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Local and global stabilization of coordination by sensory information

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Abstract In studies of rhythmic coordination, where sensory information is often generated by an auditory stimulus, spatial and temporal variability are known to decrease at points in the movement cycle coincident with the stimulus, a phenomenon known as anchoring (Byblow et al. 1994). Here we hypothesize that the role of anchoring may be to globally stabilize coordination under conditions in which it would otherwise undergo a global coordinative change such as a phase transition. To test this hypothesis, anchoring was studied in a bimanual coordination paradigm in which either inphase or anti-phase coordination was produced as auditory pacing stimuli (and hence movement frequency) were scaled over a wide range of frequencies. Two different anchoring conditions were used: a single-metronome condition, in which peak amplitude of right finger flexion coincided with the auditory stimulus; and a double-metronome condition, in which each finger reversal (flexion and extension) occurred simultaneously with the auditory stimuli. Anchored reversal points displayed lower spatial variation than unanchored reversal points, resulting in more symmetric phase plane trajectories in the double- than the single-metronome condition. The global coordination dynamics of the double-metronome condition was also more stable, with transitions from antiphase to inphase occurring less often and at higher movement frequencies than in the single-metronome condition. An extension of the Haken-Kelso-Bunz model of bimanual coordination is presented briefly which includes specific coupling of sensory information to movement through a process we call parametric stabilization. The parametric stabilization model provides a theoretical account of both local effects on the individual movement trajectories (anchoring) and global stabilization of observed coordination patterns, including the delay of phase transitions.

Key words Coordination dynamics · Stabilization · Bimanual · Transitions · Human

Introduction

In the last decade or so, many studies have shown that, when coordinative systems are driven through a range of control parameter values, phase transitions, or qualitative changes in coordination, occur (see Haken 1996; Kelso 1995 for reviews). More recent brain-behavior experiments (Fuchs et al. 1992; Fuchs et al. 2000; Kelso et al. 1992; Mayville et al. 1999; Wallenstein et al. 1995) have demonstrated that neural activity picked up by the magnetoencephalogram (MEG) and electroencephalogram (EEG) also shows spatiotemporal phase transitions when the movement pattern switches. Subsequent theoretical studies (Fuchs et al. 2000; Jirsa and Haken 1996, 1997; Jirsa et al. 1998) connected dynamics on the behavioral and neural levels and provided a neurally based derivation of the Haken-Kelso-Bunz (HKB; Haken et al. 1985) model of biological coordination. The biological advantages of phase transitions are transparent: they provide a mechanism for flexibility, allowing the system alternative ways to coordinate itself under changing environmental or task conditions. Here we consider the other side of the coin, namely the mechanism(s) through which the central nervous system (CNS) functionally stabilizes coordination under conditions in which it may otherwise become unstable and switch. What strategies are used to stabilize coordinative patterns at values of the control parameter where the pattern typically becomes unstable and switches? In an experimental setting, stabilization of coordination may be seen in a delay or absence of transitions from a typically unstable state. Previous research has suggested that transitions can be delayed or eliminated by a number of factors, including: (a) intentional forcing (Kelso et al. 1988; Lee et al. 1996; Scholz and Kelso 1990); or (b) making use of biomechanical redundancy in the system by recruiting degrees of freedom other than those required for nominal execu-

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tion of the task (Buchanan and Kelso 1999; Fink et al. 2000; Kelso et al. 1993). Here we investigate the hypothesis that global coordination can be stabilized through specific local coupling to task-specific sensory information from the environment.

Coordination or coupling between an individual and the environment is an important feature of biological systems, enabling production of consistent movement patterns even in a continuously varying environment. Such coupling has been studied extensively, for example, in research that seeks to understand the relationship between postural sway and sensory inputs, either visual (van Asten et al. 1988; Bertenthal et al. 1997; Delorme et al. 1989; Dijkstra et al. 1994) or somatosensory (Jeka and Lackner 1994; Jeka et al. 1997). Sway was coupled to sensory information through phase and frequency locking, a process that appears to be due to a velocity-dependent coupling (Dijkstra et al. 1994; Jeka et al. 1997; see also Kelso et al. 1998). Such interaction is two-way, in the sense that, while the perceptual information affects the movement patterns, the movement patterns in turn alter the perceptual information. In rhythmic movement, a similar environmental coupling has been observed in between-subject coordination (Amazeen et al. 1995; Schmidt et al. 1990) and in coordination with auditory (Kelso et al. 1990) and visual signals (Wimmers et al. 1992; see also Lang et al. 1984), both of which also demonstrated features common to bimanual coordination (Haken et al. 1985; Kelso 1981, 1984), including stable phase and frequency locking and phase transitions between antiphase (syncopation) and inphase (synchronization) as the control parameter of frequency is increased.

In most rhythmic coordination experiments, coupling with the environment has usually been provided in a nonspecific way in the sense that metronome signals merely drive the system through a variety of coordinative states. In some cases, however, the metronome is used in a more specific way, in which a particular point in the movement cycle is synchronized with the metronome, an effect referred to as anchoring (Byblow et al. 1994; Carson 1995; see also Beek 1989; Kelso et al. 1991). Anchoring stabilizes the coordinative pattern at the point synchronized with the metronome (the anchored point) by: (1) decreasing spatial variability of the point in the movement cycle, seen in a thinning of the phase plane trajectory at that point in the movement cycle; and (2) reducing the standard deviation of relative phase at the anchored point. These effects as previously described are purely local, altering the coordinative pattern at specific times in the perception-action cycle near the metronome signal.

Here we explore whether this “local” effect of anchoring on individual movement trajectories also carries global consequences for the overall coordinative pattern. We embedded anchoring in the familiar bimanual coordination paradigm, but, unlike in previous experiments, we used two different metronome conditions: a single-metronome condition in which there was a single auditory stimulus for each movement cycle; and a double-metro-

nome condition in which there were two auditory stimuli per movement cycle. Based on many prior experiments, it is expected that, under parametric variation of movement frequency, one pattern (antiphase) will become unstable and switch. However, if anchoring also has a global stabilizing effect on coordination we would expect differences between the two metronome conditions in the critical frequencies at which coordinative patterns lose stability and switch. The double-metronome condition, with two local anchoring points available to help stabilize coordination, should delay transitions, i.e., exhibit a higher critical frequency, when compared with the single-metronome condition, which contains only one anchoring point per movement cycle.

Materials and methods

Participants

Six right-handed volunteers (three men, three women) took part in the experiment. Participants were volunteers from the undergraduate psychology subject pool and received course credit in accordance with the rules of the Department of Psychology at Florida Atlantic University. All procedures were cleared by the local Human Subjects Committee and participants signed consent forms before taking part in the experiment.

