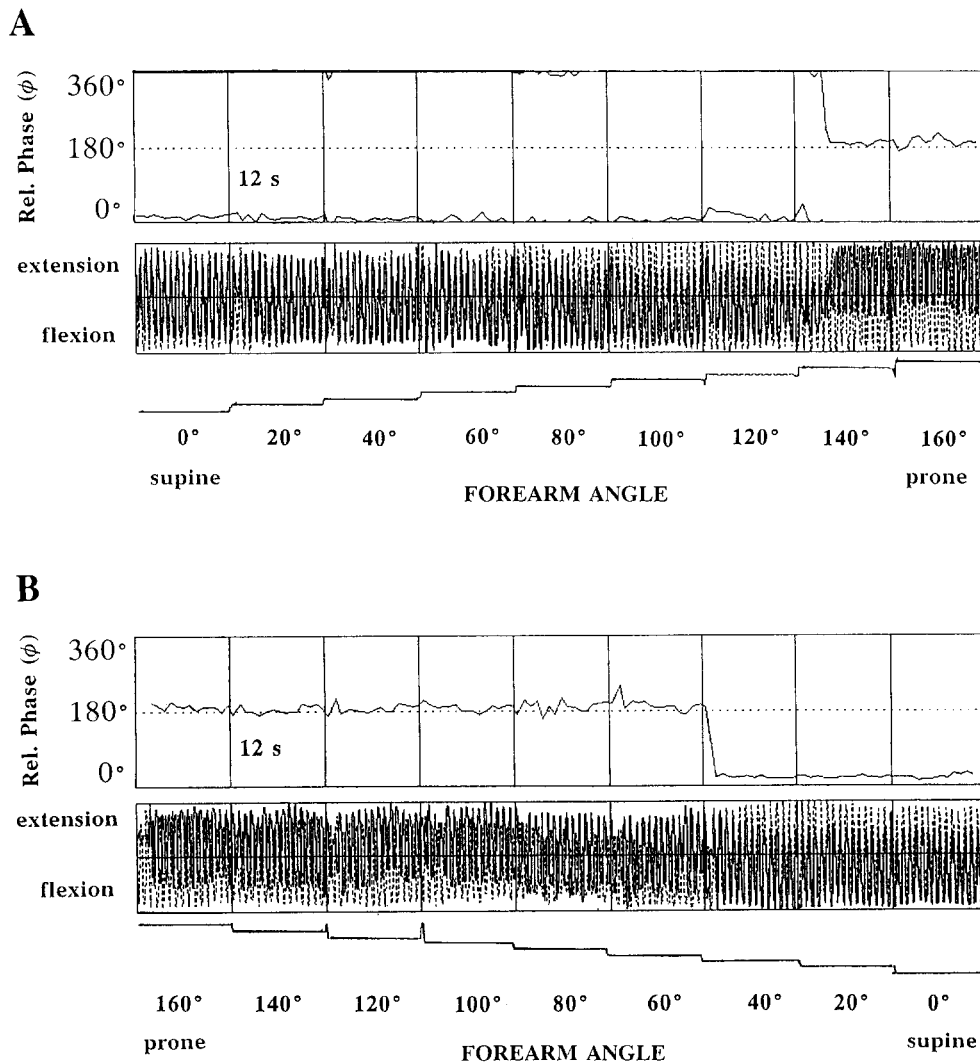


Fig. 2. Two complete individual trials showing switching from the in-phase ($\Phi=0^\circ$) to anti-phase ($\Phi=180^\circ$) pattern (**A**) and from the anti-phase ($\Phi=180^\circ$) to in-phase ($\Phi=0^\circ$) pattern (**B**) for subject BM. Time flows from left to right in both graphs. The bottom traces show the change in forearm angle, the middle traces, the time series of angular displacement for the elbow (---) and wrist (-), plotted in arbitrary units, and the top traces the point estimate of relative phase (Φ) calculated from the time series and plotted on the interval 0° – 360° .

Table 1. Number of transitions occurring over a given range of forearm angles as a function of direction of forearm rotation

Subject	In- ϕ to anti- ϕ	Supine to prone (degrees)	Anti- ϕ to in- ϕ	Prone to supine (degrees)
PC	9/10	100–140	4/6	40–0
RJ	2/2	140	7/10	100–60
MK	9/9	40–140	9/10	120–80
BM	4/6	120–160	7/10	40–0
JM	7/7	120–160	7/10	100–60
VC	–	–	9/10	100–80

Enhancement of phase fluctuations: relative phase SD

The SD of relative phase is shown in Fig. 4B. Relative phase variability was analyzed statistically with coordination pattern and forearm angle as factors. The most interesting result was the significant pattern \times forearm angle interaction [$F(5,594)=2.28$, $p<0.05$]. Although the increase in variability was larger in the anti-phase pattern going from prone to supine, simple main effects tests

revealed that the variability increased significantly ($p<0.01$) for both patterns as a function of forearm rotation. This fluctuation enhancement effect, although on the small side, is highly significant and indicates the sensitivity of the patterns to the parameter of forearm orientation. Further, the increasing phase fluctuations suggest that loss of stability in the pattern occurs as the transition point is approached, especially in the case of the anti-phase pattern. Following the transition, regardless of switching direction, the variability of the new pattern is at the level of the pretransition pattern.

