

Recruitment of Degrees of Freedom Stabilizes Coordination

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By showing that transitions may be obviated by recruiting degrees of freedom in the coupled pendulum paradigm, the authors reveal a novel mechanism for coordinative flexibility. In Experiment 1, participants swung pairs of unconstrained pendulums in 2 planes of motion (sagittal and frontal) at 8 movement frequencies starting from either an in-phase or antiphase mode. Few transitions were observed. Measures of spatial trajectory showed recruitment effects tied to the stability of the initial coordinative pattern. When the motion of the pendulums was physically restricted to a single plane in Experiment 2, transitions were more common, indicating that recruitment delays—or even eliminates—transitions. Such recruitment complements transitions as a source of coordinative flexibility and is incorporated in a simple extension of the Haken–Kelso–Bunz (1985) model.

At the core of modern dynamical approaches to the study of coordination is the recognition that such behavior results from a self-organized process involving multiple degrees of freedom (see, e.g., Beek & van Wieringen, 1994; Kelso & Schöner, 1987; Schöner & Kelso, 1988a; Turvey, 1990). Analysis of the transition properties of a system is important for understanding the nature of these self-organized coordination dynamics. Numerous experiments on different kinds of coordination have shown that salient features of the coordination dynamics can often be elucidated by driving the system toward a point of instability in which a qualitative change or phase transition occurs. Near such critical points, new modes of coordination arise that permit one to delineate the system's relevant collective variables or order parameters and the collective variable dynamics (see Haken, 1996; Kelso, 1995, for reviews). A prototypical system that has been explored in detail is bimanual coordination (Haken, Kelso, & Bunz, 1985; Kelso, 1981, 1984; Schöner, Haken, & Kelso, 1986), in which relative phase was shown to be a significant collective variable. Subsequent experiments have demonstrated the informational nature of coordination dynamics (Kelso, 1994; Turvey, 1994): The same collective variable—relative phase—and the same basic collective variable dynamics capture the coordination behavior between similar components within an organism (e.g., Byblow, Carson, & Goodman, 1994; Carson, Goodman, Kelso, & Elliott, 1995; Kelso, 1984), between stimulus and response (e.g., Kelso, DelColle, & Schöner, 1990; Wimmers, Beek, & van Wieringen, 1992), between stimulus and manipulandum

(Stins & Michaels, 1999), and between organisms (e.g., Amazeen, Schmidt & Turvey, 1995; Schmidt, Carello, & Turvey, 1990). To say that coordination dynamics is informational is not to downplay biomechanical properties that may influence these dynamics. For example, eigenfrequency differences between components have been shown to tailor the coordination dynamics in significant ways, such as by systematically shifting the fixed points of the relative phase (e.g., Kelso & Jeka, 1992; Schmidt, Shaw, & Turvey, 1993; Treffner & Turvey, 1996) as well as by causing phase drift and relative coordination effects (Kelso, de Guzman, & Holroyd, 1991).

By and large, transitions among coordination patterns are induced by instabilities effected, typically, through a frequency or movement-speed control parameter (but see also Buchanan and Kelso, 1993; Buchanan, Kelso, & de Guzman, 1997; Kelso, Buchanan, & Murata, 1994, for examples of transitions driven by changes in spatial control parameters). An apparent anomaly in the literature, however, exists in the coupled pendulum paradigm advanced by Turvey, Kugler, and colleagues (see Amazeen, Amazeen, & Turvey, 1998; Schmidt & Turvey, 1995; Turvey & Schmidt, 1994, for reviews). Transitions between modes of coordination have not been observed in this system despite clear indications that one pattern (antiphase) is less stable than the other (in phase). This differential stability of the in-phase and antiphase patterns is evident in the standard deviations of relative phase near frequency regions where transitions were expected on the basis of results from other similar experiments (Schmidt et al., 1993; Sternad, Turvey, & Schmidt, 1992; Turvey & Schmidt, 1994). Because the frequencies tested in the coupled pendulum experiments by Turvey and colleagues (Schmidt et al., 1993; Sternad, Turvey, & Schmidt, 1992; Turvey & Schmidt, 1994) fall in the range of frequencies in which transitions occurred in other movements, it is possible that certain factors not considered or measured in the coupled pendulum paradigm act to functionally stabilize the antiphase pattern in the coupled pendulum paradigm. Such factors are conceptually and theoretically important. The basic theoretical model used to explain

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coupled pendulum movements is the Haken–Kelso–Bunz (HKB) model (see, e.g., Sternad, Amazeen, & Turvey, 1996), suitably extended to include symmetry breaking (Kelso et al., 1990) and stochastic fluctuations (Schöner et al., 1986). Yet, a significant feature of this modified HKB model is transitions from antiphase to in-phase coordination, conspicuously absent in the conventional coupled pendulum paradigm studies thus far (but see Mitra, Amazeen, & Turvey, 1997). Thus, previously unsuspected processes that serve to delay or even inhibit transitions in the coupled pendulum paradigm may need to be incorporated into theoretical accounts.

What might these processes be? One possibility, pursued here, is that additional, typically unobserved biomechanical degrees of freedom are active in the coupled pendulum paradigm, the role of which is hypothesized to stabilize coordination according to task or environmental requirements (Kelso, Buchanan, de Guzman, & Ding, 1993). Early experiments in bimanual coordination showed that degrees of freedom may be recruited or suppressed depending on temporal or spatial constraints (Buchanan, Kelso, de Guzman, & Ding, 1997; Kelso & Scholz, 1985). More recently, Kelso et al. (1993) proposed that this recruitment and suppression of degrees of freedom complements pattern switching in cases in which the repertoire of stable coordination modes has been exhausted (e.g., at high movement frequencies when even the in-phase mode becomes unstable). This mechanism requires that the system is biomechanically redundant; that is, the number of available degrees of freedom exceeds the number required for a nominal execution of the task.

In this study, we explored putative recruitment processes in the coupled pendulum paradigm. In the first experiment, we examined the behavior of the pendulum in multiple planes in the typical situation, that is, in situations during which participants are instructed to maintain the original plane of motion but movements are not mechanically fixed. A stronger test of the effects of recruitment of degrees of freedom was performed in the second experiment, in which the behavior of the system was observed when the additional degrees of freedom available in the first experiment were physically constrained. Our results necessitate a new theoretical account, based on the HKB model, that incorporates planes of motion other than those necessary for nominal performance of the task.

Experiment 1

Investigation into the recruitment hypothesis in the coupled pendulum paradigm was begun by Buchanan and Kelso (1999). Buchanan and Kelso observed recruitment and suppression of degrees of freedom on the biomechanical level using three different measures: (a) deviations of the end of the pendulum from the desired planar trajectory, (b) transitions from linear to spherical trajectories, and (c) motions of other joints proximal to the end-effector. By all three measures, participants were shown to recruit degrees of freedom, indicating that the relative phase between the limbs, by itself, does not capture the full coordination

behavior. Instead, the coordinative system was shown to be a complex structure consisting of temporal variables (e.g., relative phase) and spatial variables (e.g., amplitude) that interact to stabilize the task. In the present article, we expand the work of Buchanan and Kelso and its implications for the coordination dynamics of coupled pendulum movements.

Experiment 1 differs from Buchanan and Kelso's (1999) work, which like much of the earlier research, was limited to motions taking place primarily in the sagittal plane. Here, we examine coordination in both the sagittal and frontal planes in the coupled pendulum paradigm. This is an important comparison because previous studies of frontal plane motion (Byblow et al., 1994; Carson, 1995; Carson, Byblow, & Goodman, 1994; Mitra et al., 1997) lead us to expect that coordination will become unstable in the frontal plane when movement frequency is increased, leading to other coordinative patterns. The recruitment hypothesis (Kelso et al., 1993) predicts that recruitment of degrees of freedom will occur in directions orthogonal to the direction dictated by the task regardless of the original plane of motion. Moreover, if recruitment fulfills the role of stabilizing otherwise unstable coordinative patterns, it should become manifest both in response to the energetic demands of the task (e.g., maintaining the desired frequency) and in response to the required phase difference (e.g., the less stable antiphase pattern should result in more recruitment than the more stable in-phase patterns in both planes).

Method

Participants. Eleven participants, (6 men and 5 women) from the university population volunteered for this experiment. Participants were compensated by being awarded class credit. Participants gave informed consent prior to participation in accordance with the local human subjects committee. All participants were treated in accordance with the ethical standards of the American Psychological Association (APA).

Apparatus. Participants were seated in a chair with their forearms placed parallel to each other and supported but not strapped on an armrest designed to easily allow pronation and supination of the forearm (Figure 1). Infrared-emitting diodes (IREDs) were placed in the following locations of both the right and left arm: (1) at the end of the pendulum, (2) on the articulation of the first and second phalanges of the middle finger, (3) and (4) on

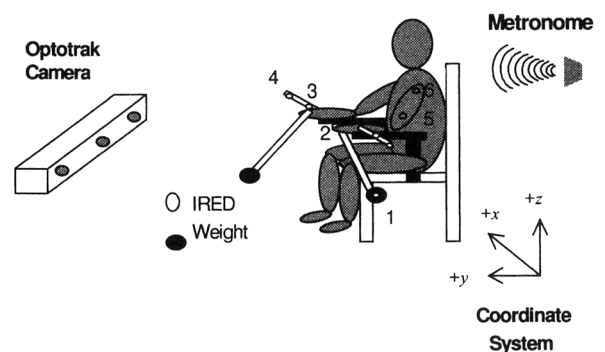


Figure 1. Setup of the coupled pendulum experiment (see text for details). IRED = infrared-emitting diodes; 1, 2, 3, 4, 5, and 6 = locations where IREDs were placed.

a metal bar fastened to the anterior portion of the styloid process (to place the markers in a visible location allowing identification of the wrist joint center), (5) on the biceps, approximately two thirds of the way from the shoulder to the elbow, and (6) on the anterior portion of the shoulder. Although the experimental apparatus allowed for measurement of joint angles as well as the end-pendular trajectory, we chose to concentrate on the latter in the present article because planar pendulum movement has been the sole focus of the many coupled pendulum studies presented in this journal.

Since recruitment may be influenced by the inertia of the pendulum (Buchanan & Kelso, 1999), three pairs of pendulums—referred to as low, medium, and high inertia pendulums—were used by each participant. The low inertia pendulum consisted of an unweighted wooden dowel (2.2 cm diameter) with a rubber hand grip placed in the middle. The medium and high inertia pendulums were constructed out of 2.2-cm-diameter wooden dowels with hand grips placed on the proximal ends and with circular lead weights placed at different locations along the pendulum. The properties of the pendulums are given in Table 1. Note that the inertial effect of the hand is not included in the moment-of-inertia calculation, as is frequently the case in the coupled pendulum paradigm (see, e.g., Turvey, Rosenblum, Schmidt, & Kugler, 1986). This omission is expected to affect the results only slightly quantitatively but not at all qualitatively.

Pacing for the participants was provided by an auditory metronome, generated by a Quick Basic program from a Macintosh Classic II computer. Both the movement and stimulus data were simultaneously collected at 128 Hz using the Optotrak 3010 and the Optotrak Data Acquisition Unit (Northern Digital Inc., Waterloo, Ontario, Canada) systems, respectively. The following conventions were used for the IRED positions: +x to the right, +y forward, and +z upward, relative to the participant (see Figure 1).

Procedure. Participants were asked to swing the pendulums in time with a metronome that increased from 1.25 Hz to 3 Hz in 0.25-Hz intervals every 10 cycles. Pendulums were swung in two planes under two initial coordinative modes: (a) parallel to the sagittal plane of the body in an in-phase mode with the pendulums moving forward and backward together, (b) parallel to the sagittal plane in antiphase mode with the right and left pendulums alternating, (c) parallel to the frontal plane in an in-phase mode with the pendulums moving in and out at the same time, and (d) parallel to the frontal plane in an antiphase mode with the pendulums moving right and left together. Thus, in the in-phase conditions, homologous muscle groups contracted simultaneously, whereas in the antiphase conditions, homologous muscle groups contracted in an alternating fashion. Participants were instructed to swing the pendulums using only wrist abduction and adduction in the sagittal plane conditions and using forearm pronation and supination in the frontal plane conditions. They were also instructed to keep their eyes closed and not to intervene if the coordinative pattern started to change but to continue with whatever pattern felt most comfortable. In each condition, two trials per participant were recorded.

Analysis. After analyzing the frequency distribution using Fourier methods, we filtered the coordinates of each IRED using a second order Butterworth filter with a cutoff of 6 Hz. Angles for the frontal and sagittal components of the pendulum motion were calculated from the angle between the line from IRED 1 to IRED 2 and the vertical line descending from IRED 2, projected onto the frontal and sagittal planes (see Figure 1). The maximum angular displacements for each hand in the two planes were found using a Matlab routine (Mathworks, 1994). A point estimate of the relative phase of the pendulum motion was found from the angular positions and velocities of the two hands using the following algorithm: $\phi_j = 2\pi \cdot [(R_i - T_j)/(R_{i+1} - R_i)]$, where R_i and R_{i+1} are the times of the peak position or velocity of the left hand and T_j is the time of the peak position or velocity of the right hand between R_i and R_{i+1} . The point estimates of relative phase using position and velocity were combined to produce a relative phase measure with two values per cycle. In-phase was defined as utilizing homologous muscle groups, so that for frontal plane movements, the right-hand frontal plane angles were multiplied by -1 . All statistical analyses on relative phase were performed using mean and standard deviations of relative phase that were obtained using circular statistics (Batschelet, 1981).