Apparatus

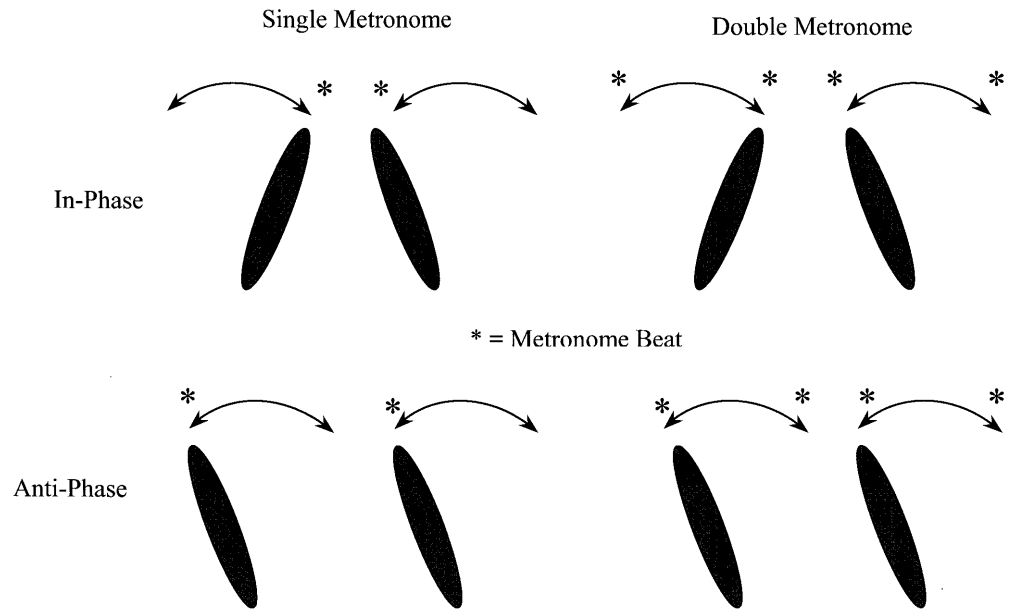
Participants placed their index fingers into two custom-built manipulanda which restricted motion of the metacarpophalangeal joints to a single plane. Two coaxial potentiometers sensed the position of the index fingers, which were sampled at 128 Hz using an ODAU analog-digital converter connected to an Optotrak 3010 system. An external metronome was generated by a Macintosh Classic computer using a program in Quick Basic.¹ The metronome signal (50 ms, 200 Hz) was sent to the ODAU unit and to a speaker (Archer mini-amplifier, speaker) placed approximately 0.5 m behind the participant.

Procedure

Participants were asked to move their index fingers in two different initial coordinative modes, inphase and antiphase, and to match their movements with two different metronome conditions, single and double, described below and shown in Fig. 1. Order of data collection was randomized for the six participants. In the inphase mode, homologous flexion and extension movements were performed simultaneously. In the antiphase mode, opposite actions of the fingers were performed simultaneously: as the right finger flexed, the left finger extended and vice versa. In all conditions, participants were instructed to keep their eyes closed during data collection. Prior to beginning each condition, the participants were told that “If at any time you feel the initial pattern start to change, do not intervene, but continue with whatever pattern feels most comfortable. Most importantly, try to stay with the metronome at all times.” A single familiarization trial was provided prior to data collection the first time each metronome condition was tested. Three trials were recorded for each condition.

¹ Standard deviation of the metronome period was found for each trial and divided by the mean period to obtain Weber’s ratio. Weber’s ratio was under 3% for each frequency plateau, a ratio at which variability is not expected to be perceived (Halpern and Darwin 1982).

Fig. 1 Schematic of the experimental conditions. The ovals represent the fingers moving in an inphase (*top*) and antiphase (*bottom*) pattern with the two metronome conditions, with the position synchronized with the metronome marked with an asterisk. Flexion is to the *middle* and extension is to the *outside*



Metronome conditions

In the single-metronome condition, participants performed ten cycles in each of nine plateaus. The metronome frequency for the plateaus ranged in frequency from 1.4 to 3.0 Hz in 0.2-Hz steps. The participants were asked to move one complete cycle for each metronome beat and to move so that right finger flexion was coincident with the metronome beat. In the double-metronome condition, as in the single-metronome condition, participants performed ten cycles in each of nine plateaus. In the double-metronome condition, metronome frequency began at 2.8 Hz and increased in 0.4-Hz steps to 6.0 Hz. Participants were instructed to move so that each metronome beat corresponded with either a finger flexion or extension. Thus, while the metronome was emitting pulses at twice the frequency of the single-metronome condition, the participant actually moved at the same frequency in both conditions.

Data processing

Finger positions were filtered using a low-pass, second-order Butterworth filter with a cutoff frequency of 10 Hz. Velocities were calculated using a first central finite difference equation applied to the raw position data. Previous research has indicated that variability of relative phase is reduced at some points in the movement cycle (Kelso et al. 1991), in particular at points synchronized with a metronome (Byblow et al. 1994). Thus, to examine the global stability of coordination, we measured continuous relative phase, which incorporates the entire movement cycle, rather than the commonly used point estimate of relative phase. Continuous relative phase between the left and right fingers was obtained by first normalizing the position and velocity of the two fingers to between -1 and $+1$ on a cycle-by-cycle basis, finding the phase as the arctangent of the instantaneous velocity over the position, and subtracting the phase of the right hand from the phase of the left hand (Kelso et al. 1986). The metronome signal was analyzed to find the onset of the metronome beats. Using this signal, the data were divided into frequency plateaus. Means and angular deviations of relative phase by plateau were calculated using circular statistics (Batschelet 1981).

A measure of anchoring was found by examining the thickness of the phase plane trajectories at the finger reversal positions. Note that we are defining anchoring as occurring at positions where participants are instructed to synchronize with the metronome rather than using the point in the movement cycle that coincided

with the metronome beat. Thickness was calculated on a plateau-by-plateau basis by first normalizing the phase plane trajectories to between -1 (flexion) and $+1$ (extension) based on the mean reversal points at that frequency plateau. Thickness of the phase plane trajectories was given by the standard deviation of the normalized reversal position. A similar measure was obtained for the phase plane trajectories across all frequency plateaus, except that overall mean reversal positions were used to normalize the data rather than the mean for each frequency plateau.