Another way to examine loss of stability is to study the evolution of phase variability up to the transition point itself, regardless of the actual position at which transitions occur. Such a procedure effectively normalizes the data across subjects and provides a more accurate estimate of the stability of the patterns in close proximity to the transition point. Figure 5 presents the adjusted variability data: number 1 on the abscissa corresponds to the last forearm position before the transition; number 2, two positions before the transition, etc. Analysis showed that the anti-phase pattern was more variable than the in-phase pattern [$F(1,594)=35.20$, $p<0.01$].

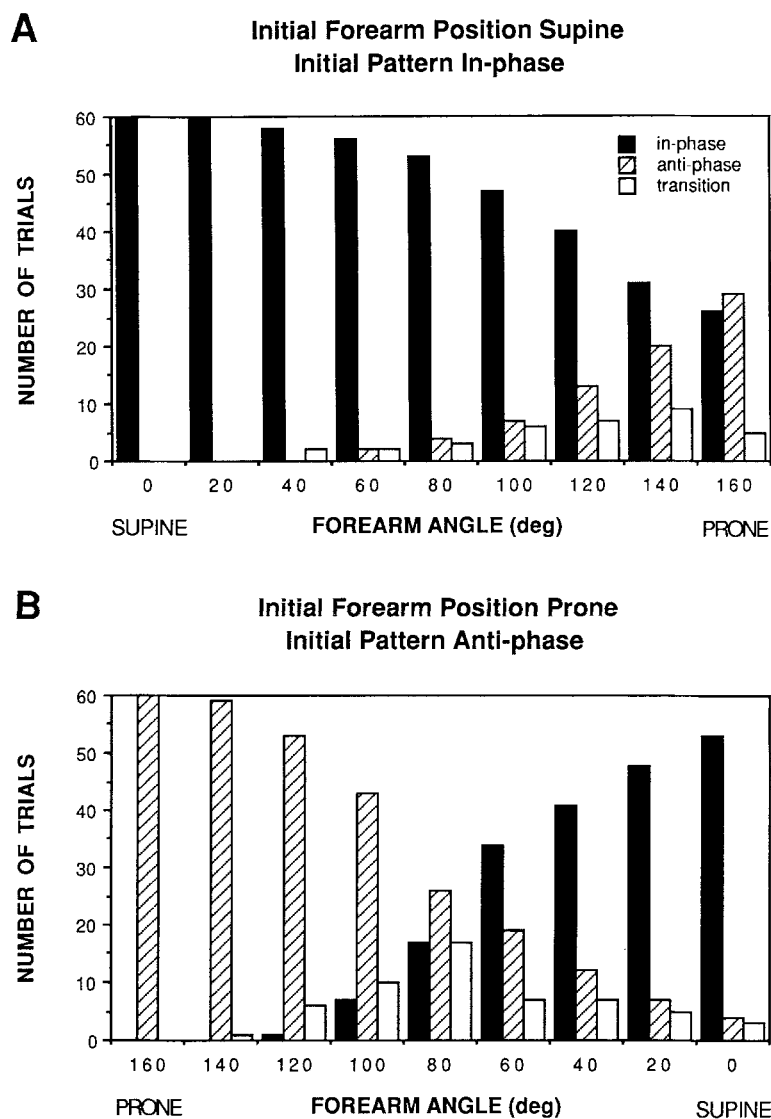


Fig. 3A, B. The change in coordinative pattern across all six subjects as a function of initial forearm position, initial coordinative pattern, and direction of forearm rotation. *Black columns* denote the in-phase pattern and *striped columns* the anti-phase pattern. The *white columns* refer to the number of switches between patterns for a specific forearm angle. **A** The initial forearm angle was 0° supine and the initial coordinative pattern in-phase. As the forearm rotates prone (0° – 160°), note the increase in the occurrence of the anti-phase pattern. As the *white columns* indicate, most switching occurred as the forearm became more prone. **B** The initial forearm angle was 160° prone and the initial coordinative pattern anti-phase. As the forearm rotates supine (160° – 0°), note the increase in the in-phase pattern. Many of the transitions occurred over the intermediate range (100° – 60°) of forearm angles

However, a significant pretransition forearm angle effect [$F(5,594) = 32.41, p < 0.01$], and the absence of an interaction effect, revealed that the increase in variability as a function of nearness to the transition point was statistically equivalent across patterns. These results indicate that the closer the system is to the transition point the greater the phase fluctuations.