Spatial deviation from the required task was calculated in two ways. First, for each trial, a linear regression was performed between the x- and y-coordinates of IRED 1 for each cycle, defined as the period between maxima in the pendulum motion in the primary plane of motion (i.e., the sagittal plane for the sagittal plane of motion or the frontal plane for the frontal plane of motion). The inclination (θ) of that line relative to the primary plane of motion (see Figure 2 for the case of the frontal plane condition) was used as a measure of deviation of the trajectory from the task. The eccentricity (ϵ), or linearity, of the paths was found by rotating the coordinate system on a cycle-by-cycle basis so that a local x-axis was defined along the regression line. The eccentricity was then defined as the ratio of the amplitude of the trajectory normal to the regression line and the amplitude of the trajectory along the regression line. Note that eccentricity is defined as a ratio of maximum excursions in two directions and does not require elliptical motion. This is not identical to the classic definition of eccentricity, but it does provide a measure of the “straightness” of the trajectory. For both measures, low values indicate adherence to the task requirement.

Statistical analyses of amplitude, inclination, and eccentricity were performed using a repeated measures analysis of variance (ANOVA) with plane of motion (2), initial coordinative mode (2), pendulum (3), and frequency (8) as factors. A similar ANOVA was used to analyze the mean and standard deviation of relative phase. Tukey’s post hoc tests were applied in the case of significant effects.

Results

Tracking. To see how well the participants paced with the metronome, correlations between the movement period

Table 1
Inertial Properties of the Three Pendulums in Experiment 1

Pendulum	Length (m)	Mass of pendulum (kg)	Added mass (kg)	Distance to added mass (m) ^a	Moment of inertia (kgm ²)
Low	0.190	0.085	0.0	0.000	0.0010
Medium	0.299	0.125	0.3	0.155	0.0112
High	0.299	0.125	0.3	0.254	0.0233

^aDistance to added mass is the distance from the proximal end of the pendulum to the added mass.

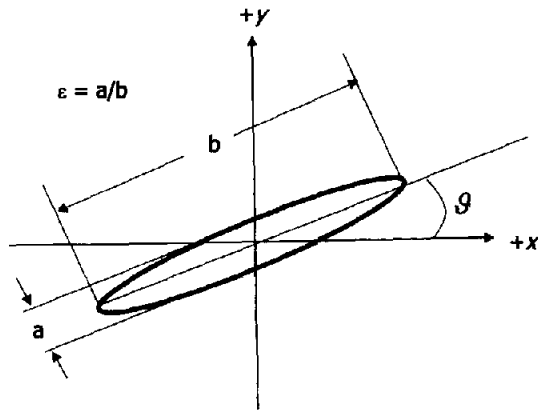


Figure 2. Measures of spatial deviation from the required task. ϵ and θ are the eccentricity and inclination of the spatial trajectory, respectively. a and b are the amplitudes perpendicular and parallel to the plane determined by the inclination, respectively. The figure assumes the frontal plane condition, and θ is the angle with respect to the $+x$ -axis.

for each pendulum and the time between metronome beats were calculated. The means of the correlations are given in Table 2. The correlations ranged from .76 to .96. The lowest correlations were found in the frontal plane antiphase condition and were due to increased occurrence of phase wrapping or intervals of systematic frequency desynchronization. Lower correlations were also found in the low inertia pendulum condition, owing in all likelihood to difficulties in controlling the pendulum because of its very low inertia.

Time series. A representative trial for the frontal plane antiphase condition with the medium inertia pendulum is shown in Figure 3 for three frequency plateaus. At a frequency of 1.5 Hz, the frontal or primary plane of motion had a large amplitude, whereas the sagittal or secondary plane motion was small and less regular (note different scales). At 2.0 Hz, the secondary plane motion grew in amplitude and was phase locked with motion in the primary plane. At 2.75 Hz, a reduction in amplitude in the primary plane occurred relative to lower frequencies along with a further growth of motion in the secondary sagittal plane. Later in the frequency plateau, at 2.75 Hz, a transition occurred in both planes of motion from antiphase to in-phase coordination.

Relative phase. Four distinct phase behaviors were identified in the data and are illustrated in Figures 4A and

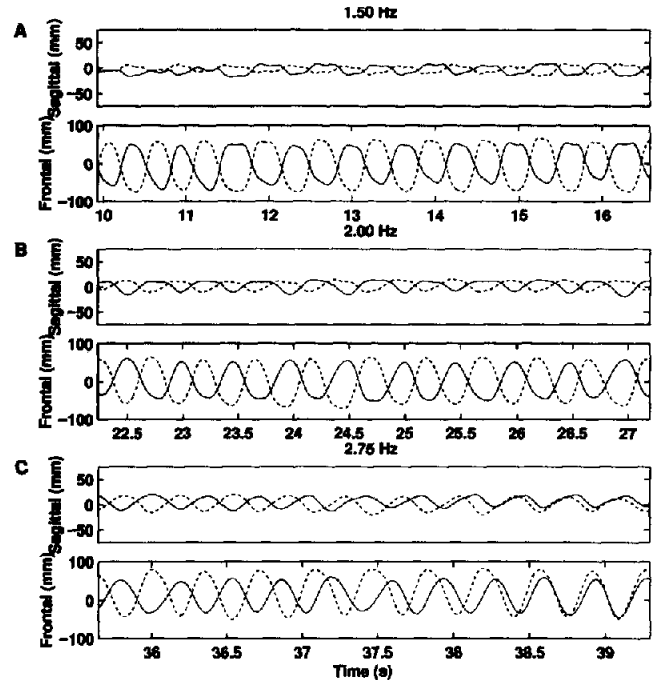


Figure 3. Time series of the left (solid lines) and right (dashed lines) pendulums for three movement frequencies in the frontal plane antiphase mode. The sagittal (secondary) plane amplitude increased with movement frequency, accompanied by a small decrease in the frontal (primary) plane amplitude. A transition from antiphase to in-phase was seen in both planes at 2.75 Hz.

4E. Vertical lines in Figure 4 separate the trial into frequency plateaus. In addition to the in-phase (Figure 4A) and antiphase (Figure 4B) patterns, phase wrapping and phase drift (Figures 4C and 4D) were observed. Phase wrapping occurred when the frequencies of the two pendulums became different for a period of time, resulting in a rapid systematic change in relative phase (Figure 4C) or a slower phase drift (Figure 4D). Transitions from antiphase to in-phase, shown in Figure 4E, consisted of an antiphase pattern changing to slow phase drift and then to an in-phase pattern. Cycles were identified as in-phase or antiphase if, when looking at a five cycle window, at least three of the five relative phases fell within 45° of either in-phase or antiphase coordination. All other cycles were classified as wrapping.

Table 2
Mean of the Correlations of Hand Frequency With Metronome Frequency for the Four Conditions and Three Pendulums

Condition	Left hand			Right hand		
	Low inertia	Medium inertia	High inertia	Low inertia	Medium inertia	High inertia
Sagittal in-phase	.93	.95	.93	.92	.95	.96
Sagittal antiphase	.89	.93	.93	.91	.95	.94
Frontal in-phase	.90	.95	.95	.91	.95	.95
Frontal antiphase	.76	.87	.88	.86	.91	.91

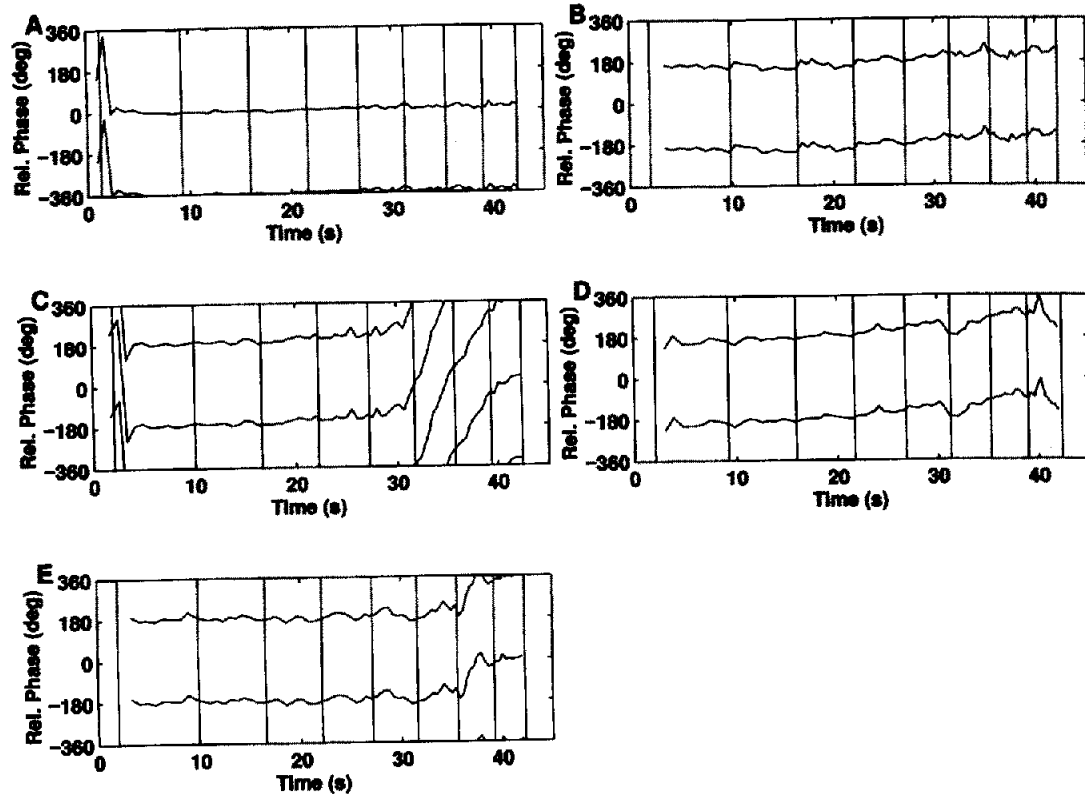


Figure 4. Relative (Rel.) phase behaviors identified in the data and shown for representative trials. Panel A: In-phase. Panel B: Anti-phase. Panel C: Rapid phase wrapping in which the frequencies of the two hands became different for a period of time, resulting in rapid systematic change in the relative phase. Panel D: Slow phase drifts usually initiated from the antiphase condition. Panel E: Transition from antiphase to in-phase.

Although the foregoing changes in coordination were often initiated from the antiphase mode (frontal or sagittal), no transitions of any type were found in the in-phase conditions. Figure 5 shows the percentage of occurrence of the different patterns for the three pendulums in the antiphase conditions as a function of movement frequency. Few transitions are present in the sagittal plane: For the majority of the trials, the sagittal plane antiphase pattern remained antiphase for the entire duration of the trial. In the frontal plane, however, the majority of the trials showed a transition from antiphase to other patterns, although in most cases not to in-phase. A chi-square test on the number of occurrences of the patterns in the last frequency plateau revealed a significant effect among the six combinations of plane and pendulum (Six Conditions \times Three Coordinative Patterns), $\chi^2(10, N = 131) = 41.26, p < .0001$. These differences were due to differences between the planes, $\chi^2(2, N = 131) = 29.13, p < .0001$, with fewer transitions away from the original antiphase mode in the sagittal plane than in the frontal plane. Although no significant effect of pendulum was found, $\chi^2(4, N = 131) = 7.06, p > .05$, there was a trend, particularly in the frontal plane, for the high inertia pendulum to transit to phase wrapping rather than to in-phase. Data for the plateau in which the transition took

place and later plateaus were excluded from further statistical analysis.

The ANOVA for the standard deviation of relative phase revealed significant main effects for pendulum, $F(2, 20) = 6.71, p < .01$, coordinative mode, $F(1, 10) = 24.90, p < .001$, and frequency plateau, $F(7, 70) = 6.59, p < .0001$. Several interactions were also significant, including a three-way interaction of pendulum, plane, and coordinative mode, $F(2, 20) = 6.51, p < .05$, and a two-way interaction of coordinative mode and frequency plateau, $F(7, 70) = 4.14, p < .001$. Figure 6 shows the standard deviation of relative phase as a function of plane, coordinative mode, pendulum, and movement frequency. In general, the frequency dependence took the form of an initial decrease in phase variability, followed by an increase as movement frequency increased. This decrease in the standard deviation, however, generally occurred only from the first to the second frequency plateau and was most likely a result of the participants needing time to settle into a pattern at the beginning of the trial. An exception to this pattern of results was found in the antiphase conditions with the medium inertia pendulums, in which decreases in variability continued until 2 Hz. Such a finding may be interpreted as a stabilizing effect that was due to the rising amplitude in the secondary plane of