Results

Auditory-movement pacing

Mean correlations between right-finger cycle time and the metronome period are given in Table 1. The correlations are, with only two exceptions, above 0.8 for every trial, with all but two of the remaining trials above 0.9. All four low correlations came from a single participant who reported difficulty in staying with the metronome. No significant differences in mean correlation were found for the four conditions ($P > 0.05$). Since the correlations only indicate that the participants increased movement frequency with the metronome, the movement frequency at the last frequency plateau was also tested, and no significant differences between conditions were found ($P > 0.05$). The lack of significant differences between conditions indicates that any differences between

Table 1 Mean and standard deviation of correlations between cycle and metronome period. There are no significant differences ($P > 0.05$) in correlation between the conditions

| | Inphase | Antiphase |
|------------------|-----------|-----------|
| Single metronome | 0.98±0.01 | 0.96±0.08 |
| Double metronome | 0.93±0.17 | 0.96±0.04 |

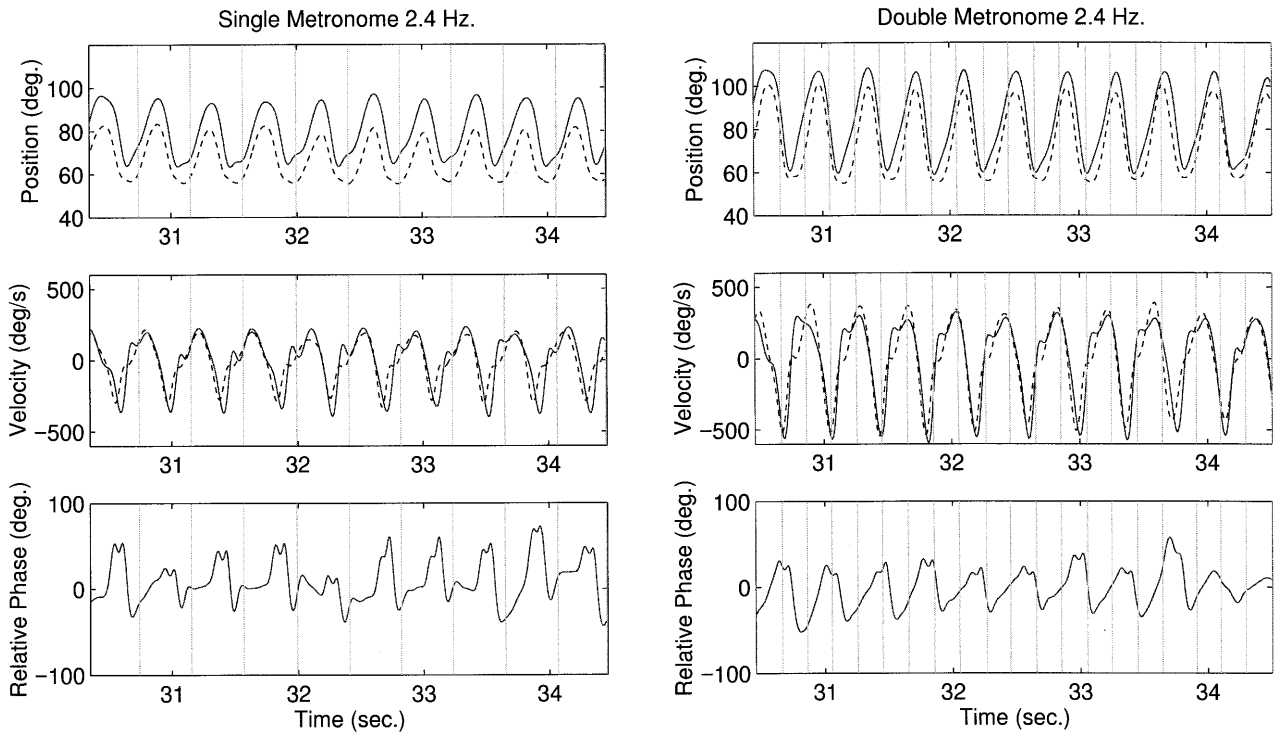


Fig. 2 Time series of the left (*solid line*) and right (*dashed line*) fingers for a single-frequency plateau (2.4 Hz) for the single- and double-metronome conditions. The *upper plots* show position with flexion increasing in angle and extension decreasing in angle, *middle plots* the velocity, and *bottom plots* continuous relative phase. *Vertical lines* indicate the presence of a metronome beat

conditions are caused by the conditions themselves and are not due to differences in movement frequency per se.

Local effects on phase plane trajectories

Time series of the position, velocity, and relative phase are shown in Fig. 2 (top, middle, bottom, respectively) for a single frequency (2.4 Hz) for the single- and double-metronome conditions for representative inphase trials. The left and right fingers are shown on the same plot in Fig. 2, with vertical lines indicating the metronome beats. Note that in the single-metronome condition peak position occurs before the metronome beat, suggesting anticipation of the stimulus (Mates et al. 1994; Engström et al. 1996). Nonharmonicities in the time series may be seen in the velocity time series, where a small pause causing slowing or deceleration of the finger can be seen as peak flexion is approached. The magnitude of this effect is larger in the single-metronome condition and in the left hand. The time series of continuous relative phase shows a large range, particularly in the single-metronome condition, but is relatively consistent at the peak finger positions.

Phase plane trajectories for the same data are shown in Fig. 3 for the single- and double-metronome conditions for an inphase trial. Boxes in Fig. 3 indicate the po-

sition at which the participant was instructed to synchronize with the metronome. In the single-metronome condition, there was a thinning of the phase plane trajectory near maximum flexion (anchored point) for both hands. By contrast, in the double-metronome condition, the phase plane trajectories had nearly equal widths at both maximum flexion and extension. Evidence for anchoring may be seen in the phase plane trajectories as a difference in the thickness of the phase plane trajectory between reversal (maximum flexion or extension) points where a metronome beat is present (anchored point) and reversal points where no metronome beat is present (unanchored point). In the single-metronome condition, metronome beats were present at the flexion reversals of both hands in the inphase mode and the flexion reversal of the right hand and extension reversal of the left hand in the antiphase mode. In the double-metronome condition, there were metronome beats at both finger reversals. Thus, if anchoring is present, small-to-zero differences should be observed between the two metronome conditions in the thickness of the phase plane trajectories where finger position coincides with the metronome beat in both metronome conditions. At the other reversals (extension of both hands in the inphase condition and left finger flexion and right finger extension in the antiphase condition), the phase plane trajectory should be less variable in the double-metronome condition than in the single-metronome condition.