Perturbations: settling time

Additional support for an instability mechanism comes from an analysis of the settling times. Figure 6 shows two examples of settling time measurements after a brake-engaged perturbation. Figure 6A shows a perturbation of the anti-phase coordination pattern as the forearm was rotated from prone to supine; Fig. 6B shows a perturbation of the in-phase coordination pattern as the forearm was rotated from supine to prone. A total of 198 perturbations of the patterns were observed (in-phase 97; anti-phase 101). Pretransition settling times were computed to determine whether an increase in settling time

occurred as the system neared the transition point. Settling times were adjusted like the variability data shown in Fig. 5, i.e., backward from the point at which transitions occurred from one pattern to another. Analysis revealed that the mean settling time of the last step (1990 ms) before the transition was significantly greater ($p < 0.05$) than the fifth (1500 ms) and sixth (1360 ms) steps before the transition. This effect did not differ between the patterns and is shown in Fig. 7A. Notably, after the transition, settling times returned to pretransition levels. These results suggest that settling time following an external perturbation (a change in forearm rotation) increased as the system approached the point at which switching occurred, and further support the hypothesis that transitions occur as a result of instability.

Perturbation-induced transitions

Of the 90 observed transitions, 72 (77%) were classified as perturbation-induced transitions resulting from the engagement of the brake (in-phase to anti-phase, $n = 24$;

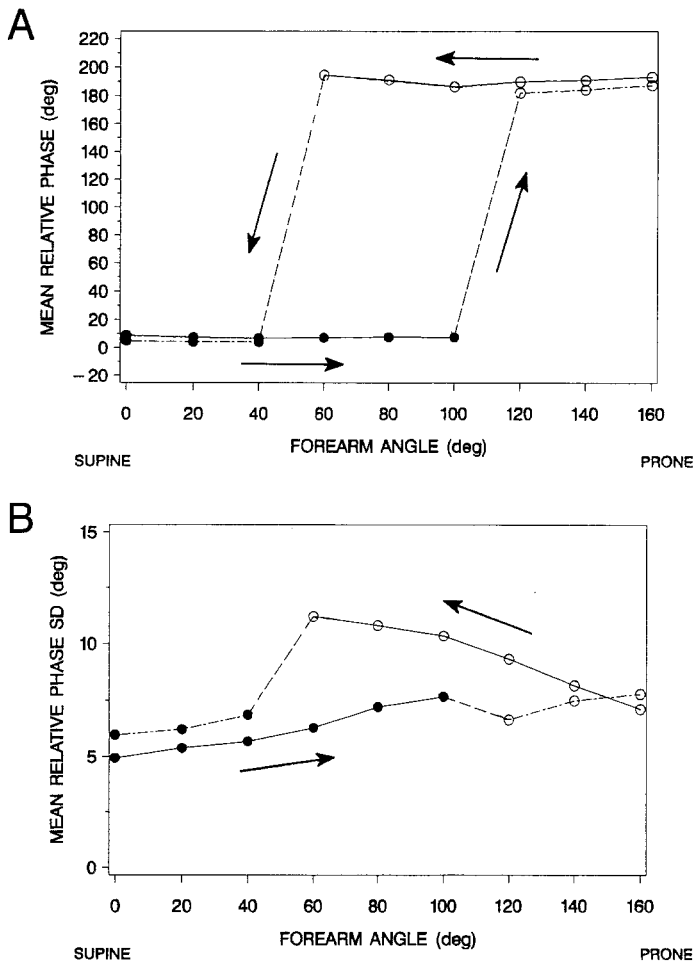


Fig. 4. The group relative phase (**A**) and relative phase variability (**B**) data are plotted as a function of forearm angle and direction of forearm rotation. The *left-right arrows* indicate the direction of forearm rotation, and the *up-down arrows*, in **A**, the direction of switching. The pretransition relative phase and relative phase variability for the anti-phase and in-phase patterns are plotted as *open circles* and *closed circles connected by a solid line* for the first six forearm angles in each condition, respectively. The posttransition relative phase and relative phase variability for the anti-phase (now in-phase) and in-phase (now anti-phase) patterns are plotted as *closed* and *open circles connected by the dotted-dashed line* for the last three forearm angles in each condition, respectively. In **A**, it is important to note that the mean relative phase remains constant both before and after the transition for both patterns; while in **B** a systematic increase in variability occurs as a function of forearm rotation in both directions across the first six forearm positions

anti-phase to in-phase, $n=48$). Two examples of perturbation-induced transitions are shown in Fig. 8. As the forearm was rotated from supine to prone, the brake perturbation induced a transition from the in- to anti-phase coordination pattern (Fig. 8A). This appears to take longer than going in the opposite direction (Fig. 8B). In Fig. 7B, the distribution of switching times is plotted as a histogram. The switching time data were examined in a direction of switch (in-phase to anti-phase vs anti-phase to in-phase) by forearm step (eight steps) ANOVA. Only the direction of switch effect was significant [$F(1,70)=6.62$, $p<0.05$ (in-phase to anti-phase, mean