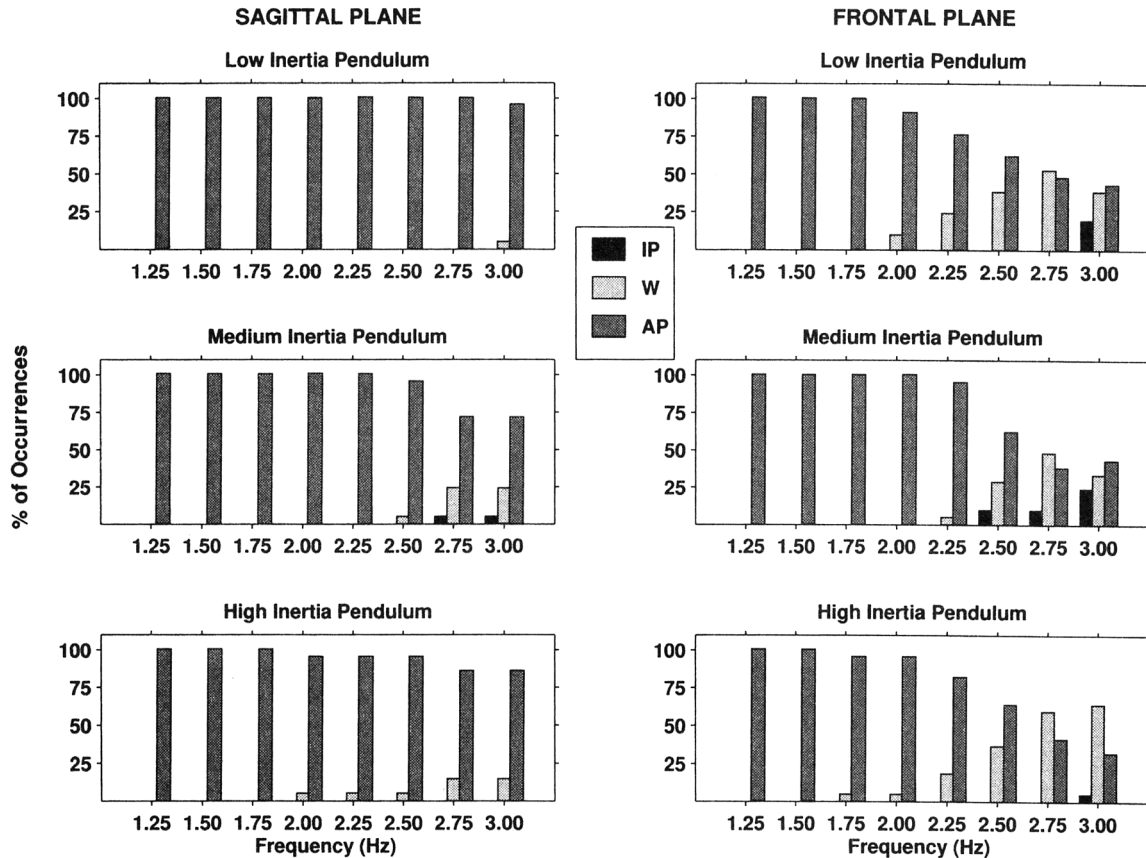


Figure 5. Percentage of occurrence of the different patterns in each plane of motion for the antiphase conditions as a function of movement frequency and out of a total of 22 trials in each condition. IP = in-phase pattern; W = wrapping pattern; AP = antiphase pattern.

motion. In all cases, the in-phase condition exhibited lower relative phase variability than the antiphase condition and increased less in variability as the frequency of motion was scaled upward. These effects were generally greater in the frontal than in the sagittal plane and were larger for the high and low inertia pendulums than for the medium inertia pendulum.

Both the data showing the number of occurrences of the basic patterns (Figure 5) and the standard deviations of relative phase (Figure 6) highlight stability differences between the patterns of coupled pendulum motion. First, for both planes, the antiphase patterns are less stable than the in-phase patterns. Second, frontal plane antiphase coordination tends to be less stable than sagittal plane antiphase. Third, in-phase patterns are equally stable on both planes. The effect of the pendulum, or the resistance, appears to relate more to the nature of the transitions, with the higher inertia pendulum tending to produce wrapping rather than transitions to in-phase patterns.

Amplitude. Figure 7 shows the effect of the plane of motion, initial coordinative pattern, and movement frequency collapsed across all pendulum pairs on the amplitudes in both the primary and secondary planes of motion. A significant main effect of initial coordinative mode, $F(1,$

$10) = 91.29, p < .0001$, and a significant interaction of pendulum, plane of motion, and movement frequency was found for amplitude in the primary plane of motion, $F(14, 140) = 1.8, p < .05$. Post hoc tests showed that the initial antiphase condition produced larger amplitudes than the initial in-phase mode ($p < .05$). In all conditions, there was a general pattern of a decrease in amplitude as frequency increased, with the amplitude in the last frequency plateau being significantly less than in the first frequency plateau ($p < .05$). Amplitude decreases were modified by both pendulum and plane of motion, with the largest percentage decreases found with the high inertia pendulums. In the secondary plane of motion, the interaction of all the main effects was significant, $F(14, 140) = 4.98, p < .0001$. In all conditions (except the sagittal in-phase condition with the low inertia pendulum), there was an increase in amplitude from the first frequency plateau to at least one of the subsequent frequency plateaus ($p < .05$), although the shape of the resulting frequency–amplitude curve (increasing or an inverted U) varied for the different conditions.

Inclination. Trajectories of the end of the pendulum for representative antiphase trials are shown in Figure 8 in the sagittal (Panel A) and frontal (Panel B) planes. Also included are values of the measures of the inclination and eccentricity

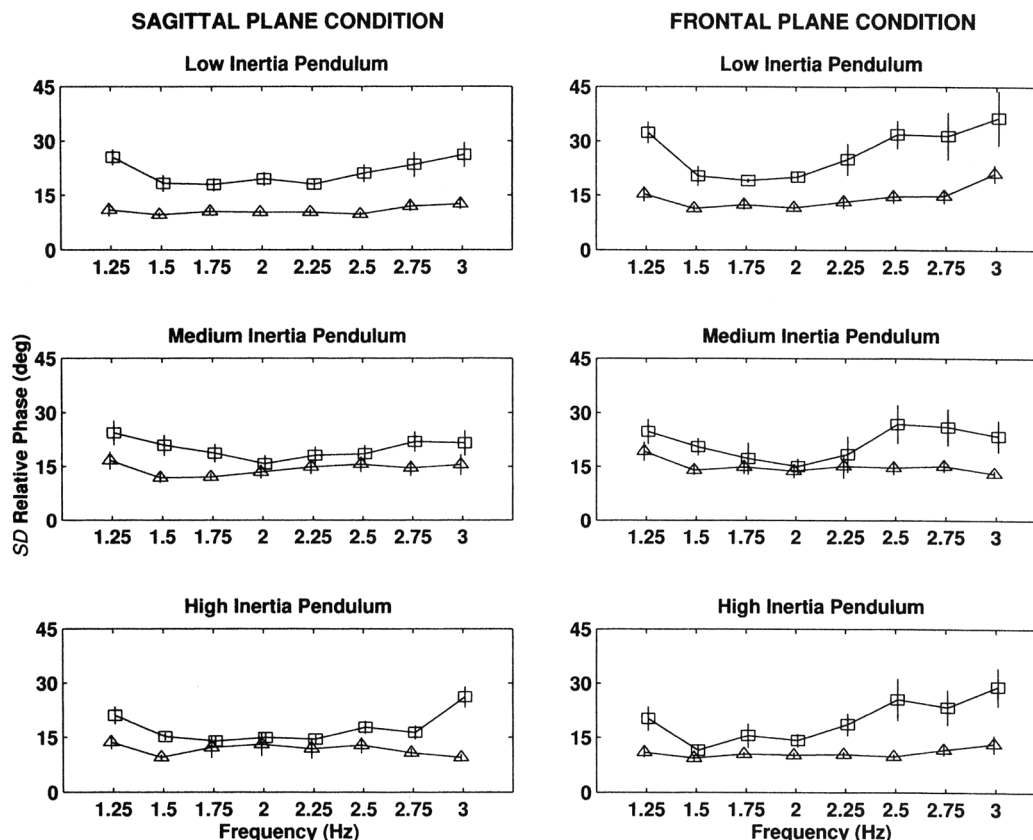


Figure 6. Standard deviations of relative phase plotted as a function of movement frequency for the three pendulums in each plane of motion. Triangles denote in-phase patterns, and squares denote antiphase patterns.

for each frequency plateau. In both planes, a systematic shift away from the instructed plane of motion occurred as frequency increased, seen in a general increase in inclination.

The means of the absolute value of the inclination from the desired plane of motion are shown in Figure 9. The ANOVA revealed significant main effects of plane of motion, $F(1, 10) = 9.21, p < .05$, initial coordinative mode, $F(1, 10) = 9.30, p < .05$, frequency, $F(7, 70) = 27.25, p < .0001$, and pendulum, $F(2, 20) = 8.15, p < .005$. The four-way interaction among these effects was also significant, $F(14, 140) = 2.45, p < .005$. Generally speaking, inclination increased with movement frequency, with significant differences between the first and at least one subsequent plateau ($p < .05$) for all cases with the exception of sagittal plane motions using the high inertia pendulum and sagittal plane in-phase coordination using the low inertia pendulum. In cases in which significant differences occurred between the antiphase and in-phase conditions, the antiphase condition had a significantly greater inclination ($p < .05$).

Eccentricity. Eccentricity measures are presented in Figure 10. A significant main effect was found only for frequency, $F(7, 70) = 34.20, p < .0001$, although the three-way interaction of pendulum, plane of motion, and frequency was also significant, $F(14, 140) = 2.80, p < .005$. Unlike inclination, the initial coordinative mode was not

significant either as a main effect or as a factor in the significant interaction for eccentricity. As seen in Figure 10, eccentricity increased as movement frequency increased, with the exception of the sagittal plane motions using the high inertia pendulums and the sagittal plane in-phase condition with the low inertia pendulum ($p < .05$). Increases in eccentricity were more pronounced in the frontal plane, particularly with the high and medium inertia pendulums.

Discussion

Experiment 1 was designed to probe an apparent anomaly in the coupled pendulum paradigm, namely the absence of transition phenomena despite differential stability of the coordinative modes and related phenomena (e.g., phase shifts, increased antiphase variability). On the basis of a hypothesis proposed by Kelso et al. (1993), we predicted that this absence of transitions was at least in part due to recruitment of previously quiescent degrees of freedom, the role of which, in a biomechanically redundant system, is to stabilize coordination under conditions in which it may otherwise be unstable. To detect signs of putative recruit-

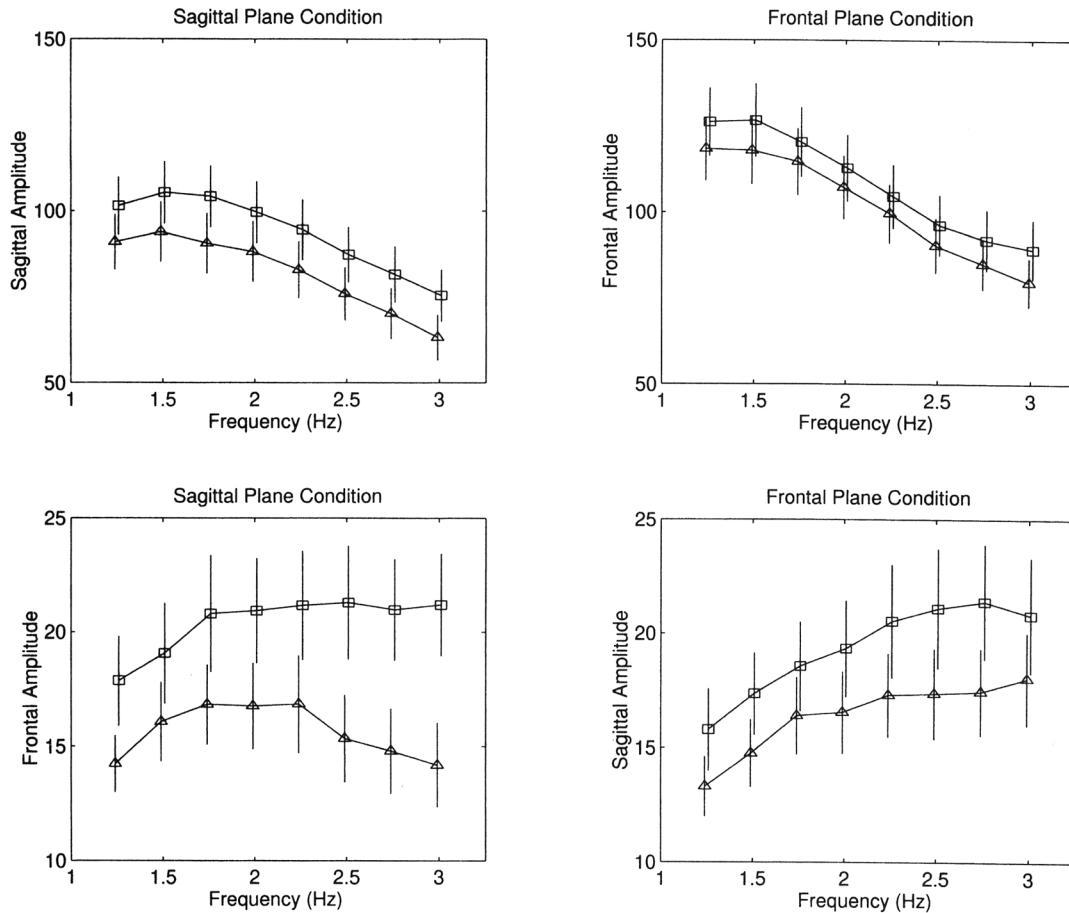


Figure 7. Mean amplitudes collapsed across all pendulums for the sagittal (left panels) and frontal (right panels) plane conditions. The top panels show the amplitude in the primary plane of motion; bottom panels show the amplitude in the secondary, or recruited, plane of motion. Triangles denote in-phase patterns, and squares denote antiphase patterns.

ment, we examined the pendulum trajectory in detail, as well as other more conventional measures (e.g., amplitude, phase).