Thickness of the normalized phase plane trajectories within a frequency plateau was tested statistically using a five-factor (two coordinative modes \times two metronome conditions \times two hands \times two positions, flexion or extension, \times nine frequency plateaus) repeated-measures ANOVA (three trials per subject) using data from all tri-

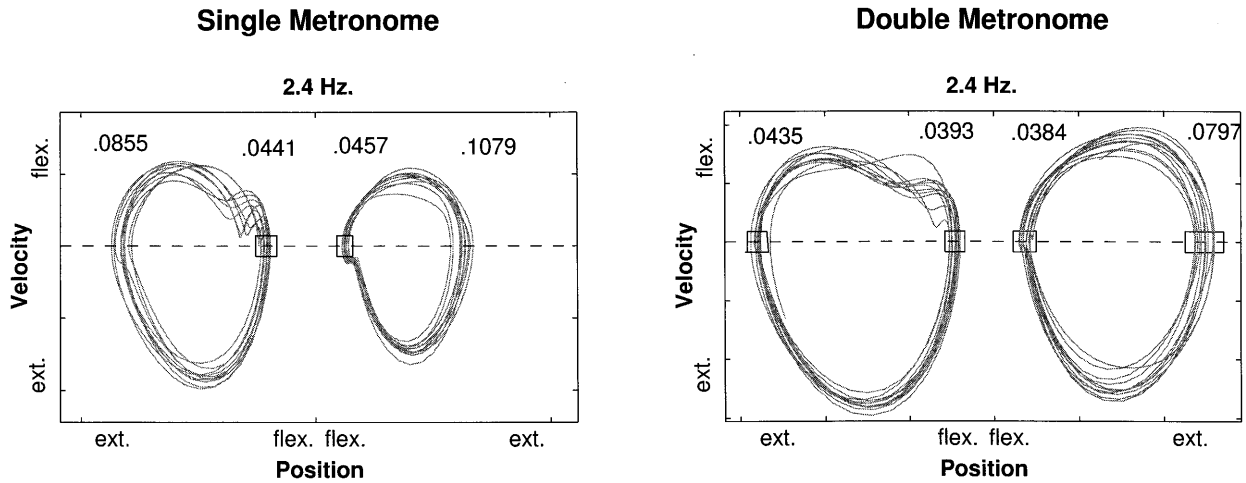


Fig. 3 Phase plane trajectories of the left and right fingers for an inphase trial with the single- and double-metronome conditions for a single-frequency plateau, with the thickness measures (normalized units) for each position shown along the *top*. *Rectangles* indicate the location where the movements were supposed to be

synchronized with the metronome. The phase plane trajectories are thinner at flexion (anchored) than at extension (unanchored) in the single-metronome condition, while in the double-metronome condition there is little difference between the flexion and extension positions

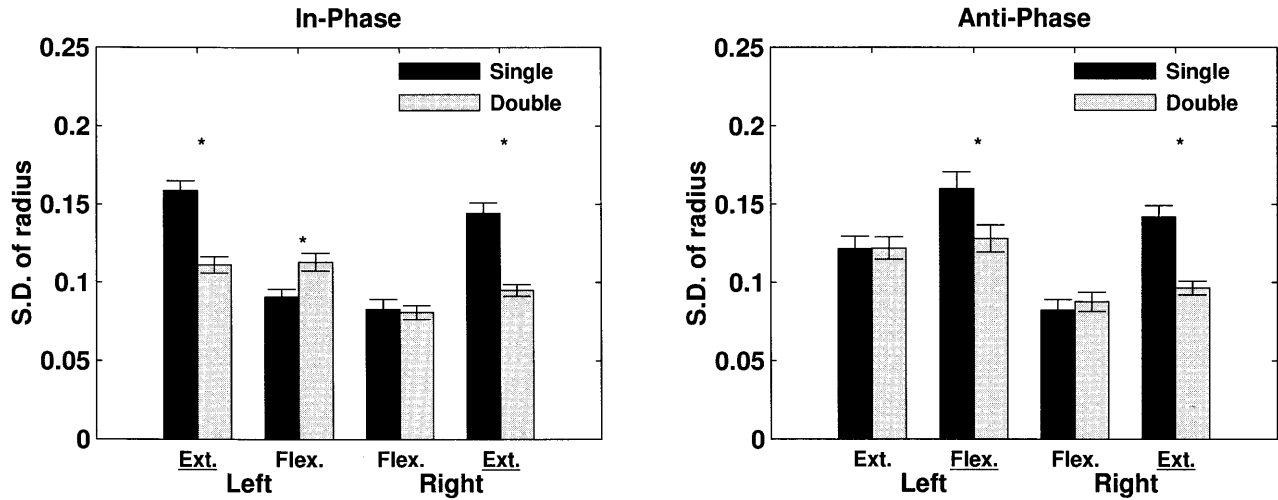


Fig. 4 Mean thickness of the normalized phase plane trajectories within a frequency plateau at flexion and extension for inphase and antiphase coordination. Positions that were not anchored in the single-metronome condition and therefore are expected to show differences are *underlined*. Significant differences are marked with an *asterisk*. Significant differences were found at all expected positions. *Error bars* indicate between-subject variability

in the double-metronome condition and not in the single-metronome condition (extension in both hands in the in-phase condition and left hand flexion and right hand extension in the antiphase condition), we concentrated on these positions. Using Tukey tests, significant differences ($P < 0.05$) between the single- and double-metronome conditions were found at each of these positions, with greater thickness in the single-metronome condition than in the double-metronome condition, confirming our hypothesis.

als at frequencies before a transition away from the original coordinative pattern occurred. Anchoring can be seen in the significant interaction of hand, coordinative mode, position, and metronome condition ($F_{1,5} = 18.00$, $P < 0.001$) shown in Fig. 4, collapsed across all frequency plateaus. Standard deviations of the radii of the phase plane trajectories for the left and right hands in the in-phase and antiphase coordinative modes are given as a function of hand and position. Since anchoring is manifested in differences in phase plane trajectory thickness in reversal positions where an anchoring point is present

An additional interaction, that of frequency plateau and position, was also significant ($F_{8,40} = 4.98$, $P < 0.0005$) and is shown in Fig. 5, in which trajectory thickness is plotted against frequency plateau for flexion and extension. In both cases the curve has a U-shape with a minimum at 2.2 Hz, possibly related to the eigenfrequency of the finger. Tukey tests confirm that a significant decrease in thickness occurred from 1.4 to 2.2 Hz in both flexion and extension. In extension there was a significant in-

Fig. 5 Mean thickness of the normalized phase plane trajectories for the flexion (*top*) and extension (*bottom*) reversal positions as a function of movement frequency. *Error bars* indicate between-subject variability