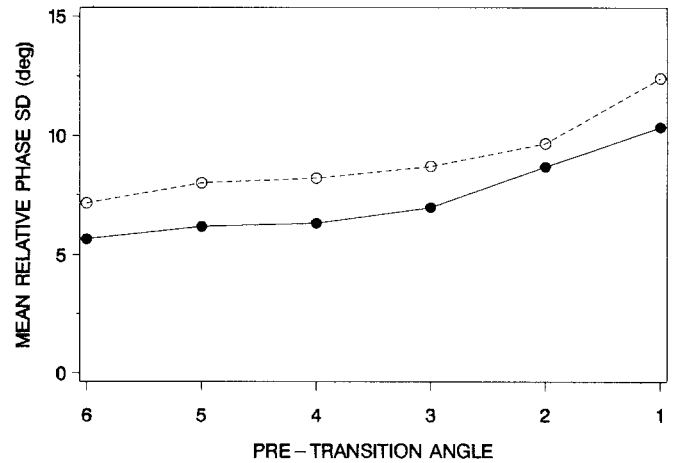


Fig. 5. The normalized group relative phase variability data in the pretransition regime are plotted as a function of forearm angle and coordinative pattern: anti-phase pattern, open circles; in-phase pattern, closed circles. On the *abscissa*, pretransition angle 1 is the forearm angle before the transition, and pretransition angle 6 is the forearm angle furthest from the transition. The systematic increase in variability across both patterns as a function of distance from the transition is quite obvious

1640 ms; anti-phase to in-phase, mean 1380 ms)], supporting the relative phase variability analysis (cf. Fig. 4B) which showed that the anti-phase pattern was inherently less stable than the in-phase pattern in this task. These results clarify the relationship between switching time and pattern stability, i.e., it takes longer to switch from a more stable to less stable pattern than vice versa.

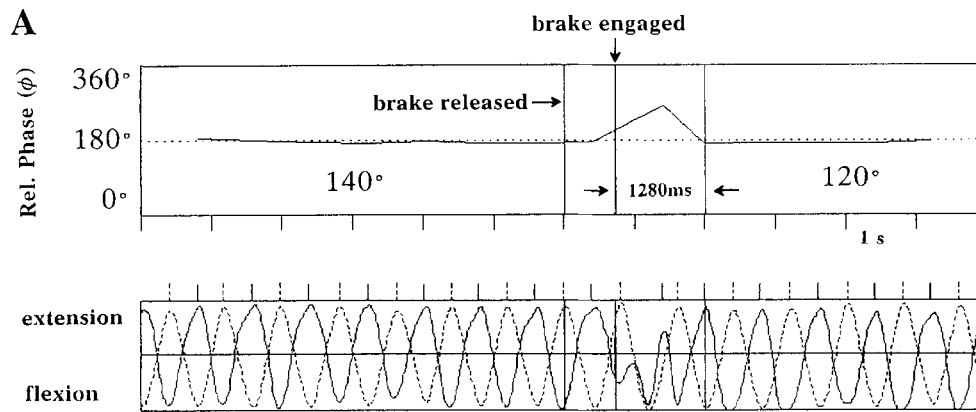
Angular displacement

Qualitative change was observed in the relative phasing between the joints when one pattern of coordination switched to another. But no such dramatic changes were observed in the angular displacements of the joints as the forearm rotated from supine to prone and vice versa. In fact, analysis showed no differences overall between the elbow (65.7°) and wrist (65.6°) displacements across conditions ($p>0.05$). Wrist angle as the forearm was rotated from supine to prone tended to be larger (68.5°) than vice-versa (62.8°), but these changes in angular displacement contributed little to the observed coordinative changes.

End-effector trajectories

In previous work we showed that the hand's trajectory was curvilinear when the joints moved in the same direction (up-up or down-down). In contrast, when the joints moved in opposite directions (up-down) a large reduction in curvature was observed. Furthermore, before a transition from different to same direction joint motion, the trajectory became much more variable, whereas after a transition the (now curvilinear) trajectory was much