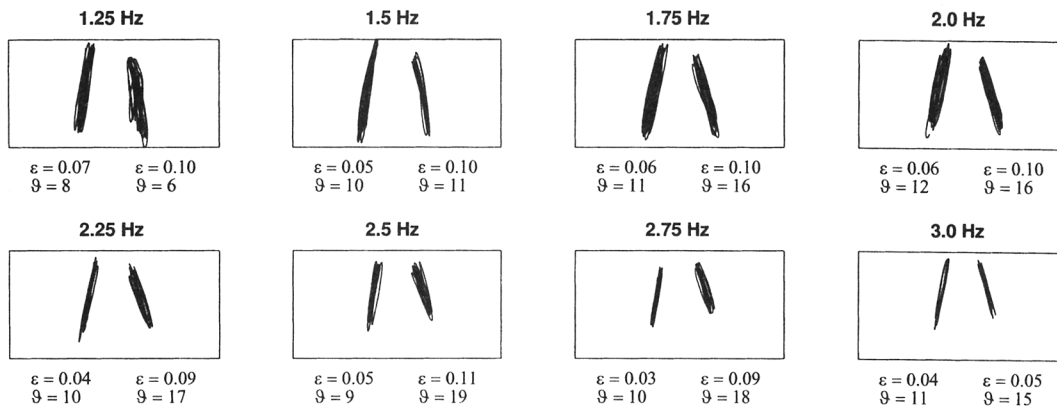
Previous studies (see Turvey & Schmidt, 1994, for a review) of coordination involving the coupled pendulum system did not report well-defined switches between antiphase and in-phase modes when participants had swung the pendulums in the sagittal plane. In this study, we reproduced the results of these previous experiments in the sagittal plane, although we also found that at high movement frequencies, a small number of trials did change from the antiphase pattern, primarily to phase wrapping. This result is consistent with much previous work (e.g., Schmidt et al., 1993; Sternad et al., 1992; Turvey & Schmidt, 1994), showing that the standard deviation of relative phase was higher for antiphase than for in-phase patterns and is indicative of differential stability. It may be safely concluded that transitions away from the antiphase pattern are rare in the typical coupled pendulum experiments in the sagittal plane.

On the other hand, we show here that transitions from

antiphase to other phasing patterns occur frequently in frontal plane motions, although the resulting pattern is rarely in-phase. Similar results were found in unconstrained motion in the frontal plane using coupled pendulums (Mitra et al., 1997) or isometric contractions (Carson, 1995). On the basis of the direct comparison conducted here, it appears that the original plane of motion has a clear effect on the occurrence of transitions, with transitions being far less frequent in the sagittal plane than in the frontal plane.

Our main finding is that recruitment of motion in the secondary plane of motion occurs in both sagittal and frontal plane conditions as movement frequency is increased. The amount of recruitment was modified by the inertial properties of individual pendulums. Some, and indeed probably most, recruitment was a result of the task requirement to produce high movement frequencies. Because additional use of the primary-joint motions merely causes an increase in the amplitude of motion along the original plane, recruitment, by necessity, entails the use of joint motions other than those specified in the task (wrist abduction-adduction in the sagittal plane, forearm pronation-supination in the frontal

A Sagittal Plane Condition



B Frontal Plane Condition

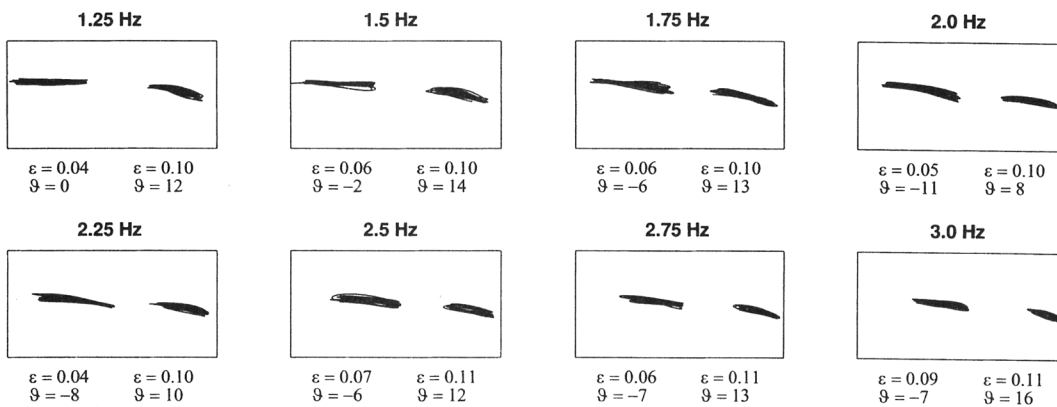


Figure 8. End-pendular trajectory for each frequency plateau for representative trials in the antiphase sagittal (Figure 8A) and frontal (Figure 8B) conditions. ϵ = eccentricity; ϑ = inclination.

plane condition). Such recruitment occurred in every single trial, despite clear instructions to restrict motion to a single plane of motion.

Despite the observed dependence of movement frequency and pendulum inertia on recruitment, not all of the recruitment can be attributed to biomechanical factors. If biomechanical factors alone were responsible for recruitment, there is no reason to expect that the stability of the relative phase pattern between limbs has an effect on the amount of recruitment. Instead, what we see is that recruitment, as measured either by absolute amplitude in the secondary plane of motion or by inclination away from the primary plane of motion, is a function of the initial relative phase pattern, with the less stable antiphase pattern producing more recruitment than the in-phase pattern. Moreover, the manner in which the additional plane of motion is recruited (i.e., in a phase- and frequency-locked manner, as evidenced by a nonzero inclination) strongly suggests that the dynamics of such recruitment are of a similar nature to those seen between limbs (i.e., informational or neural), implying that recruitment is, in large part, the result of a self-organizing central nervous system strategy. Our results are consistent with the hypothesis tested here, namely that recruitment of

previously quiescent degrees of freedom acts to functionally stabilize coordinative patterns at values of the control parameter at which instability and transitions are normally present. At the same time, they point to a limitation of the HKB model, which does not include a mechanism for recruitment.

Experiment 2

A strong test of the recruitment hypothesis would be to restrict pendulum motion to a single plane of motion coinciding with the required task. On the basis of previous results in which motion was confined to a single plane (e.g., Byblow et al., 1994; Kelso & Jeka, 1992) and thereby restricted the number of available degrees of freedom to perform the task, transitions in both planes of motion may be expected to occur. If the lack of transition behavior in the sagittal plane observed in Experiment 1 is due to the recruitment of motion in planes other than the original or task plane, transition behavior should be observed when these additional planes of motion are no longer available. We designed an apparatus to perform a simple experiment to

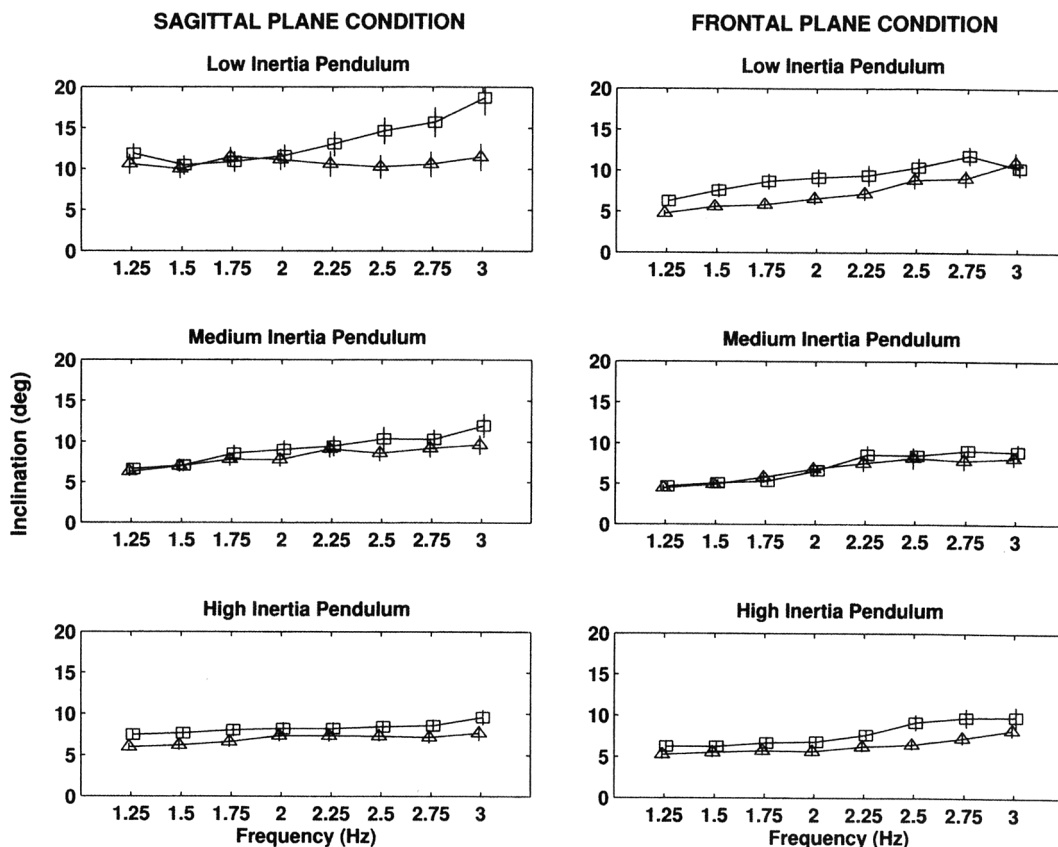


Figure 9. The means of the inclination are plotted against movement frequency for the three pendulums for sagittal (left panels) and frontal (right panels) plane conditions. Triangles denote in-phase patterns, and squares denote antiphase patterns.

check out this prediction with the aim of obtaining converging evidence for the recruitment interpretation.

Method

Participants. Six participants (5 women and 1 man) from the university population volunteered for this experiment. None of the 6 participants took part in Experiment 1. Participants received course credit for their participation and gave informed consent prior to participation in accordance with the local human subjects committee. All participants were treated in accordance with the ethical standards of the APA.

Apparatus. The apparatus constrained pendulum movements to a single plane. A horizontal axle was connected to a manipulandum, which in turn consisted of a metal bar leading to an unweighted pendulum (total mass was 0.61 kg, moment of inertia was 0.0097 kgm², similar to the medium inertia pendulum in Experiment 1) that was grasped by the participants. The axes of rotation of the manipulandum were aligned with either the antero-posterior axis of the wrist in the sagittal plane condition or the longitudinal axis of the ulna in the frontal plane condition. By aligning the axis of rotation of the pendulum mechanism with the axis of the appropriate joint motion, the contribution of other joints was minimized. Participants were seated with forearms positioned in an armrest to further limit unwanted joint motion. Pendulum position was recorded with a coaxial potentiometer and sent to an ODAU analog-digital converter connected to an Optotrak 3010

system. A metronome signal, generated by a Quick Basic program from a Macintosh Classic II computer, was used to pace the movement frequency. Pendulum positions and the metronome signal were recorded at 256 Hz.

Procedure. Participants were asked to swing the pairs of pendulums in either the frontal or sagittal planes in time with an auditory metronome that increased in frequency from 1.25 to 3 Hz in 0.25-Hz intervals every 10 cycles. In each plane, five in-phase and five antiphase trials were collected for each participant, with the order of the planes and trials within a plane randomized. As in Experiment 1, we defined in-phase as movements requiring simultaneous contraction of homologous muscles (e.g., pendulums moving forward and backward at the same time in the sagittal plane or in and out at the same time in the frontal plane), whereas antiphase patterns were produced with alternating contractions of homologous muscles. Participants were told to keep their eyes closed and not to intervene if the coordinative pattern started to change but to continue with whatever pattern felt most comfortable.

Results

Metronome pacing. As in Experiment 1, correlations were calculated between movement period and metronome period. Correlations were again high, ranging from .87 to .98. No significant differences were found between conditions ($p > .05$).

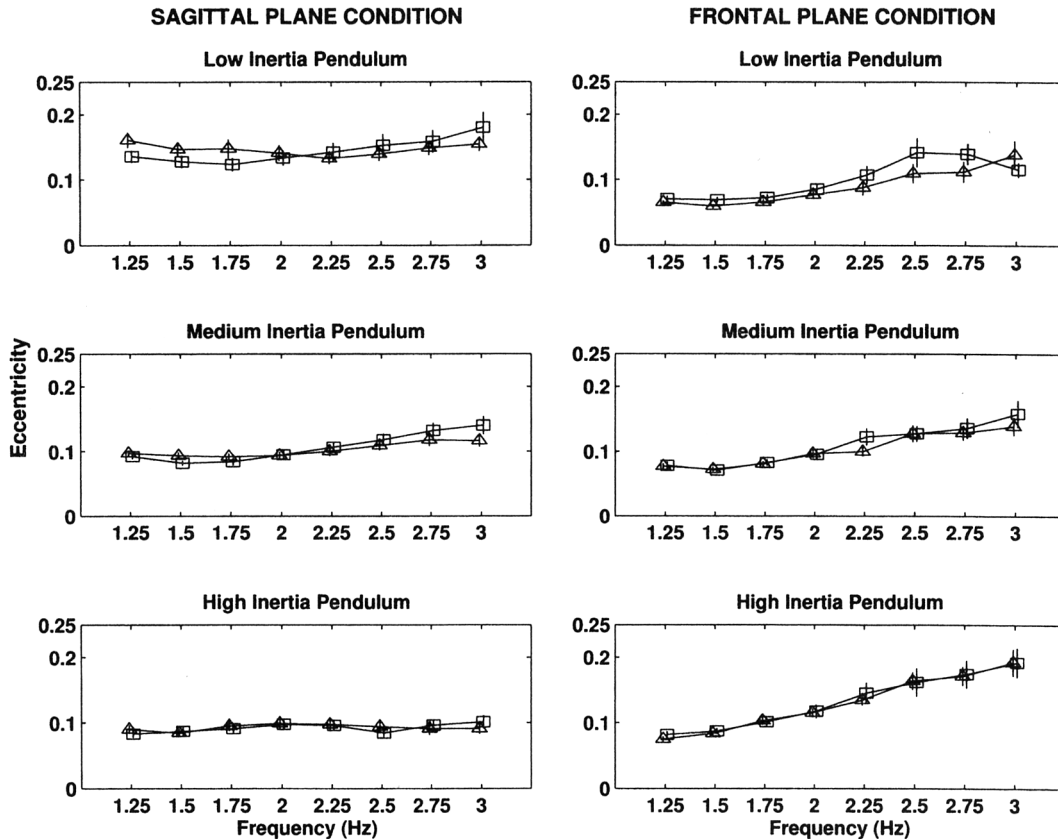


Figure 10. The means of the eccentricity are plotted against plateau frequency for the three pendulums for sagittal (left panels) and frontal (right panels) plane conditions. Triangles denote in-phase patterns, and squares denote antiphase patterns.