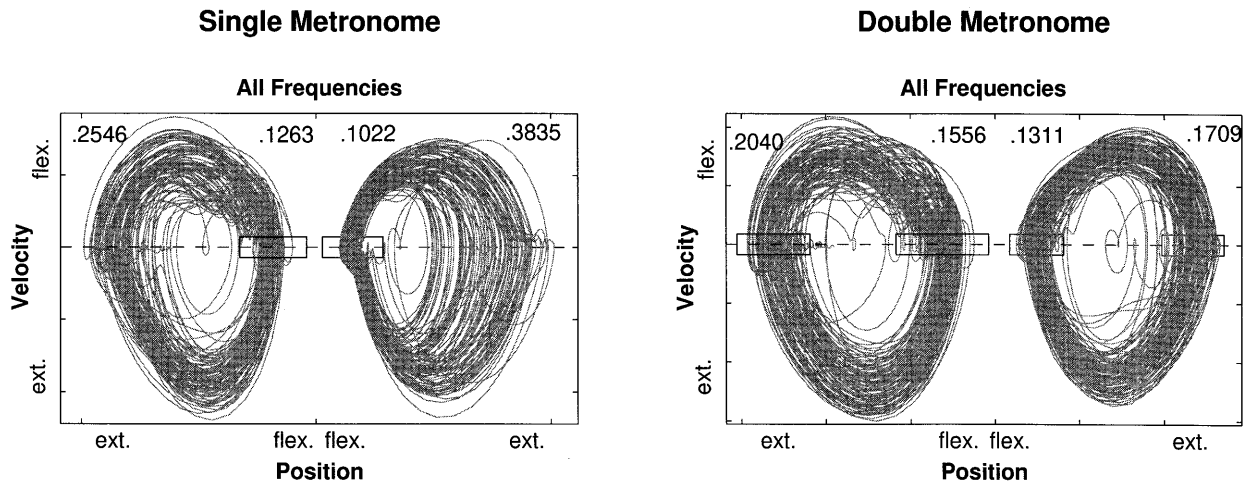
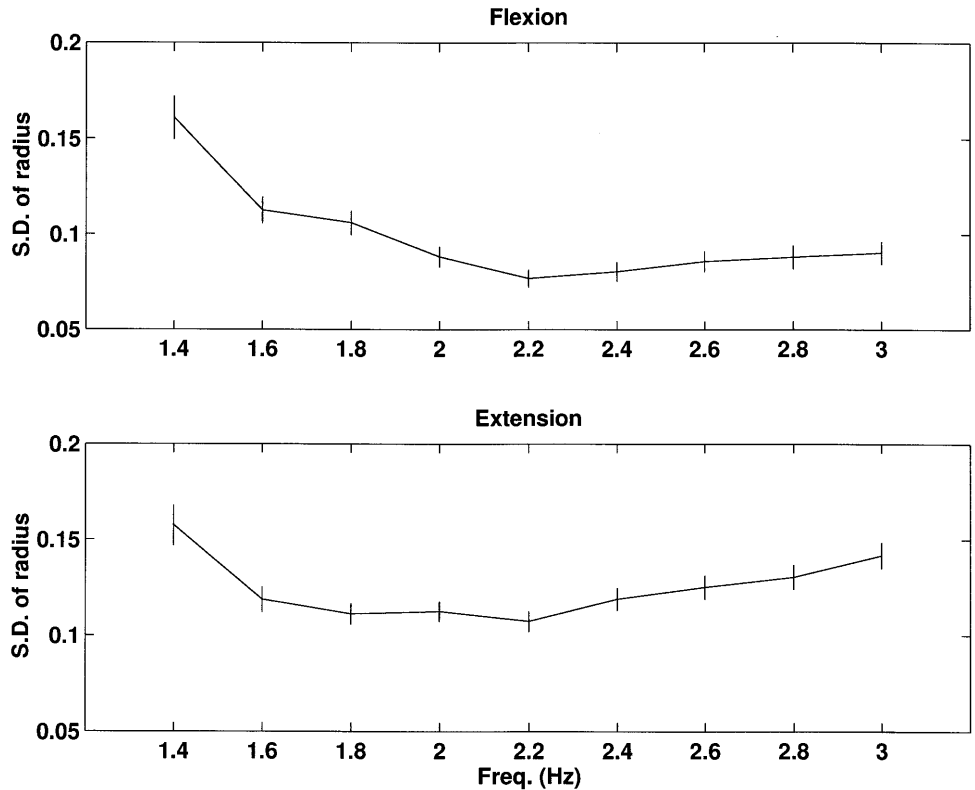


Fig. 6 Phase plane trajectories of the left and right fingers for an inphase trial with the single- and double-metronome conditions across all frequency plateaus with the thickness measures (normalized units) shown at the *top*. *Rectangles* indicate the location where the movements were supposed to be synchronized with the metronome. In the single-metronome condition, there is little change in the reversal positions at flexion (anchored), while the trajectory at the extension (unanchored) reversal was thicker. In the double-metronome condition, there is little difference in trajectory thickness between flexion and extension positions

shows representative phase plane trajectories across all movement frequencies for a single- and double-metronome inphase trial. As in Fig. 3 (within a single-frequency plateau), the phase plane trajectories are thinner in the single-metronome condition near the anchored point (flexion) than near the unanchored point (extension). This shows that, in addition to the decrease in reversal position variability within a frequency plateau, the anchored reversal point stays relatively constant as movement frequency is increased, whereas the unanchored reversal position becomes more variable across changes in frequency. In the double-metronome condition, the phase plane trajectories are of equal width at both flexion and extension, implying that position changes occurred equally at both reversal points.

increase in thickness from 2.2 to 3 Hz. In flexion there was a general trend for an increase in thickness as frequency increased from 2.2 Hz, but the trend was not significant.

Anchoring may also be seen in the phase plane trajectories over multiple movement frequencies. Figure 6

