Are frequency-induced transitions in rhythmic coordination mediated by a drop in amplitude?

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Abstract. The coordination of rhythmic movements is characterized by attraction to stable modes as well as by loss of stability due to the manipulation of external control parameters. For isochronous coordination between two oscillating components, frequency-induced transitions from antiphase to inphase coordination are frequently observed. Such transitions have been understood on the basis of a dynamical model, the HKB model, consisting of both a potential function for relative phase and a description of the oscillating limbs in terms of nonlinearly coupled limit cycle oscillators. According to the latter aspect of this model, the loss of stability of the antiphase pattern, which precedes the transition to the inphase pattern, is mediated by the decrease in movement amplitude that occurs when the movement frequency is scaled up. This amplitude-based transition mechanism was examined experimentally in the context of a unimanual tracking task. Subjects were instructed to maintain a prescribed amplitude, while tracking an oscillating visual stimulus in either the inphase or the antiphase mode. Three different movement amplitudes were used to examine the prediction that larger amplitudes lead to more stable coordination. When the frequency of oscillation was gradually increased, transitions from antiphase to inphase coordination were observed in the majority of the trials, despite constant or sometimes even slightly increasing amplitudes. No significant effects of amplitude on pattern stability, as indicated by the variability of relative phase and by the critical frequency, were observed. To the extent that these findings can be generalized beyond the present task domain, they suggest that frequency-induced transitions in coordinated rhythmic movements may not be mediated by a drop in amplitude and that alternative directions in modeling may have to be considered.

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1 Introduction

In performing daily activities, our movement system constantly has to adapt to changing conditions. Whereas such adaptations often involve merely quantitative scaling of relevant variables, qualitative changes between different coordination patterns are also observed. For instance, increase in the speed of locomotion results in transitions between gait patterns in a large number of species. Quadrupeds walk at slow speeds but change to trot and subsequently to canter, transverse gallop, or rotary gallop at higher speeds. Such transitions in gait have been interpreted as functional adaptations on the basis of considerations of mechanical stability, metabolic cost, mechanical interference between the limbs, and maneuverability (e.g., Grillner et al. 1979; Hildebrand 1980; Hoyt and Taylor 1981). In certain quarters, it is believed that the switches between coordination patterns result from the selection of specific motor programs (e.g., Shapiro et al. 1981).

The dynamical systems approach to movement coordination, however, seeks an explanation for such qualitative changes in coordination in principles of pattern formation and self-organization (e.g., Beek et al. 1995; Diedrich and Warren 1995; Haken 1996; Kelso 1994, 1995; Turvey 1990). Within this perspective, it has been proven useful to capture the order in the system (i.e., the coordination pattern) by one or a few collective variables or order parameters. The dynamics of these order parameters and, thus, the stability of the coordination patterns are influenced by aspecific control parameters. Gradual scaling of a control parameter may result in loss of stability of the initial coordination pattern followed by an abrupt transition to another, still stable pattern. As a result, various coordination modes may be captured by a single dynamical system with order parameter dynamics that undergo qualitative (nonlinear) changes at critical values of a control parameter. During such 'phase transitions', the system reveals itself in the sense that the order parameter (the dimension

along which the sudden nonlinear change occurs) and the control parameter (the linearly scaled parameter that inflicts the transition) can be determined. For this reason, the study of phase transitions plays an essential role in the dynamical systems approach to movement coordination.

Phase transitions between coordination patterns were originally demonstrated in the context of isochronous rhythmic interlimb coordination (e.g., Kelso 1984; Kelso et al. 1987). If two limbs cycle with the same sufficiently low frequency, two coordination patterns can be stably performed without specific training: the inphase pattern (simultaneous movements in identical directions, resulting in a phase difference of 0°) and the antiphase pattern (simultaneous movements in opposite directions, resulting in a phase difference of 180°). When starting in antiphase coordination, a gradual increase in the frequency of the movements (control parameter) results in an abrupt transition to the inphase pattern. The occurrence of critical fluctuations (Kelso et al. 1986) and critical slowing down (Scholz et al. 1987), indicators of pattern instability, revealed that this transition indeed resulted from loss of stability of the antiphase pattern.

Building on this original line of research, transitions from the antiphase to the inphase mode have also been demonstrated in the coordination between wrist movements in a pronation-supination task (Byblow et al. 1994), between different limbs (e.g., an arm and a leg; Jeka and Kelso 1995), between a limb and a visual (Wimmers et al. 1992) or auditory stimulus (Byblow et al. 1995; Kelso et al. 1990), and between the lower legs of two different persons (Schmidt et al. 1990). In addition, frequency-induced transitions have been demonstrated in multifrequency tapping tasks, where transitions from one frequency ratio (e.g., 5:8) to another, less complex, frequency ratio (e.g., 2:3) were observed (Haken et al. 1996; Peper et al. 1991, 1995).