Time series. Figure 11 shows a time series for a representative frontal plane antiphase trial for three frequencies. A reduction in movement amplitude was seen as frequency was increased, and a transition from antiphase to in-phase occurred at 2.5 Hz. When compared with the time series for Experiment 1 (Figure 3), the same general decrease in amplitude occurred in both cases, but in Experiment 2, the secondary plane amplitude was restricted to zero. Notably, a phase transition occurred at a lower frequency than in Experiment 1.

Stability of the coordinative pattern. Three distinct relative phase patterns were identified in the data—in-phase, antiphase, and phase wrapping—using the procedure described in Experiment 1. The frequency of occurrence of each of the patterns in the initial antiphase condition is shown in Figure 12. As frequency was increased, there was an increase in the number of transitions away from antiphase, seen in this experiment in both planes of motion. Table 3 shows the percentage of trials in which the patterns were observed for at least part of the trial for both Experiment 1 and Experiment 2. Transitions away from the initial coordinative mode were observed in all four experimental conditions in Experiment 2; at high frequencies, even in-phase coordination sometimes became unstable and displayed wrapping behavior. The four conditions differed in

the number and type of transitions, as confirmed by a significant chi-square value, $\chi^2(6, N = 58) = 13.35, p < .05$, on the presence of three patterns: the initial coordinative mode, phase wrapping, and the opposite coordinative mode (i.e., in-phase for the initial antiphase mode). A significant chi-square value was found for initial coordinative mode, $\chi^2(2, N = 58) = 9.63, p < .01$, with the antiphase mode showing more deviations from the initial relative phase pattern than the in-phase mode, although this difference resulted more from the difference between the two coordinative modes in the frontal plane, $\chi^2(2, N = 58) = 8.96, p < .05$, than from the sagittal plane, $\chi^2(2, N = 58) = 2.35, p > .05$.

More important is the comparison between the number of transitions from antiphase to in-phase coordination between Experiment 1 (seen on the left side of Table 3), in which additional degrees of freedom were available to be recruited, and Experiment 2, in which they were not. In Experiment 2, such transitions occurred more often in both planes of motion, including 23% of the trials in the sagittal plane as compared with 2% in Experiment 1 (and none in the many previous studies on the coupled pendulum paradigm). The difference in number of transitions between Experiments 1 and 2 was confirmed by a significance test between the sagittal plane antiphase condition in the two experiments (2

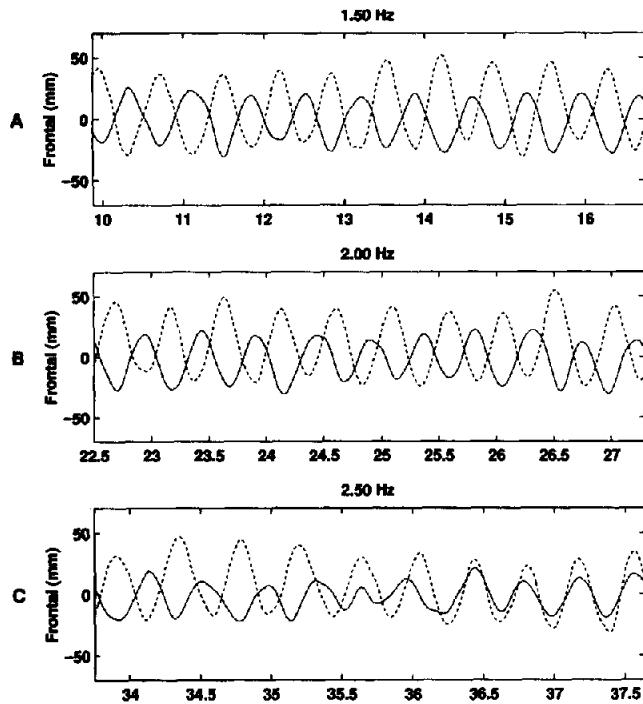


Figure 11. Representative time series for three frequency plateaus in the frontal plane antiphase condition. A transition from antiphase to in-phase was observed at 2.5 Hz.

experiments \times 3 patterns), $\chi^2(2, N = 160) = 9.08, p < .05$, and between the two experiments in the frontal antiphase condition, $\chi^2(2, N = 160) = 9.08, p < .05$. Although these results could be interpreted as meaning that participants in Experiment 2 were more likely to display transitions, this explanation seems unlikely, given the complete absence of transitions reported in the numerous studies of sagittal plane antiphase coordination to date. The observed increase in the percentage of transitions in Experiment 2 strongly supports our hypothesis that recruitment of degrees of freedom serves to stabilize coordination under conditions in which it would otherwise become unstable and change.

Amplitude. Movement amplitude, shown in Figure 13, followed the same general pattern as shown in Experiment 1, with a decrease in amplitude as movement frequency increased. Significant main effects were found for the initial coordinative mode, $F(1, 5) = 93.25, p < .0005$, plane of motion, $F(1, 5) = 13.65, p < .05$, and frequency plateau, $F(7, 35) = 5.21, p < .0005$, with no significant interactions among the variables. Tukey tests revealed significantly larger amplitudes in the antiphase mode and in the sagittal plane ($p < .05$). Significant differences were found between the first three frequency plateaus and the last three frequency plateaus ($p < .05$).

Discussion

We explored the hypothesis that recruitment of additional degrees of freedom serves to stabilize coordination. By physically constraining the pendulum motion to a single

plane, participants were prevented from using additional degrees of freedom, at least as measured by pendulum motion. This procedure, of course, does not consider additional sources of variation, such as forces applied to the pendulum or activity in additional joints (e.g., elbow flexion and extension). Despite this caveat (which applies to all coupled pendulum studies), transitions from antiphase to in-phase were observed in both planes of motion. Previous experiments in the coupled pendulum paradigm have not revealed transitions from antiphase to in-phase in the sagittal plane (see Amazeen et al., 1998, for a review). Here, however, we show transitions from antiphase to in-phase on 23% of the trials, a figure that although lower in the sagittal than in the frontal plane, clearly supports our hypothesis that the complete lack of transition behavior reported earlier is due, in part, to the availability and use of additional degrees of freedom. There also appears to be an effect of the plane of motion, with transitions in the frontal plane more frequently observed than in the sagittal plane. This effect could have several causes, among which are (a) the use of different joint motions in the two planes (an unavoidable concern because moving to a new plane of motion necessitates a change in either the joint motion used—as in the current experiment—or a change in the position of other joints [see Carson, 1996, for effects of the latter]), (b) symmetry properties, or (c) the fact that many tasks performed primarily in the sagittal plane (e.g., walking or running) are performed in what may be described as an antiphase pattern. Additional research is needed to resolve these issues.

General Discussion

From the perspective of elementary coordination dynamics, essential sources of task-specific flexibility have been shown both empirically and theoretically to arise in at least three basic forms: (a) multistability and switching among states of absolute coordination, including hysteresis; (b) partial, or relative, coordination characterized by metastability in which individual components express their independent variation while remaining globally coordinated; and (c) spontaneous recruitment of previously quiescent biomechanical degrees of freedom and the suppression of others. The two experiments reported here are among the first to explore the effects of recruitment of degrees of freedom on the stability of coordinative patterns in the coupled pendulum paradigm. In previous coupled pendulum experiments (many reported in this Journal; Amazeen et al., 1997; Schmidt et al., 1993; Sternad et al., 1992; Treffner & Turvey, 1996; Turvey et al., 1986), motions in planes other than those designated by the task were not constrained, under the assumption that behavior was adequately described by motion in a single plane. In Experiment 1, we found systematic recruitment of planes of motion orthogonal to the initial plane of motion when movement frequency was increased. This recruitment occurred despite instructions to maintain coordinated behavior on the original plane of motion throughout the trial. In light of these results, it appears unlikely that participants in previous studies were able to remain in the initial plane of motion, especially at higher movement frequencies.

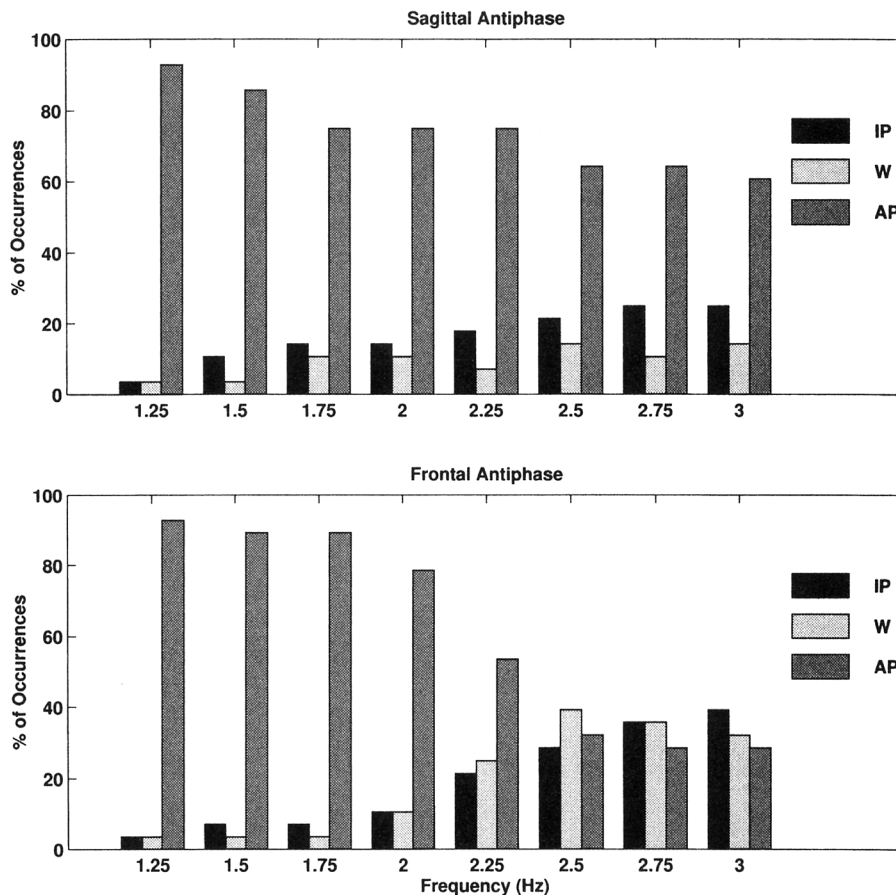


Figure 12. Percentage of occurrence out of 30 trials of the basic patterns in the initial antiphase condition in Experiment 2. Note that some participants failed to keep pace with the metronome, so the number of patterns reported for each plateau does not always add up to 100%. IP = in-phase pattern; W = wrapping pattern; AP = antiphase pattern.

What role does this recruitment play in coordinated behavior? In Experiment 1 recruitment, seen in the inclination of the pendulum trajectory, was dependent on the stability of the relative phase pattern being performed, with the less stable antiphase pattern producing greater inclinations than the in-phase pattern. This fact is consistent with the proposal of Kelso et al. (1993) that recruitment of additional degrees of freedom serves to stabilize coordinative patterns. Converging on the recruitment interpretation

are the results of Experiment 2, showing that when the number of available degrees of freedom are limited to the task plane of motion, the number of transitions, especially in the sagittal plane, increases. This provides one explanation for an apparent anomaly in previous coupled pendulum experiments, namely the rarity or complete absence of transition behavior. Lack of transitions, then, can be attributed to the fact that additional degrees of freedom were used to delay, or even eliminate, transitions. In this light, recruit-

Table 3
Percentage of Occurrences of the Basic Patterns in Experiments 1 and 2

Condition	Unconstrained (Exp. 1)			Constrained (Exp. 2)		
	In-phase	Wrapping	Antiphase	In-phase	Wrapping	Antiphase
Sagittal in-phase	100	0	0	100	27	3
Sagittal antiphase	2	14	100	23	23	93
Frontal in-phase	100	0	0	97	43	0
Frontal antiphase	15	44	100	30	37	93

Note. The three pendulum types in Experiment 1 were collapsed. When a transition from one pattern to another occurred, both patterns were counted for that trial. Thus, percentages can add up to more than 100% in some conditions. Exp. = Experiment.