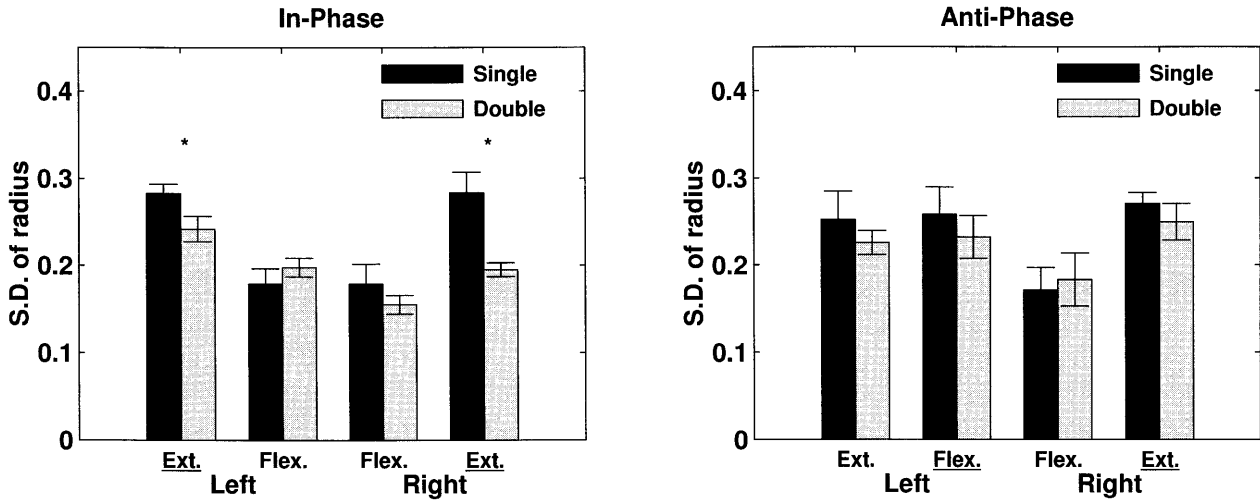
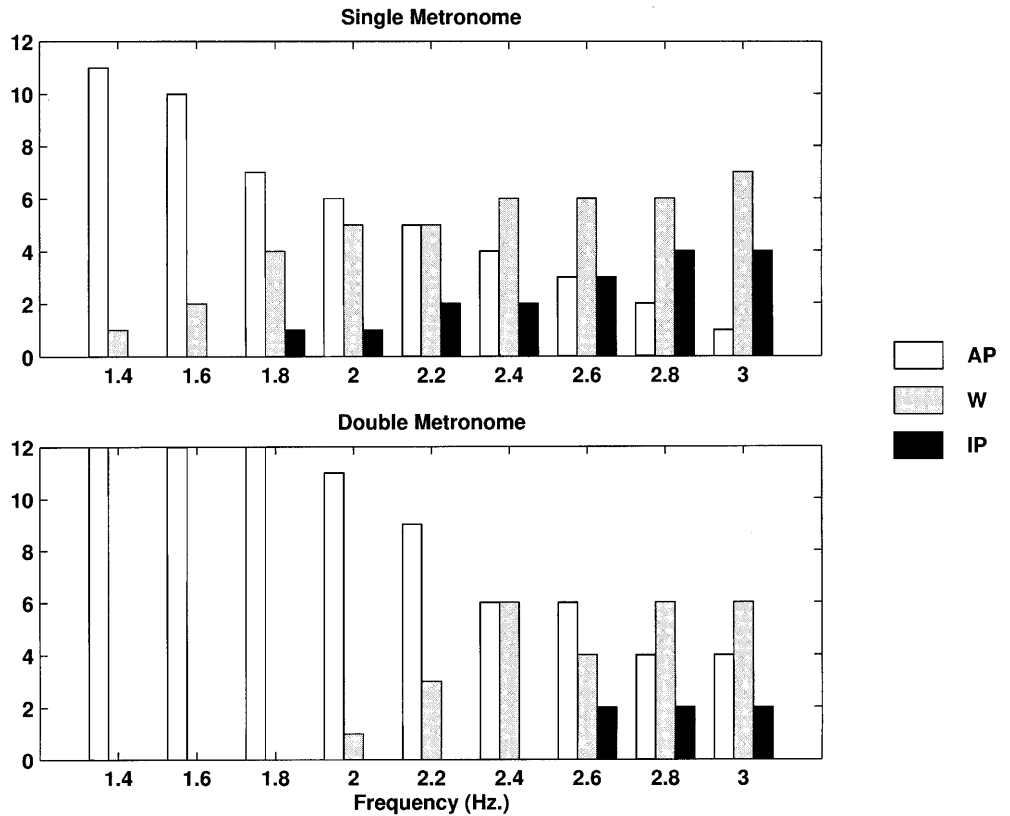


Fig. 7 Mean thickness of the normalized phase plane trajectories across all frequencies at flexion and extension are shown for the inphase and antiphase modes. Positions that were not anchored in the single-metronome condition and therefore are expected to show differences are *underlined*. Significant differences are

marked with an *asterisk*. Significant differences were found in the inphase mode, whereas in the antiphase mode there was a general trend toward greater trajectory thickness in the single-metronome condition. *Error bars* indicate between-subject variability

Fig. 8 Number of occurrences of the three different patterns (*AP* antiphase, *W* wrapping, *IP* inphase) for participants who displayed at least one transition from antiphase. Although both metronome conditions show an increasing number of departures from antiphase as frequency increases, the single-metronome condition results in more frequent transitions at all movement frequencies



Anchoring across plateaus was tested using a similar ANOVA to that used for within-frequency plateau thickness, using – to stay on the conservative side of our hypothesis – only those trials in which no transition occurred. Anchoring is seen here in significant interactions for coordinative mode, metronome condition, and hand ($F_{1,4}=16.66, P<0.05$), and coordinative mode and posi-

tion ($F_{1,4}=4.98, P<0.05$).² A plot of the thickness of the phase plane trajectory at maximum flexion and extension across all frequency plateaus is shown in Fig. 7. Tukey tests were again performed comparing the single- and

² One subject displayed transitions on every single antiphase trial, so the denominator degrees of freedom are changed from the previous analysis.

double-metronome conditions at finger reversals where a metronome beat was present in one condition and not in the other. In the inphase condition, significantly greater ($P < 0.05$) thickness was found in the extension position in the single-metronome condition than in the double-metronome condition. In the antiphase condition, no significant differences were found, although a general trend toward greater thickness in the single-metronome condition was present.

Global coordinative stability

Relative phase patterns were divided into three types of behavior: inphase, antiphase, and transient behavior. Included in the latter category was phase wrapping, in which no steady state was realized. Four of the six subjects showed a deviation from the initial antiphase mode in at least one trial. The other two subjects remained in antiphase coordination throughout all trials. A histogram of the occurrence of the three patterns in the initial antiphase condition for the four subjects who demonstrated transitions is shown in Fig. 8. At every frequency, including the first frequency, there were more departures from antiphase in the single-metronome condition than there were in the double-metronome condition. This was most evident at 2.0 Hz., where in the single-metronome condition the initial antiphase pattern was not present in half of the trials, while in the double-metronome condition there was only a single departure from the antiphase mode.

Another indication of the stability of coordination is the angular deviation of relative phase. We performed a t -test comparing the angular deviations of the two metronome conditions using the standard deviation of continuous relative phase at all movement frequencies before a transition. A significant difference was found between the two conditions ($t(34) = 2.05$, $P < 0.05$), with the single-metronome condition being more variable (SD 0.47 radians) than the double-metronome condition (SD 0.39 radians). Taken together, the greater number of departures from antiphase in the single-metronome condition, shown in Fig. 8, and the higher angular deviation of relative phase in the single-metronome condition point to the fact that the double-metronome condition reduces variability of relative phase and delays or even eliminates transitions.