Perturbation of Anti-phase Pattern



Perturbation of In-phase Pattern

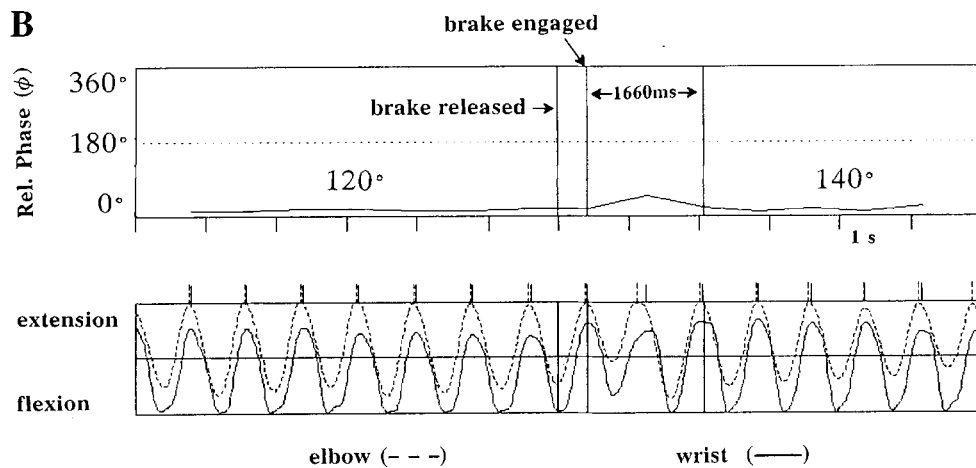


Fig. 6A, B. Two examples of brake-engaged perturbations are used to graphically represent the calculation of settling time. The time series of elbow (---) and wrist (—) angular displacement are plotted in the *bottom traces* in arbitrary units. The relative phasing (Φ) computed from the time series is plotted on the interval 0° – 360° in the *top traces* of both graphs. In all traces, the *first vertical line* indicates the release of the brake, the *second line* the engagement of the brake, and the *third line* the time at which the pattern returned to the pre-perturbation relative phase value. **A** Anti-phase pattern ($\Phi = 180^\circ$) for subject BM. After the brake release, the forearm rotates from forearm angle 140° to 120° . **B** In-phase pattern ($\Phi = 0^\circ$) for subject RJ. After the brake release, the forearm rotates from forearm angle 120° to 140° . Note that the relative phase change in **A** and **B** returns to its pre-perturbation value

less variable (Kelso et al. 1991, Fig. 9). In this experiment, the trajectory was curvilinear for the initial forearm positions, supine in-phase, forearm angle 0° (Fig. 9A, B), and prone anti-phase, forearm angle 160° (Fig. 9C, D). Rotating the forearm did not seem to alter the curvilinear nature of the trajectories, suggesting that the hand trajectory is strongly tied to the directional (up-down) relationship between the components and the inherent stability of the pattern.

Discussion

Insights into how the nervous system assembles patterns of coordinated behavior may be gleaned by studying transitions from one multijoint coordination pattern to another. The reason is that at transitions one pattern must be disassembled and a new or different pattern assembled. If such transitions are accompanied by an instability, pattern formation and change are said to be self-organized. In self-organizing systems, due to non-linear interactions among the components, patterns arise and change spontaneously when a control parameter is

systematically varied. The role of the control parameter is not to prescribe specific patterned states, but rather to drive the system through available states. Fluctuations play a key role in probing the stability of a given pattern and allow the system to discover new patterns. Notions of self-organization have attracted neuroscientists in the past (e.g., Katchalsky et al. 1974),¹ but rigorous analysis has had to await detailed experimental examples and theoretical models (e.g., Haken et al. 1985; Kelso 1984; see Schönner and Kelso 1988, and Turvey 1990 for reviews).

In the present experiment, three specific lines of evidence converge on an instability interpretation of coordinative change: (1) a growth in phase fluctuations was found as the transition region was approached (Figs. 4B, 5); (2) settling time increased following a perturbation as

¹ At a special Neurosciences Research Program on "Dynamic Patterns in Brain Cell Assemblies", Katchalsky et al. (1974, p. 152) concluded that, "The *possibility* [our italics] of ... macrostates emerging out of cooperative processes, sudden transitions, pre-patterning etc., seem made to order to assist in the understanding of integrative processes ... of the nervous system ... that remain unexplained by contemporary neurophysiology"