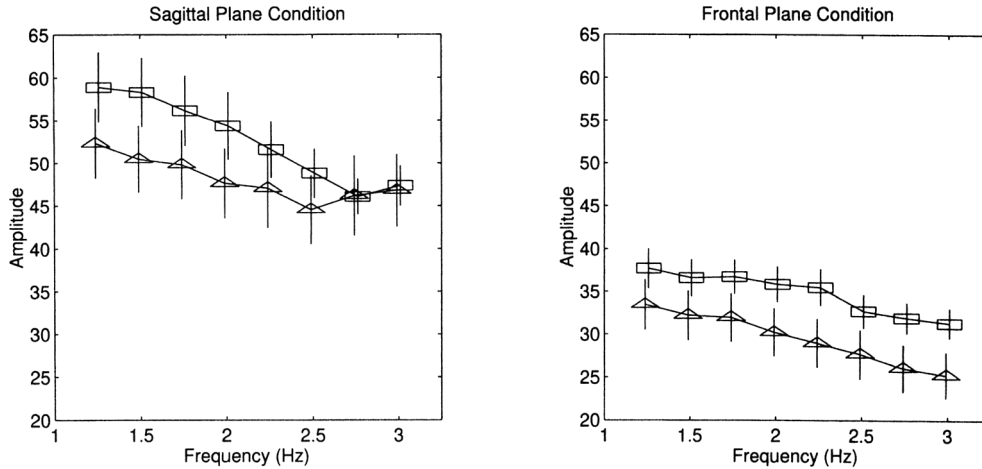


Figure 13. Mean amplitudes collapsed across all pendulums for the sagittal (left panel) and frontal (right panel) plane conditions. Triangles denote in-phase patterns, and squares denote antiphase patterns.

ment of degrees of freedom serves as a stabilization mechanism, enhancing the flexibility of the system by increasing the number of available stable coordinative states.

Theoretical Modeling

Given the present experimental results, it seems obvious that coordination behavior cannot be described fully by a single relative phase variable. Rather, the recruitment of other planes of motion must be incorporated into the coordination dynamics. This is not to deny the validity of the HKB model or its extension to include frequency differences between the components (Kelso et al., 1990). On the contrary, on the basis of the agreement of results from coupled pendulum experiments with various predictions based on the extended HKB model (e.g., relative variability of in-phase and antiphase coordination, shift in the fixed points owing to asymmetries in the pendulums, relative coordination effects, etc.), it is clear that the HKB model is valid for describing the coordination of coupled pendulums in terms of a single phase variable. However, the HKB model and its later modifications were not intended to model coordination in more than a single plane of motion. Thus, it is necessary to modify the basic HKB model to accommodate additional degrees of freedom, such as has been done for unconstrained bimanual coordination (Kelso et al., 1993), multifrequency tasks (de Guzman & Kelso, 1991; Haken, Peper, Beek, & Daffertshofer, 1996), four-limb movements (Schöner, Jiang, & Kelso, 1990), environmental information (Schöner & Kelso, 1988b, 1988c), the influence of intention (Kelso, Scholz, & Schöner, 1988; Schöner & Kelso, 1988c), learning (Schöner, Zanone, & Kelso, 1992), handedness (Treffner & Turvey, 1996), attention (Amazeen, Amazeen, Treffner, & Turvey, 1997), and trajectory formation (de Guzman, Kelso, & Buchanan, 1997).

Any modified model must retain the essential properties of the HKB theory at both the coordinative (e.g., multistabil-

ity, phase transitions, hysteresis) and component (e.g., frequency–amplitude–velocity relations, limit cycle stability features) levels. Vis-à-vis recruitment, several new properties must be incorporated into the model. First, phase locking is present not only between hands in the primary plane but also in the secondary plane and between the two planes. The latter effect is seen in the inclination data (Figure 9), in which a nonzero inclination indicates phase locking between the planes at values near zero or 180°. Second, the amount of recruitment increases as movement frequency is increased (Figures 3, 8, 9, and 10). Finally, recruitment serves to stabilize the coordinative pattern by delaying or eliminating phase transitions (cf. Figures 5 and 12).

Coordination with recruitment: Component oscillator model. In the following, we present a modified HKB model that captures the features of the old model while incorporating the novel properties observed experimentally. Frontal motion of the left and right pendulums is represented by the oscillators $x_1(t)$ and $x_2(t)$, whereas the left and right sagittal motions are given by $y_1(t)$ and $y_2(t)$, respectively. When uncoupled, these are assumed to be of the hybrid van der Pol–Rayleigh type (Beek, Rikkert, & van Wieringen, 1996; Haken et al., 1985; Kay, Kelso, Saltzman, & Schöner, 1987; Kay, Saltzman, & Kelso, 1991). The basic model is given as

$$\begin{aligned}
 \ddot{x}_1 + (A_f x_1^2 + B_f \dot{x}_1^2 - \gamma_f) \dot{x}_1 + \omega^2 x_1 & \\
 = (\alpha_f + \beta_f [x_1 - x_2]^2)(\dot{x}_1 - \dot{x}_2) & \\
 - \lambda_f (y_1^2 + y_2^2)(\dot{x}_1 + \dot{x}_2) + \xi_1^f(t) & \quad (1) \\
 \ddot{x}_2 + (A_f x_2^2 + B_f \dot{x}_2^2 - \gamma_f) \dot{x}_2 + \omega^2 x_2 & \\
 = (\alpha_f + \beta_f [x_2 - x_1]^2)(\dot{x}_2 - \dot{x}_1) & \\
 - \lambda_f (y_1^2 + y_2^2)(\dot{x}_1 + \dot{x}_2) + \xi_2^f(t) &
 \end{aligned}$$

and

$$\begin{aligned} \ddot{y}_1 + (A_f y_1^2 + B_f \dot{y}_1^2 - \gamma_f) \dot{y}_1 + \omega^2 y_1 \\ = (\alpha_f + \beta_s [y_1 - y_2]^2) (\dot{y}_1 - \dot{y}_2) \\ - \lambda_s (x_1^2 + x_2^2) (\dot{y}_1 + \dot{y}_2) + \xi_1^y(t) \end{aligned} \quad (2)$$

$$\begin{aligned} \ddot{y}_2 + (A_s y_2^2 + B_s \dot{y}_2^2 - \gamma_s) \dot{y}_2 + \omega^2 y_2 \\ = (\alpha_s + \beta_f [y_2 - y_1]^2) (\dot{y}_2 - \dot{y}_1) \\ - \lambda_f (x_1^2 + x_2^2) (\dot{y}_1 + \dot{y}_2) + \xi_2^y(t) \end{aligned}$$

for the frontal and sagittal components, respectively. This is similar to the HKB model but involves four components and additional frontal and sagittal couplings (terms in bold) with parameters λ_f and λ_s , respectively. The HKB coupling provides the requisite relative phase behavior (Haken et al., 1985). Terms with λ_f and λ_s factors act both as a damping

force as well as a phase stabilizing influence on the basis oscillators. To simulate the fact that all real systems contain noise, we have added the Gaussian, delta-correlated functions $\xi_k^x(t)$ and $\xi_k^y(t)$. All the parameters except α_f and α_s are taken to be positive. To see the feasibility of such a system, we numerically integrated Equations 1 and 2 for a representative set of parameter values close to those used in the HKB model (Haken et al., 1985). The initial conditions were set up to simulate the task of swinging the pendulums on the frontal plane in the antiphase mode and correspond to the frontal antiphase task of Figure 3. Because the case of synchronizing antiphase in the sagittal plane is formally the same as the above condition, we limited analysis to the frontal antiphase task. Plotted in Figure 14 are the time series at strategic values of the frequency parameter, showing the system's behavior around the points of recruitment of the sagittal plane and the phase switch in the frontal plane. For frequencies below 1.6 (not shown) and after the system has settled down to a well-defined oscillation, frontal motion remains stable at antiphase with equal amplitudes for both

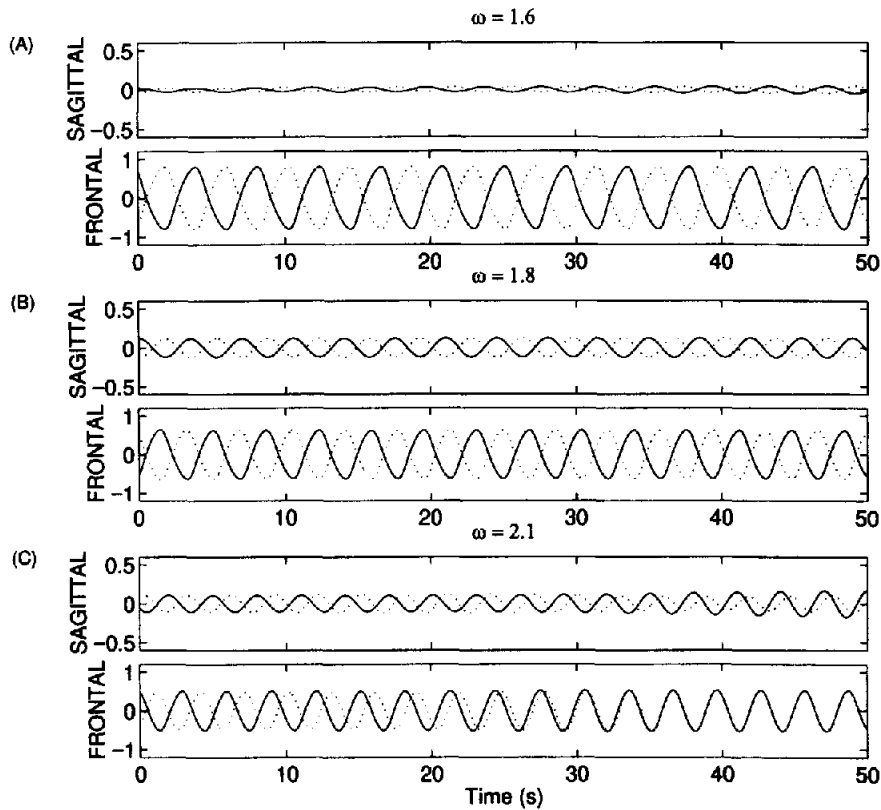


Figure 14. Simulation of the Haken–Kelso–Bunz dynamics with recruitment (Equations 1–2) for the case when the primary task is antiphase in the frontal plane. The parameters used were $A_f = A_s = 1$, $B_f = B_s = 1$, $\gamma_f = 1$, $\gamma_s = 0.3$, $\alpha_f = -0.2$, $\beta_f = 0.5$, $\alpha_s = -0.13$, $\beta_s = 0.5$, $\lambda_f = 1.0$, $\lambda_s = 0.4$, and a noise level of 10^{-3} . The initial conditions were set to antiphase frontal and zero amplitude for the sagittal component. For frequencies below 1.6 (not shown), sagittal motion was minimal and was dominated by noise. Panel A: Recruitment of the sagittal degree of freedom at $\omega = 1.6$. Panel B: At a higher frequency, $\omega = 1.8$, motion remained phase locked but with a slight decrease in the frontal and increase in the sagittal amplitude. Panel C: Near $\omega = 2.1$, both sagittal and frontal motions became unstable and coordination switched to in-phase in both planes.

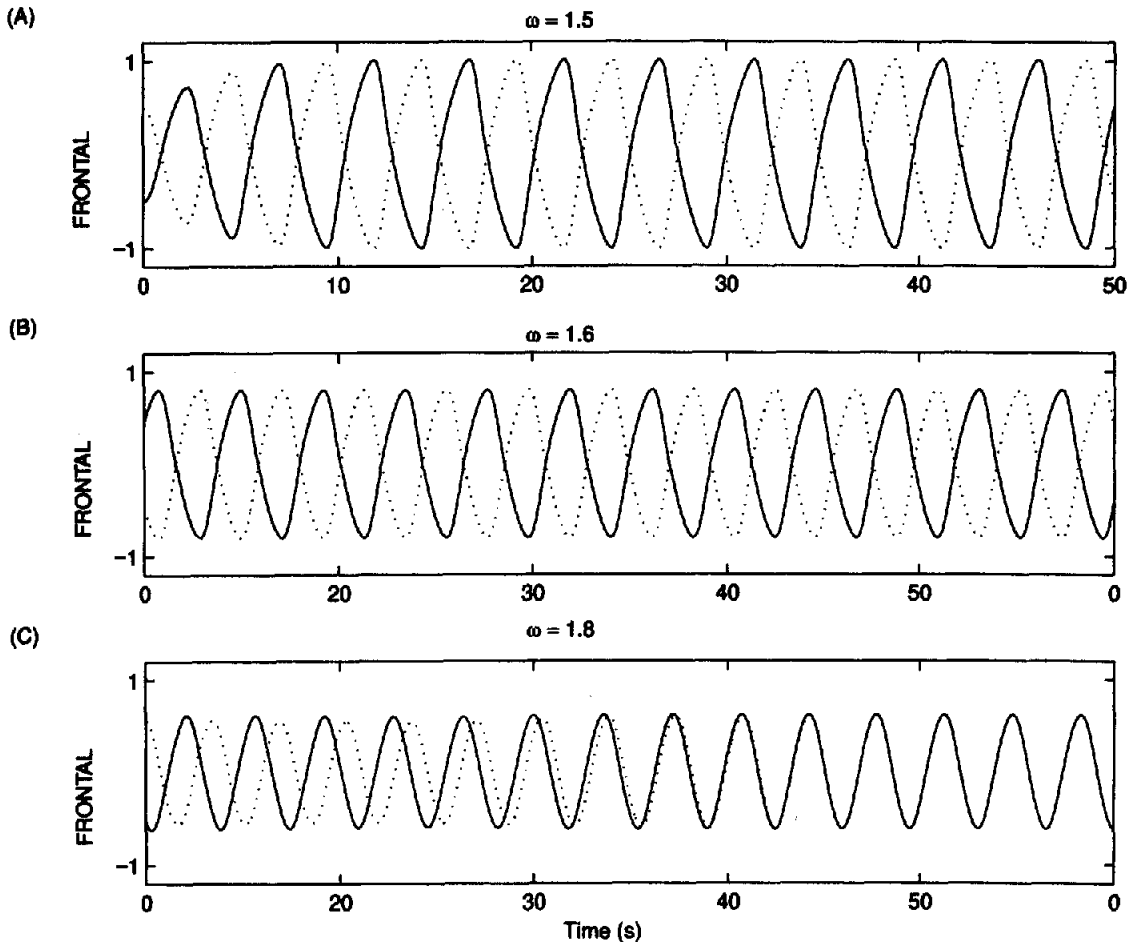


Figure 15. Simulation of the frontal Haken–Kelso–Bunz dynamics without recruitment (constrained case). Here, $y_1(t)$ and $y_2(t)$ were identically set to zero, and only the frontal components (Equation 1) were integrated using the same parameters of Figure 14. Panel A: At the starting frequency, $\omega = 1.5$, frontal motion was phase locked at antiphase. Panel B: At a higher frequency, $\omega = 1.6$, motion remained phase locked at antiphase but with a lower amplitude. Panel C: Transition from antiphase to in-phase in the frontal relative phase occurred around $\omega = 1.8$. Note that this frequency was earlier than the frontal transition frequency ($\omega = 2.1$) of Figure 14C.

limbs. Sagittal motion, which was minimal at low frequencies, is recruited and becomes coherent at $\omega \approx 1.6$ (cf. Figure 3A). For $\omega > 1.6$, the sagittal amplitude rises, and frontal and sagittal motion remain phase locked (between left and right pendulums) within each plane (cf. Figure 3B). The frontal and sagittal components then switch to in-phase at $\omega \approx 2.1$ (cf. Figure 3C). In short, the model reproduces three of the main features seen in Experiment 1: frequency-dependent recruitment, phase locking between planes, and transitions.