Discussion

One of the most remarkable features of the CNS is its plasticity, the ability to modify behavior according to specific sensory inputs from the environment. Previous research on coupling with the environment, or anchoring, has shown that the environment exerts a local effect, stabilizing the movement cycle at places near the occurrence of environmental events. Here we have observed a second property of coupling with the environment: by lo-

cally coupling points of maximal excursions of individual finger movements to specific auditory inputs, stability of overall coordination is altered. In addition to previously observed local effects of anchoring (i.e., thinning of the phase plane trajectory), global changes in behavior, seen as delays in coordinative transitions, occurred as the environmental information was manipulated. We show below that local and global effects may be modeled in a simple extension of the HKB model through the inclusion of specific coupling to the metronome, a process we refer to as *parametric stabilization*.

Local effects

The intentional coupling of action and perception is operationalized here in terms of an interaction between rhythmic movement and a metronome, a process called anchoring. One of the ways in which anchoring has been demonstrated previously is in asymmetries in phase plane trajectories (Byblow et al. 1994; Carson et al. 1994), with thinning of the phase plane trajectories, or stabilization of the movement pattern in space, at the anchored point. We have reproduced this effect within frequency plateaus (Figs. 3, 4) with thinner phase plane trajectories at reversals coincident with the metronome beat than at other reversal points. Anchoring is also seen across frequency plateaus (Figs. 6, 7), indicating that not only is the anchored point stabilized, but also the anchored point is fixed in space across changes in frequency and amplitude. Thinning of the phase plane trajectories is a purely local effect, with no changes to the phase plane trajectories other than those near the anchored point.

Theoretically, local effects of anchoring have been considered only in discrete models of coordination, which do not attempt to handle the phase plane trajectories of the individual components being coordinated (Beek 1989; DeGuzman and Kelso 1991; Kelso and DeGuzman 1988). Obviously, any theoretical model of coordination must accommodate: (a) local effects of sensory stimuli on the individual movement trajectory; and (b) global effects on the coordination states themselves, including the enhancement of coordinative stability and (correspondingly) delays or even elimination of phase transitions. One characteristic of the HKB model at the component level and subsequent versions is that the oscillators themselves are symmetric; flexion and extension positions may be exchanged without affecting the phase plane trajectory (Beek et al. 1995, 1996; Kay et al. 1987). As long as all parameters of the oscillators, including eigenfrequencies, are the same the phase plane trajectories generated by the model are symmetric, with left-right exchanges leaving the phase plot invariant (Fuchs et al. 1996). We see in Fig. 3 that experimentally derived phase plane trajectories do not share this trait. Phase plane trajectories in the single metronome are narrower at the reversal coincident with the metronome beat than at the other reversal, a feature also noted by others

(Carson et al. 1994) that may be attributed to the effect of synchronizing with a metronome. By contrast, in the double-metronome condition, the phase plane trajectories are more symmetric, since information is available at both flexion and extension reversal points.

Global effects

The present hypothesis is that local sensory inputs may serve to stabilize global coordination. When an appropriate kinematic property, say peak flexion, must be coordinated with a metronome, we show here that the entire coordination dynamics (stability, loss of stability, etc.) are altered. The single-metronome condition, the metronome condition typically used in experiments to date, was far less stable than the double-metronome condition as readily observable in the number of transitions seen between the two metronome conditions (Fig. 8). Even the single-metronome condition appears to stabilize coordination: two subjects showed no transitions from anti-phase in either metronome condition even though previous (not specifically anchored) experiments would suggest that transitions are typically present before 3 Hz. This phenomenon is consistent with previous research (Byblow et al. 1994; Carson 1995), which indicated that anchoring at a single point in a movement cycle acts to decrease the angular deviation of relative phase at the anchoring point coincident with the metronome beat. However, in previous work, this decrease in the variability of relative phase was not associated with any changes in the global coordinative behavior such as phase transitions. Here we see that stabilizing relative phase at two positions in the movement cycle has the effect of reducing the propensity to switch coordinative patterns, indicating that although the environmental information was available only at discrete points in time, the stabilizing effects of coupling with the environment extend to the entire coordinative system.

The global effect of delaying transitions is crucial in that it allows for flexibility in coordinative patterns. One important source of flexibility in coordination is multistability, which means that several different patterns can be adopted for the same environmental or task conditions. Here we have observed that by anchoring, or coupling to the environment, transitions can be delayed or eliminated, thus preserving (bi)stable coordination states through a broader range of the control parameter than would otherwise be possible. This effect has been used by others to produce coordinative patterns not normally available such as multifrequency movements (De Guzman and Kelso 1991; Haken et al. 1996) or relative phase patterns other than inphase or antiphase (Tuller and Kelso 1989; Zanone and Kelso 1992) through coupling with a metronome. The importance of the ability to use a metronome to produce new coordination patterns was highlighted by Zanone and Kelso (1997), who found that the component level dynamics were altered near the synchronization point with a metronome, enabling pro-

duction of new stable patterns during learning (see Figs. 7, 8 by Zanone and Kelso 1997).

Modeling

The local and global effects of anchoring described above are not accounted for by any existing model of coordination (to our knowledge). Previous attempts of modeling coupling of bimanual coordination and an external stimulus via linear driving of the HKB model (Schöner and Kelso 1988a, 1988b) do not explain the changes in coordination observed here; namely the increase in critical transition frequency and changes to the phase plane trajectory. Here, we introduce a simple extension of the HKB model that includes these effects. This extension is important in that it not only accounts for the anchoring behavior observed here, but carries implications for the underlying neural dynamics as well. In recent years, various attempts have been made to biologically motivate phenomenological models of human coordination (see Haken 1996; Kelso 1995 for reviews). In particular, the HKB model of coordination has been derived from the level of excitatory and inhibitory neural ensembles in the neocortex, connected via intra- and corticocortical fibers (Jirsa et al. 1998). This has allowed the behavioral HKB coupling to be expressed in terms of physiological and anatomical measures. Thus, an extension of the HKB model that involves the presence of auditory coupling (i.e., anchoring) not only provides a behavioral model for coordination dynamics under environmental influence, but also suggests the presence of qualitative changes in the dynamics at the neural level due to the auditory coupling.