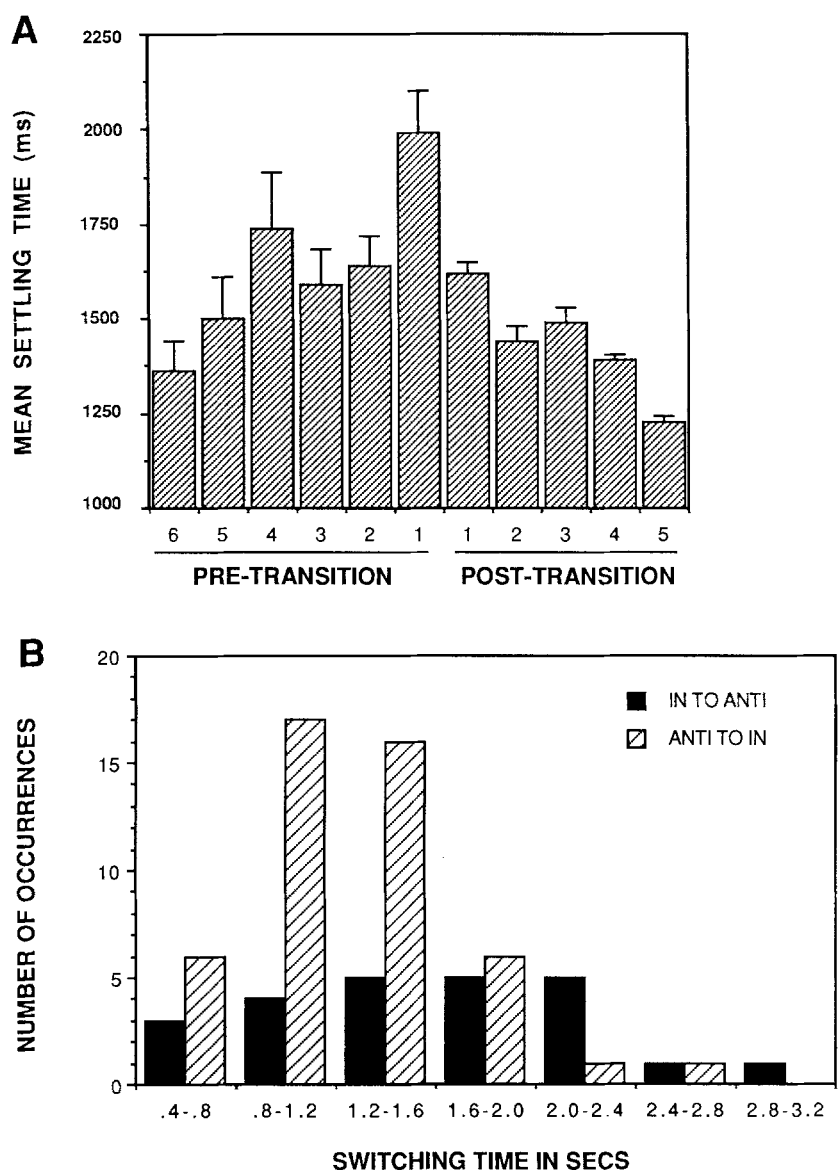


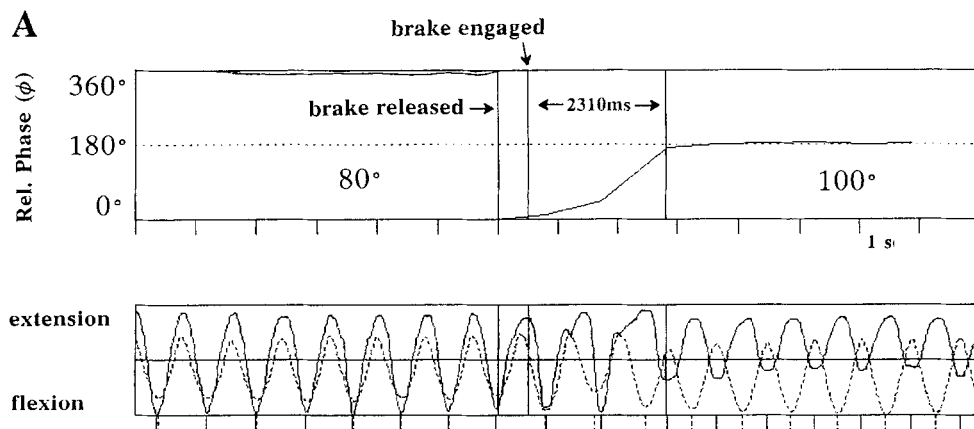
Fig. 7. A The normalized group pretransition and posttransition mean settling times across conditions are plotted as a function of the step (change in forearm angle) before and after the transition, respectively. On the *abscissa*, pretransition step 1 is the step before the transition and pretransition step 6 is the step furthest from the transition; posttransition step 1 is the step after the transition and posttransition step 5 is the step furthest from the transition. The *bars* on each column represent 1 SD around the mean. Note the fairly systematic increase and decrease in settling times as a function of pretransition and posttransition step, respectively, around the transition. **B** The number of perturbation-induced switches are plotted as a function of switching time (*abscissa*) and direction of switch. Note the differences in distribution between the anti-phase to in-phase transition (*striped columns*) and the in-phase to anti-phase transitions (*black columns*)

the system neared the transition point (Figs. 6, 7A); and (3) the probability of an external perturbation kicking the system into a more stable coordinative state increased near the transition region (Figs. 7B, 8). Observed increases in phase fluctuations and settling times are consistent with the predictions of *critical fluctuations* and *critical slowing down* in theories of self-organization in non-equilibrium systems (Haken 1983; Haken et al. 1985; Schönner and Kelso 1988).

Previous research has demonstrated unidirectional transitions between coordinative patterns in a wide variety of experimental settings. Usually, frequency or speed of motion was increased and spontaneous switching from an intrinsically less stable coordination pattern to a more stable coordination pattern was observed (e.g., Kelso 1984; Kelso et al. 1991; Schmidt et al. 1990; Wimmers et al. 1992; for exceptions, however, see Scholz and Kelso 1990; Walter and Swinnen 1990). For example, Baldissera et al. (1982) demonstrated directionally depen-

dent transitions between multijoint patterns across limbs (the wrist and ankle) as a function of movement frequency. Although their work hinted that loss of stability might be the cause of such transitions (see Fig. 2F in Baldissera et al. 1982), an analysis of pattern variability was not undertaken. Recently, we demonstrated that loss of stability is present when direction-dependent coordinative changes occur between joints of a single limb (Kelso et al. 1991) and between limbs (e.g., Kelso and Jeka 1992). In the experiment by Kelso et al. (1991; and probably in Baldissera et al. 1982), the transition always occurred from a less stable to more stable form of coordination. In the present experiment, a spontaneous transition between two stable coordinative patterns – a bidirectional transition – was observed. Our work shows that not only movement frequency but also spatial orientation is an important system parameter: systematically changing forearm posture from prone to supine induced switching from an anti-phase ($\Phi \approx 180^\circ$) to in-