In Figure 15, our model system is constrained to move only on the frontal plane as in Experiment 2. This is accomplished by keeping $y_1(t) = y_2(t) = 0$ at all times in Equation 1 or, alternatively, by setting the frontal coupling $\lambda_f = 0$ and disregarding the sagittal component dynamics altogether. Thus, only the x -components of Equation 1 are integrated. When we focus on just the frontal motions, $x_1(t)$ and $x_2(t)$, we note stable antiphase coordination at low

frequencies (cf. Figures 15A and 11A). As frequency increases, coordination remains antiphase but with a lower amplitude (cf. Figures 15B and 11B). Then, at a still higher frequency ($\omega = 1.8$), coordination switches from antiphase to in-phase (cf. Figures 15C and 11C). A key point to note is that switching under constrained conditions (Experiment 2) occurs at an earlier frequency than in the unconstrained conditions. It is thus possible to stabilize a coordination mode within the HKB framework by recruiting biomechanical components from other planes and coupling them appropriately. These theoretical results are meant to demonstrate the essential properties of the model. No attempt has been made to fit the data.¹

¹ To produce the requisite dimensions and correct parameter values, Equations 1 and 2 need to be scaled appropriately in time and space (see e.g., Fuchs, Jirsa, Haken, & Kelso, 1996).

Phase and amplitude dynamics. Since phase locking within and between planes is a prominent feature of our experiments, we turn now to a consideration of the phase and amplitude dynamics. Just as in the two-component HKB model, wherein the stability of the coordination depends on the amplitudes in the primary plane of movement, the amplitude of the recruited degrees of freedom also affects the stability of a pattern in the initial plane. We see this more explicitly in the following case, in which we extract the amplitude and phase dynamics corresponding to Equations 1 and 2. To do this, we assume the system exhibits a dominant oscillation at frequency ω and then apply the slowly varying amplitude and rotating wave approximations (Minorsky, 1962; see Appendix for details). Additional simplifications are possible by noting that after the system has stabilized, the left and right components of the same plane have equal amplitudes. We may therefore set $r_1 = r_2 \equiv r$ and $\rho_1 = \rho_2 \equiv \rho$, where r and ρ refer to the frontal and sagittal amplitudes (see Appendix for the resulting equations of motion). Because there are four phases ($\phi_1, \phi_2, \varphi_1, \varphi_2$) available, we can define at most three independent relative phases at one time. We have chosen to define the following combinations: $\phi \equiv \phi_1 - \phi_2$, $\varphi \equiv \varphi_1 - \varphi_2$, and $\delta \equiv \varphi_1 - \phi_1 + \varphi_2 - \phi_2$. We refer to ϕ , φ , and δ as the frontal, sagittal, and within-limb relative phases, respectively. For the case of equal amplitudes, we obtain the relative phase equations

$$\dot{\phi} = [\alpha_f + 2\beta_f r^2 - 2\lambda_f(2 - \cos \delta \cos \varphi)r^2] \cdot \sin \phi - \beta_f r^2 \sin 2\phi \quad (3a)$$

$$\dot{\varphi} = [\alpha_s + 2\beta_s \rho^2 - 2\lambda_s(2 - \cos \delta \cos \phi)\rho^2] \cdot \sin \varphi - \beta_s \rho^2 \sin 2\varphi \quad (3b)$$

$$\dot{\delta} = -4\left(\lambda_s r^2 \cos^2 \frac{\varphi}{2} \cos \phi + \lambda_f \rho^2 \cos^2 \frac{\phi}{2} \cos \varphi\right) \sin \delta \quad (3c)$$

We note that for $\lambda_f = \lambda_s = 0$, Equation 3 yields two independent HKB systems, one for the frontal (ϕ) and one for the sagittal (φ) planes. Because the coupling between planes in this case is nonexistent, the within-limb relative phase dynamics (δ) is not fully determined. For nonzero λ_f and λ_s , it is clear that a subset of fixed points of Equation 3 is of the form $\phi^*, \varphi^*, \delta^*$, where each component phase takes the value 0 or π .² Such fixed points correspond to the basic coordination modes seen in Experiment 1. Note that Equation 3 may have other fixed points aside from these basic modes, but this goes beyond the scope of the present article. To illustrate the amplitude and phase dynamics of our model and to verify the approximations and assumptions, we consider the circumstances of Experiment 1, in which the primary task is to coordinate antiphase motion in the frontal plane.

In Figure 16, we have plotted the mean amplitudes and circular mean of the relative phases as a function of movement frequency for our model. The means were

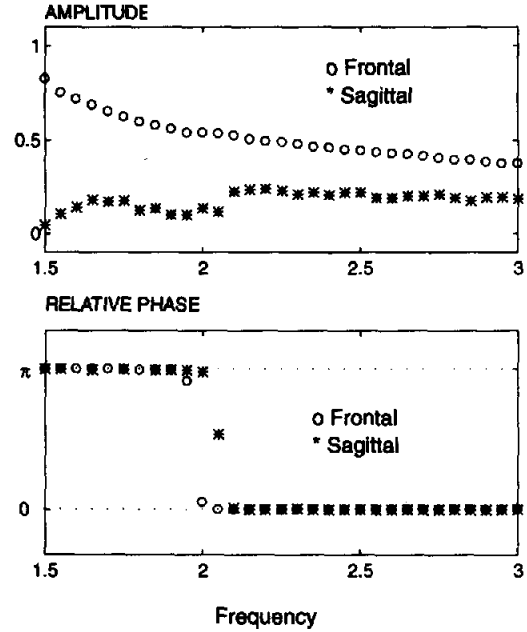


Figure 16. Mean values of the amplitudes and relative phases as a function of movement frequency in the frontal antiphase task. Each point is an average of the time series generated by numerical integration of amplitude (Equations A5 and A6) and relative phase equations (Equation 3), on the basis of the oscillator parameters in Figure 14.

computed using the time series generated by direct integration of Equation 3 and the amplitude equations (see Appendix) for each frequency plateau.

Parameter values are the same as in Figure 14. Note that since there is no sagittal amplitude at the beginning of the task, there is no (one) initial condition that can be imposed on the relative phases φ and δ . Thus, we have set these phases to π and 0, respectively. Figure 16 simulates some of the mean features seen experimentally. A drop of frontal amplitude with frequency is accompanied by a rise in sagittal amplitude as frequency is increased. Initially, the frontal and sagittal relative phases are stable at π , become unstable at $\omega \approx 2.1$, and switch to 0. At higher frequencies, both frontal and sagittal relative phase are stable and phase locked. Comparing Figure 16 with our model Figure 14, we see agreement between the oscillator and the phase–amplitude dynamics simulation in terms of the recruitment

² The above assumes a left–right, fully symmetric condition. The empirical situation is, however, slightly different because observations reveal asymmetry both in time and space. Temporally, one sees not only in-phase and antiphase modes but also slight deviations from these generic phases. In addition, phase wrappings and slow drifts occur. As in the extended, symmetry-breaking version of the HKB model (Kelso et al., 1990; Kelso & Jeka, 1992), introducing slight differences in the left- and right-component oscillators may accommodate these additional effects. At the phase dynamics level, this involves the introduction of constant terms in Equation 3. Thus, both the temporal and spatial features of the trajectory may show the asymmetry.

frequency ($\omega \approx 1.6$) and the relative phase transition frequency ($\omega \approx 2.1$). Note the general increase in the sagittal amplitude as the frontal amplitude decreases (cf. Figure 7).

We now consider in more detail how sagittal motion stabilizes the frontal phase dynamics. Assuming that both frontal and sagittal amplitudes are already active, we express the ϕ equation (Equation 3a) for the frontal relative phase as

$$\dot{\phi} = -\tilde{a}_f \sin \phi - \tilde{b}_f \sin 2\phi, \quad (4)$$

where $\tilde{a}_f \equiv -[\alpha_f + 2\beta_f r^2 - 2\lambda_f(2 - \cos \delta \cos \varphi)\rho^2]$ and $\tilde{b}_f \equiv \beta_f r^2$. Note that except for the extra λ_f term in the \tilde{a}_f coefficient, Equation 4 is identical to the standard HKB model of bimanual coordination (Haken et al., 1985). Assuming the other phases remain stable, Equation 4 is bistable at in-phase and antiphase when $\tilde{a}_f < 2\tilde{b}_f$ and monostable at in-phase when $\tilde{a}_f > 2\tilde{b}_f$. The transition from bistability to monostability occurs when $\tilde{a}_f = 2\tilde{b}_f$. Because $\lambda_f > 0$ and $\rho > 0$, the result is a decrease in the magnitude of \tilde{a}_f (compared with when $\rho = 0$, as in the standard HKB model). This in turn extends the bistable region to smaller frontal amplitudes r , or, equivalently, higher values of omega. The result of this effect is seen in a delay in relative phase switch in the frontal plane. This is consistent with the experimental finding that less phase switching occurs in the primary plane when the secondary plane is involved (see experimental comparison in Figures 5 and 12 and in Table 3).

To see how the onset of recruitment and phase switching depend on the spatial coupling, we computed the critical recruitment frequency (Ω_p) and the frontal phase transition frequency (Ω_ϕ) for the unconstrained case for a combination of λ_s and λ_f . The result is shown in Figure 17, in which we have plotted Ω_p and Ω_ϕ versus λ_s , $\lambda_s \in [0, 1]$, for the cases $\lambda_f = 0.25$ and $\lambda_f = 1$. For comparison, we also plotted $\Omega_\phi^{(0)}$, the frontal phase transition frequency were recruitment not allowed (constrained case). Note that for the latter case, the critical frequency is independent of the spatial coupling and that the curve is given by the horizontal line $\Omega = \Omega_\phi^{(0)}$. We see that $\Omega_\phi^{(0)}$ is consistently greater than Ω_p and less than Ω_ϕ when λ_s is below a critical value λ_s^* , the latter being defined by the point at which the frequency curves intersect. We therefore take the interval $[0, \lambda_s^*]$ as the valid region for the sagittal parameter λ_s . For fixed λ_f , low values of λ_s correspond to earlier sagittal recruitment and more delayed relative phase switching on the frontal plane. When the frontal degree of freedom is strongly coupled to the sagittal degree of freedom ($\lambda_s \approx \lambda_s^*$), there is a competition between recruitment and phase switching, and the outcome may very well be determined by noise.