In a separate paper (see Jirsa et al. 2000 for more details), we have extended the HKB model to accommodate these new effects by adding a parametric driving term to each oscillator x . The equations take the form:

$$\begin{aligned}\ddot{x}_1 + f(x_1, \dot{x}_1)\dot{x}_1 + \omega^2 x_1 &= g(x_1, \dot{x}_1, x_2, \dot{x}_2) + \varepsilon(t)x_1 \\ \ddot{x}_2 + f(x_2, \dot{x}_2)\dot{x}_2 + \omega^2 x_2 &= g(x_2, \dot{x}_2, x_1, \dot{x}_1) + \varepsilon(t)x_2\end{aligned}$$

where f is a nonlinear damping function, g represents the HKB bimanual coupling function, ω is the eigenfrequency of the oscillator. $\varepsilon(t)$ represents the environmental information, here specified by an auditory metronome, which is periodic, with $\varepsilon(t) = \varepsilon(t+T)$, where T is the time between two metronome beats. The conceptual difference here to earlier approaches (Schöner and Kelso 1988b) is the introduction of periodically changing environmental information by a periodically changing parameter (parametric driving) rather than a linear additive driving. The exact form of the parametric driving term may be subject to change. Here we couple auditory input to finger position, since the task requires peak finger position to coincide with the stimulus. A parametric driving term coupling the stimulus to the velocity rather than to the amplitude produces qualitatively similar results. We refer to the global stabilization effect of the parametric driving term as parametric stabilization.

While retaining the qualitative behavior of the HKB model (bistable coordination, spontaneous phase transitions as movement frequency is increased, hysteresis, etc.), parametric driving generates a vast variety of dynamics not achievable by earlier approaches because they were restricted to 1:1 coupling between effector and environment. The new effects observed experimentally (i.e., stabilization of the relative phase pattern and changes in the phase plane trajectories) are described by the parametric stabilization model as well. Table 2 shows estimates of transition frequencies derived from the HKB model using standard parameters and from the parametric model using the same parameters as the HKB model and an estimate of the coupling strength ϵ for both the single- and double-metronome conditions. For a relative comparison, experimentally obtained transition frequencies in the two metronome conditions are also in-

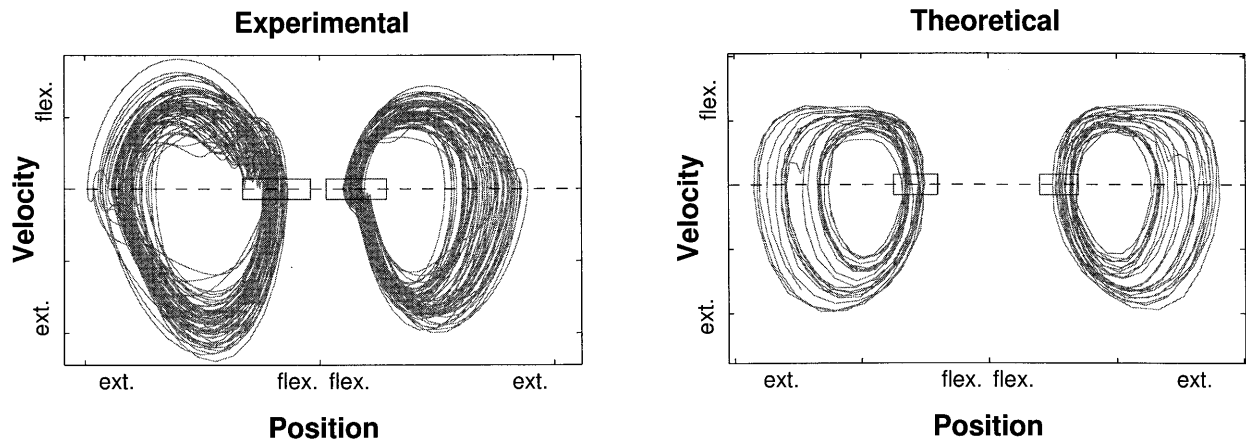
cluded in Table 2. The addition of coupling with a metronome increases the transition frequency when compared with the HKB model, with the highest transition frequency in the double-metronome condition. This agrees very well with Fig. 8, which shows that transitions occur earlier, i.e., at lower frequencies in the single-metronome condition. The addition of the parametric stabilization term reproduces the local effects on phase plane trajectories, resulting in a thinning of the phase plane trajectories, seen in Fig. 9 for both data and theoretical model, near the metronome beat. Note that no attempt is made here to fit parameters of the model to the data, but rather to demonstrate the main qualitative effect, namely thinning of the phase plane trajectory at the anchored point. In addition, the concept of parametric stabilization can accommodate previous experimental results, including single-limb coordination with rhythmic auditory or visual stimuli (Kelso et al. 1990; Stins and Michaels 1999; Wimmers et al. 1992).

Table 2 Transition frequencies for the Haken-Kelso-Bunz (HKB) and parametric stabilization models of coordination. A standard set of parameters for the HKB model and an estimate of the coupling strength ϵ were used to generate the transition frequencies ($A=B=1$, $\alpha=-0.2$, $\beta=0.2$, $\epsilon=3$, $\lambda=0.01$; see Jirsa et al. 2000 for details). For comparative purposes transition frequencies from the experimental data are included. Only the relative values matter here

| | Transition frequency | |
|------------------|----------------------|--------------------------------|
| | Model (Hz) | Experimental (Hz) ^a |
| HKB model | 1.2 | |
| Parametric model | | |
| Single metronome | 1.6 | 2.1 |
| Double metronome | 2.4 | 2.4 |

^a Transition frequencies were calculated as the mean frequency at which a departure from antiphase coordination was first observed. Since the single-metronome condition produced more departures, the difference in transition frequencies is most probably greater than indicated here

Fig. 9 Phase plane trajectories for the single-metronome condition across frequency plateaus from the experimental data (left) and theoretical model (right). Boxes indicate the position synchronized with the metronome beat. The theoretical model reproduces the thinning of the phase plane at the flexion (anchored) position. Parameters for the model are the same as those used in Table 2



Conclusion

Anchoring, or intentionally synchronizing a particular point in the movement with a particular sensory input, has previously been seen as a purely local effect, influencing coordinative stability and movement variability only at times and places close to the stimulus. Here we examined whether the local effects of anchoring (observed, for example in thinning of the phase plane trajectory) also carry global consequences for the stability of the coordinative patterns. Through a manipulation of the environmental information available at discrete points in time (i.e., an auditory metronome), we demonstrated that global stability of the coordination system is altered, delaying or even eliminating transitions. Such delays are shown theoretically to be due to parametric stabilization of the coordination dynamics and are expected to result in qualitative changes in the neural dynamics as revealed, for example, by EEG and MEG recordings (see Kelso et al. 1992; Mayville et al. 1999). The stabilizing effect is important because it provides a mechanism by which multistability is preserved, allowing the CNS to produce coordinative patterns at values of the control pa-

parameter at which coordination typically becomes unstable and changes. Preserving multistability enhances coordinative flexibility, allowing the brain to adapt both its component and coordinative behavior to suit task and environmental conditions.

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