Perturbation Induced Switching: In-phase to Anti-phase



Perturbation Induced Switching: Anti-phase to In-phase

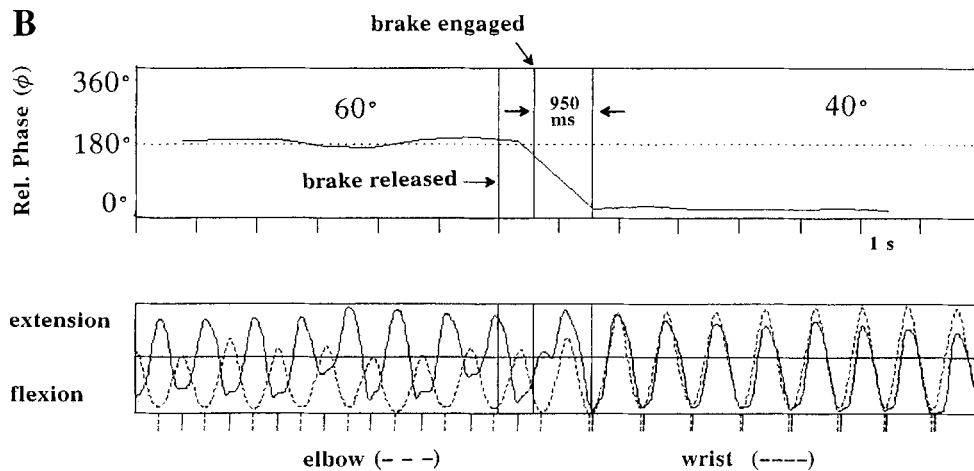


Fig. 8A, B. Two examples of perturbation-induced transitions are used to graphically represent the calculation of switching time. The time series of elbow (---) and wrist (—) angular displacement are plotted in arbitrary units in the *bottom traces*. The relative phasing (Φ) computed from the time series is plotted in the *top traces* on the interval 0–360°. In all traces, the *first vertical line* indicates the release of the brake, the *second line* the engagement of the brake, and the *third line* the time at which the new pattern was established. **A** A transition from the in-phase ($\Phi=360^\circ$) to anti-phase ($\Phi=180^\circ$) pattern for subject BM as the forearm rotates from forearm angle 80 to 100°. The relative phase near 360° for the in-phase pattern indicates that the wrist reaches maximum flexion before the elbow. **B** A transition from the anti-phase ($\Phi=180^\circ$) to in-phase ($\Phi=0^\circ$) pattern for subject BM as the forearm rotates from forearm angle 60 to 40°. Note the slowing of the wrist in **A** and the quickening in **B** during the transition

phase ($\Phi \approx 0^\circ$) pattern of coordination. Reversing the direction of forearm rotation from supine to prone, induced switching from an in-phase ($\Phi \approx 0^\circ$) to anti-phase ($\Phi \approx 180^\circ$) pattern. Bidirectionality of pattern switching reveals the hysteretic nature of the transitions and draws attention to a common but frequently ignored property of biological coordination, namely, multifunctionality, i.e., the ability to produce several patterns of coordination for the same parameter value.

In a previous paper (Kelso et al. 1991), we entertained two possible explanations for direction-dependent transitions observed in our earlier work and the work of others (cf. Baldissera et al. 1982; see also Kelso and Jeka 1992). One possibility is that incoming proprioceptive information fed to supraspinal structures (e.g., parietal cortex, cerebellum) alters descending signals, thereby producing abrupt spontaneous changes in behavior (see Georgopoulos and Grillner 1989). Another possibility is that proprioceptive input to spinal cord interneurons leads to spontaneous transitions by gating descending signals (cf. Baldissera et al. 1982). An important consideration in each case is the putative role of propriocep-

tive information for the maintenance of multijoint coordinative patterns. There are a couple of reasons for stressing the importance of proprioceptive information. One stems from work by Kots et al. (1971) on single multijoint limb movements, and Kelso (1977) and Polit and Bizzi (1979) on single joint movements (see also Jeannerod 1988, Chap. 6, for review). Basically, Kots et al. demonstrated that a lack of kinesthetic sensitivity due to parietal lesions produced deficient performance in elbow and wrist flexion/extension movements similar to the ones examined here. Kelso, in humans, and Polit and Bizzi, in monkeys, demonstrated that removal of sensory feedback did not drastically diminish performance on *single* joint movements. The latter authors also showed significant deficits in pointing behavior when the posture of the upper arm was changed unbeknownst to the monkey. Taken together, such results suggest that proprioceptive information is necessary for sustaining coordination *between* the joints. A second reason why proprioception may be important concerns the occurrence of phase fluctuations observed here before the transition. These fluctuations are a sign of instability in the coord-