Spatial trajectory. We now consider the trajectories traversed by each limb in space. Assuming equal amplitude solutions, the k th limb traverses a path given parametrically by $x_k(t) = 2r \cos(\omega t + \phi_k)$ and $y_k(t) = 2\rho \cos(\omega t + \varphi_k)$. The equation of the curve in space, found by eliminating t from the parametric equations, is given by $\rho^2 x_k^2 + r^2 y_k^2 - 2r\rho \cos \delta_k x_k y_k = 4r^2 \rho^2 \sin^2 \delta_k$, where $\delta_k = \varphi_k - \phi_k$ is the relative phase between the frontal and the sagittal motion of

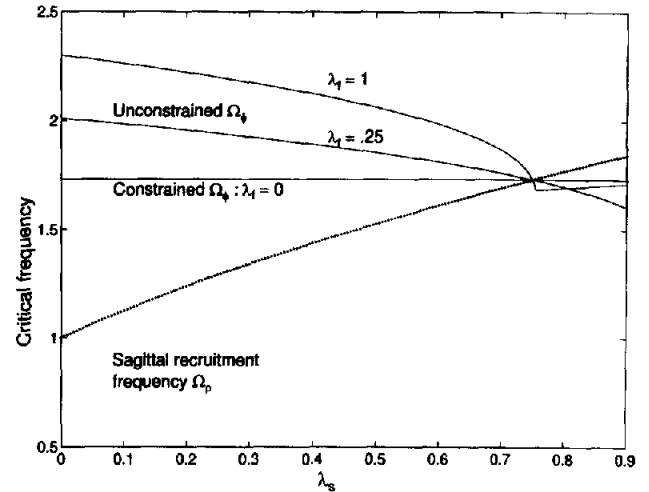


Figure 17. Plot of the sagittal recruitment frequency Ω_p (solid line) and the frontal phase transition frequencies Ω_ϕ (dotted lines) in the frontal antiphase task as a function of the sagittal coupling λ_s for the frontal coupling $\lambda_f = 0.25$ and $\lambda_f = 1$. The horizontal solid line represents what the frequency in the frontal phase would be were recruitment not allowed (constrained condition) and may be considered as representing a third case (i.e., $\lambda_f = 0$, $\Omega = \Omega_\phi^{(0)}$). The phase values used were $(\phi^*, \varphi^*, \delta^*) = (\pi, \pi, 0)$. Comparing the Ω_ϕ curves for $\lambda_f = 1, 0.25$, and 0 , we see that as we decreased the effect of the sagittal on the frontal motion, the unconstrained curve approached the constrained case, as expected. For a given λ_f , $\Omega_p < \Omega_\phi^{(0)} < \Omega_\phi$, provided λ_s is below a critical value λ_s^* , defined as the parameter point at which these three curves intersect. Note also that low values of λ_s correspond to much earlier sagittal recruitment and more delayed relative phase switch. As λ_s increased, recruitment occurred later and consequently did not delay the frontal phase switch as much.

the k -th limb. For stable r , ρ , and δ_k , the curve is an ellipse with inclination ϑ_k , given by $\tan 2\vartheta_k = 2r\rho(r^2 - \rho^2)^{-1} \cos \delta_k$. The ratio of the minor to the major axis (denoted by ϵ_k), a measure similar to the eccentricity of an ellipse, can also be expressed in terms of the amplitudes and phases and is given by

$$\epsilon_k^2 = \frac{r^2 + \rho^2 - \sqrt{(r^2 + \rho^2)^2 - 4r^2\rho^2 \sin \delta_k}}{r^2 + \rho^2 + \sqrt{(r^2 + \rho^2)^2 - 4r^2\rho^2 \sin \delta_k}}$$

The relative phase between the planes can be expressed as $\delta_1 = \frac{1}{2}(\delta - \phi + \varphi)$ and $\delta_2 = \frac{1}{2}(\delta + \phi - \varphi)$. Thus, the inclination and axes ratio depends on the amplitudes and the overall coordination pattern. In Figure 18, we show the different geometries arising from the basic phase patterns. Note that there is a slight indeterminacy in the variables δ_1 and δ_2 because each of the phases ϕ , φ , and δ are defined to within a multiple of 2π . This results in two spatial trajectories for each basic pattern (ϕ, φ, δ) .

Simulations starting from the basic modes tend asymptotically toward linear trajectories so that the eccentricity ϵ_k remains largely at zero. This occurs because the more stable basic mode yields δ_k equal to either zero or π , which renders

ϵ_i equal to zero, as is easily verified using Equation 5. Such is not the case if strict left-right symmetry is broken. For example, an eigenfrequency difference (a feature sometimes considered germane to the problem of handedness; see, e.g., Treffner & Turvey, 1996) may be accommodated by constant correction terms on Equation 3 (see, e.g., Fuchs, Jirsa, Haken, & Kelso, 1996, for an analysis of a comparable problem). This results in fixed points that are offset from the basic coordination modes of Figure 18, and, consequently, more elliptical trajectories. Because of recruitment in the secondary plane, a trajectory not only may change shape but also may reorient from its initial condition, a feature captured in the inclination measure ϑ . In Figure 19, we plotted the predicted inclinations ϑ_1 and ϑ_2 as a function of frequency for the case when both planes are already active at the start of the task. Because the sagittal degree of freedom participates immediately in the first frequency plateau, ϑ_1 and ϑ_2 start at nonzero values. Because the sagittal amplitude increases while the frontal amplitude decreases with frequency, we also expected increasing tendencies in inclination. This compares favorably with the empirical findings (e.g., right column of Figure 9).

Conclusion

Transitions have been demonstrated time and again to provide human beings with a source of flexibility, enabling them to switch easily from one mode of behavior to another under changing environmental and task demands. Here we have asked, what other sources of flexibility do biological systems possess? Specifically, using the well-established coupled pendulum paradigm as a tool, we have inquired whether other (previously unsuspected) processes may serve to stabilize coordinated behavior under conditions in which it might otherwise become unstable and change. The motivation is twofold. First, despite much empirical and theoretical work on the coupled pendulum paradigm and despite much

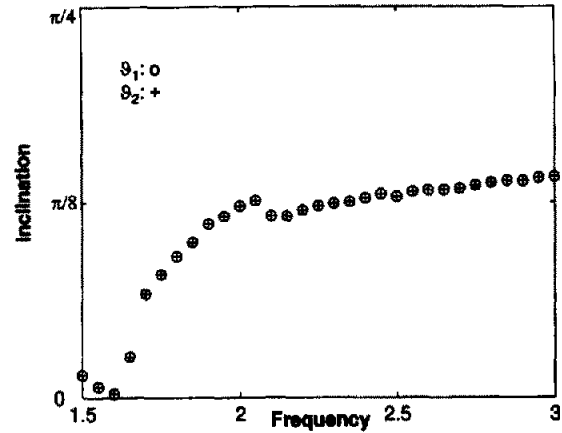


Figure 19. Predicted inclinations of the spatial trajectory as a function of the frequency for the case when the task was frontal antiphase. The inclinations were computed from the mean values of the amplitudes and relative phases generated from Figure 16. Initially, there was a general increase in the inclination with increasing frequency consistent with what has been found empirically. ϑ_1 and ϑ_2 = inclinations of the first and second trajectories, respectively.

empirical validation of the (extended) HKB model, transition effects have been largely absent. The present work was based on the hypothesis that in biomechanically redundant systems, (e.g., those not constrained to a single plane of motion), recruitment of degrees of freedom may serve to stabilize coordination states. Second, previous work on bimanual coordination in which motions were allowed on multiple planes revealed a rich set of recruitment-annihilation effects, suggesting that like mechanisms may be active in the coupled pendulum paradigm, thereby explaining the lack of observed transitions.

The results of our experiments highlight the important role that recruitment of degrees of freedom plays in stabilizing coordination. When other previously quiescent degrees of freedom are allowed to participate, we have shown experimentally that coordination may be stabilized over a broader range of environmental and task conditions than when they are not. By using additional spatial-dependent coupling in a theoretical model, we show that recruitment inhibits phase transitions, thereby resolving an anomaly in the coupled pendulum literature of some theoretical and empirical import. That anomaly concerns the use of the extended form of the HKB theory to explain coupled pendulum coordination despite the fact that transitions in that paradigm have seldom been observed. Our model analysis modifies but certainly does not destroy the general spirit of the HKB model and is consistent with the notion that modulation of the component amplitudes enhances flexibility in coordination tasks. More generally, by challenging the completeness of current accounts of coupled pendulum coordination, this work elucidates an alternative mechanism—recruitment—through which animals and human beings can adjust to environmental and task-related change.

		FRONTAL IN-PHASE							
(ϕ, φ, δ)		$(0, 0, 0)$		$(0, 0, \pi)$		$(0, \pi, 0)$		$(0, \pi, \pi)$	
(δ_1, δ_2)		$(0, 0)$	(π, π)	$(\frac{1}{2}\pi, \frac{1}{2}\pi)$	$(\frac{3}{2}\pi, \frac{3}{2}\pi)$	$(\frac{1}{2}\pi, \frac{1}{2}\pi)$	$(\frac{3}{2}\pi, \frac{3}{2}\pi)$	$(0, \pi)$	$(\pi, 0)$
Spatial Trajectory									

		FRONTAL ANTIPHASE							
(ϕ, φ, δ)		$(\pi, 0, 0)$		$(\pi, 0, \pi)$		$(\pi, \pi, 0)$		(π, π, π)	
(δ_1, δ_2)		$(\frac{1}{2}\pi, \frac{1}{2}\pi)$	$(\frac{3}{2}\pi, \frac{3}{2}\pi)$	$(0, \pi)$	$(\pi, 0)$	$(0, 0)$	(π, π)	$(\frac{1}{2}\pi, \frac{1}{2}\pi)$	$(\frac{3}{2}\pi, \frac{3}{2}\pi)$
Spatial Trajectory									

Figure 18. Basic coordination modes of the relative phase dynamics and the corresponding spatial trajectories for the case when both degrees of freedom are active. Note that for each mode, there are two left-right symmetric trajectories.

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Appendix

Reduction From the Oscillator to the Phase–Amplitude Dynamics

Typical derivation of the phase and amplitude equations from the component oscillators involves the rotating wave and slowly varying amplitude approximations (see e.g., Minorsky, 1962). To make those approximations, we assumed first that the system exhibits a dominant oscillation at frequency ω and has solutions of the form $x_k = a_k e^{i\omega t} + a_k^* e^{-i\omega t}$ and $y_k = b_k e^{i\omega t} + b_k^* e^{-i\omega t}$, where $k = 1, 2$ and a_k and b_k are complex numbers with conjugates a_k^* and b_k^* . The first and second derivatives of x_k with respect to time are given by

$$\dot{x}_k = \dot{a}_k e^{i\omega t} + i\omega a_k e^{i\omega t} + c.c. \quad (A1)$$

$$\ddot{x}_k = \ddot{a}_k e^{i\omega t} + 2i\omega \dot{a}_k e^{i\omega t} - \omega^2 a_k e^{i\omega t} + c.c.,$$

where the notation *c.c.* signifies complex conjugation of the preceding term. The slowly varying amplitude approximation implies $|\dot{a}_k| \ll \omega |a_k|$ and $|\ddot{a}_k| \ll \omega^2 |a_k|$. Using these in Equation A1, we obtained

$$\dot{x}_k \approx i\omega a_k e^{i\omega t} + c.c. \quad (A2)$$

$$\ddot{x}_k + \omega^2 x_k \approx 2i\omega \dot{a}_k e^{i\omega t} + c.c.$$

Similarly for the sagittal component, this means $|\dot{b}_k| \ll \omega |b_k|$ and $|\ddot{b}_k| \ll \omega^2 |b_k|$. Direct substitution of the assumed solutions x_k and y_k and the approximations (Equation A2) and their sagittal version into the oscillator Equations 1 and 2 yield linear combinations of $e^{i\omega t}$, $e^{2i\omega t}$, and $e^{3i\omega t}$ as well as their complex conjugates. To apply the rotating wave approximation to the result, we neglected oscillations faster than $e^{\pm i\omega t}$. The result yields equations for a_k and b_k as follows:

$$2\dot{a}_k \approx -(A_f |a_k|^2 + 3\Omega^2 B_f |a_k|^2 - \gamma_f) a_k + \sigma_k (\alpha_f + \beta_f |a_1 - a_2|^2) (a_1 - a_2) - \lambda_f [2(a_1 + a_2)(|b_1|^2 + |b_2|^2) - (a_1^* + a_2^*)(b_1^2 + b_2^2)] \text{ and} \quad (A3)$$

$$2\dot{b}_k \approx -(A_s |b_k|^2 + 3\Omega^2 B_s |b_k|^2 - \gamma_s) b_k + \sigma_k (\alpha_s + \beta_s |b_1 - b_2|^2) (b_1 - b_2) - \lambda_s [2(b_1 + b_2)(|a_1|^2 + |a_2|^2) - (b_1^* + b_2^*)(a_1^2 + a_2^2)], \quad (A4)$$

where $\sigma_1 = -\sigma_2 = 1$. Next, we express a_k and b_k in terms of phase and amplitude as follows: $a_k = r_k e^{i\phi_k}$ and $b_k = \rho_k e^{i\varphi_k}$. Differentiating these with respect to t , we found $\dot{a}_k = (\dot{r}_k + ir_k \dot{\phi}_k) e^{i\phi_k}$ and $\dot{b}_k = (\dot{\rho}_k + i\rho_k \dot{\varphi}_k) e^{i\varphi_k}$, or, upon inverting,

$$\dot{r}_k = \Re(\dot{a}_k e^{-i\phi_k}) \quad \dot{\rho}_k = \Re(\dot{b}_k e^{-i\varphi_k}) \quad (\text{A5})$$

$$\dot{\phi}_k = r_k^{-1} \Im(\dot{a}_k e^{-i\phi_k}) \quad \dot{\varphi}_k = \rho_k^{-1} \Im(\dot{b}_k e^{-i\varphi_k}), \quad (\text{A6})$$

where the symbols $\Re(\)$ and $\Im(\)$ refer to the real and imaginary parts, respectively. Using Equations A3 and A4 in Equations A5 and A6, it is now straightforward to derive the relative phase and amplitude equations. Amplitude equations (symmetric case) are as

follows (where $r_1 = r_2 = r$ and $\rho_1 = \rho_2 = \rho$):

$$\dot{r} = \frac{1}{2} r \cdot [\gamma_f + 2\alpha_f \sin^2 \frac{1}{2}\phi - [A_f + 3\omega^2 B_f - 8\beta_f \sin^4 \frac{1}{2}\phi] \cdot r^2 - 4\lambda_f [1 + \cos \phi - \cos(\delta - \frac{1}{2}\phi) \cos \varphi \cos \frac{1}{2}\phi] \cdot \rho^2] \quad (\text{A7})$$

$$\dot{\rho} = \frac{1}{2} \rho \cdot [\gamma_s + 2\alpha_s \sin^2 \frac{1}{2}\varphi - [A_s + 3\omega^2 B_s - 8\beta_s \sin^4 \frac{1}{2}\varphi] \cdot \rho^2 - 4\lambda_s [1 + \cos \varphi - \cos(\delta + \frac{1}{2}\varphi) \cos \phi \cos \frac{1}{2}\varphi] \cdot r^2]. \quad (\text{A8})$$

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