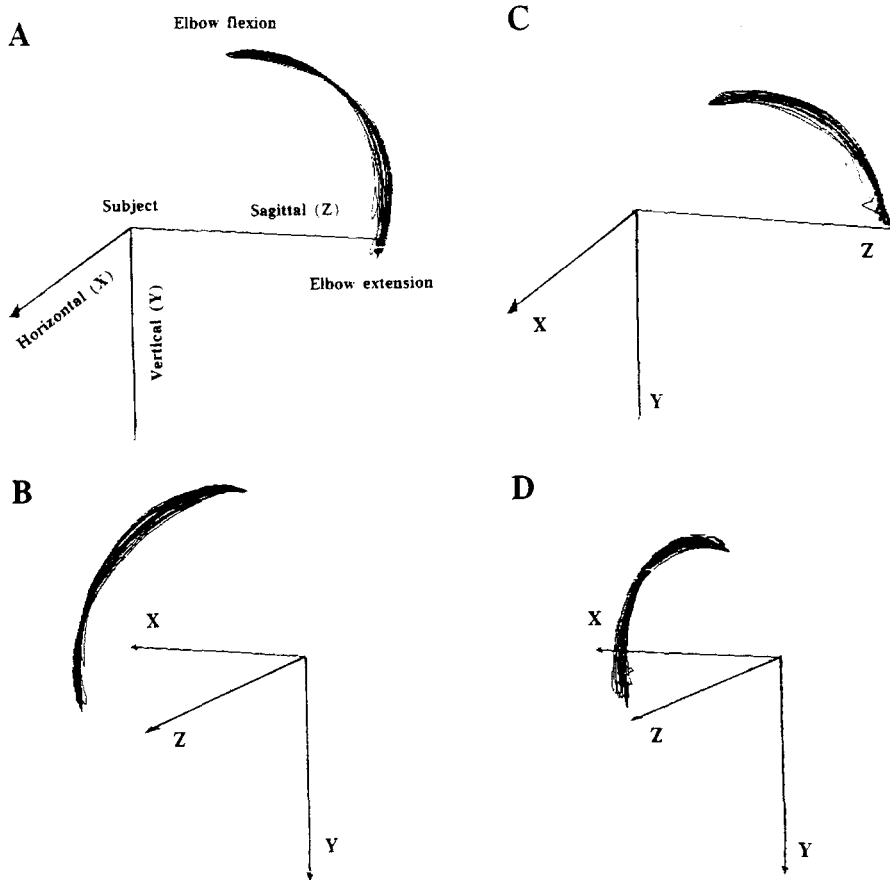


Fig. 9A–D. Representative examples of hand trajectories for subject JM are plotted as a function of the X , Y , and Z displacements of infrared-emitting diode (IRED) 1. The subject's position is centered near the origin with the Z -axis representing motion in the sagittal plane, the Y -axis representing vertical motion, and the X -axis representing horizontal motion. **A, C** A view as if standing to the right of the subject; **B, D** a view as if standing to the left of the subject. **A, B** The coordinative pattern producing the trajectory is in-phase and the forearm angle is 0° supine. **C, D** The coordinative pattern producing the trajectory is anti-phase and the forearm angle is 160° prone. Note the similarity in the curvature of the trajectories for the different forearm positions and corresponding coordination patterns

dination between the joints (e.g., Haken et al. 1985; Schöner and Kelso 1988). Neural systems may require proprioceptive information about such fluctuations for the purpose of intentionally stabilizing coordinated states (e.g., Scholz and Kelso 1990).

How do the present results relate to current and future work in the area of multijoint coordination and trajectory formation? First, the work on minimum jerk principles (e.g., Flash and Hogan 1985) and curvature-speed tradeoffs (e.g., Viviani and Schneider 1991) in arm movements describes in detail the kinematics of the end-effector trajectory, but pays little attention to how the individual joints of the limb are coordinated. The trajectory data presented here (Fig. 9) and elsewhere (e.g., Hollerbach and Atkeson 1987; Kelso et al. 1991; Soechting et al. 1986) suggest that an analysis relating the trajectory path of the hand to the coordination dynamics of the joints may help in clarifying how the nervous system controls multijoint movements in different functional contexts. A second point concerns how the present results on rhythmical coordination relate to discrete, single limb multijoint movements. Recently, Schöner (1990) has modelled single and interlimb discrete targeting tasks building on models of rhythmic movement (Haken et al. 1985) and experimental work by Kelso and colleagues (Kelso et al. 1979, 1983). In Schöner's formulation, postural states, discrete movements from one posture to another, and rhythmic movements are all shown to be governed by the same algorithm (an equa-

tion of motion), depending only on the parameters selected. A third point concerns neural network models of multijoint coordination (e.g., Bullock and Grossberg 1991; Jordan 1990). Although these models reproduce a wide variety of behavior while the system is operating in the linear range, they do not presently account for the effects we have demonstrated here, which are typical properties of self-organizing, i.e., synergetic systems. Pattern switching and hysteresis are obviously produced by real neural networks, but they present a challenge to artificial neural network models.

Finally, we want to stress that on *any* given level of description (e.g., planning, joint, muscle) stability is a key concept. But stability of what? In complex, multi-degree-of-freedom movements, relevant variables are not given a priori, but have to be found. Two criteria for defining relevant variables are that they should: (1) change much more slowly compared to other possibilities (e.g., component amplitudes and velocities); and (2) exhibit qualitative change at a critical value of some parameter (here the spatial orientation of the forearm). Relative phase between the joints qualifies as a system-relevant variable because the phase (and only the phase) remains "invariant" or stable before and after the transition. Moreover, relative phase is the only variable that shows signs of instability, before switching at a critical parameter value. Thus coupling through relative phase appears to be an important way to coordinate events in the nervous system and behavior.

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