To account for the transition from antiphase to inphase coordination during isofrequency coordination tasks, a dynamical model was developed by Haken et al. (1985). This model, referred to in the literature as the Haken-Kelso-Bunz (or HKB) model, involves two interrelated levels of modeling, namely that of the dynamics of the order parameter relative phase (i.e., the phase difference between the moving limbs) and that of the individual limb movements and their interactions. At the first level, the dynamics of relative phase were accounted for by means of the potential function:

$$V(\phi) = -a\cos\phi - b\cos(2\phi) \tag{1}$$

where ϕ denotes relative phase and a and b are two parameters. The minima of this function represent the attractor states of the system, where the corresponding values of the order parameter are stable. Indeed, for $b/a > 0.25$, (1) results in minima for 0° and 180°, implying that both the inphase and antiphase coordination pattern can be performed stably (see Fig. 1). To account for the observed transition between these coordination modes, scaling of the control parameter was translated
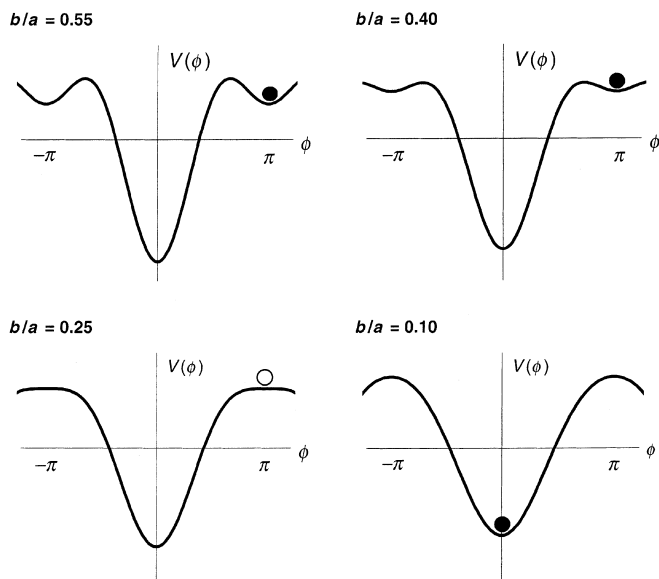

Fig. 1. The potential $V(\phi)$ for different values of b/a. Behavioral changes are represented by the overdamped motion of a rolling ball in the potential. At $b/a = 0.25$, the antiphase pattern becomes unstable (white instead of black ball), resulting in a transition to the inphase pattern

into annihilation of the attractor for antiphase coordination. This was accomplished by assuming that changes in movement frequency inflict parametric changes in the potential function: Increasing movement frequency was associated with a decrease in the ratio between the parameters b and a. This results in a differential decrease in stability for the two coordination modes and culminates in the observed transition at $b/a = 0.25$ (see Fig. 1; cf. Haken et al. 1985).

Although the potential function (1) can account for the observed transition, it is unclear at this level of analysis why the ratio between the coupling parameters b and a would be affected by changes in the frequency of oscillation. In the HKB model, this issue was resolved by modeling the system also at the level of the equations of motion that describe the kinematics of the limb movements. At this level, the model is tailored more specifically to the movements of the limbs and the way in which they interact. In general terms, the resulting model of coupled oscillators is defined by

$$\ddot{x}_1 + h(x_1, \dot{x}_1) + g(x_1) = I_{12}(x_1, \dot{x}_1, x_2, \dot{x}_2) \tag{2a}$$

$$\ddot{x}_2 + h(x_2, \dot{x}_2) + g(x_2) = I_{21}(x_2, \dot{x}_2, x_1, \dot{x}_1) \tag{2b}$$

where x_j ($j = 1, 2$) denotes the limb position in time and the dot notation is used to indicate time derivatives. On the basis of the kinematics of the movements, the moving limbs were modeled as nonlinearly damped oscillators with both a Van der Pol ($x^2\dot{x}$) and a Rayleigh ($\dot{x}^3$) damping term (Haken et al. 1985; Kay et al. 1987). Such oscillators involve both positive and negative damping and are therefore self-sustaining. Moreover, they are characterized by specific spatiotemporal properties: With increasing frequency, peak velocity increases

due to the Van der Pol damping term, whereas amplitude decreases due to the Rayleigh term. As will be discussed below, the latter aspect of the model plays an essential role in the explanation of the observed transition from antiphase to inphase coordination.

The mutual interactions between the two oscillators were modeled by Haken et al. (1985) in terms of their state variables x and $\dot{x}$. The coupling functions I_{12} and I_{21} in (2) had to be defined in such a way that the collective dynamics, i.e., the dynamics of the order parameter ϕ, of the resulting system was adequately modeled by the potential function (1). From the relation

$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = -\frac{\mathrm{d}V(\phi)}{\mathrm{d}\phi} \tag{3}$$

it follows that the dynamics of ϕ, as defined by the HKB potential function (1), are captured by the order parameter equation

$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = -a \sin\phi - 2b \sin(2\phi) \tag{4}$$

Although a variety of coupling functions may lead to the required order parameter equation (4), two specific formulations were suggested by Haken et al. (1985). Whereas the functional form of the coupled oscillators has been validated (Kay et al. 1987; but see also Beek et al. 1996), the form of the proposed coupling functions still awaits empirical evaluation. Such an evaluation is important for at least three reasons. First, the identification of the proper coupling functions for the coordination of rhythmic movements is an essential step in the formal characterization of such movements qua instances of coupled limit cycle oscillators, which is (still) of theoretical relevance in its own right, especially in cases where no potential function can be derived, such as in the production of multifrequency patterns (Haken et al. 1996). Second, the construction of coupled oscillator models may provide a means for evaluating the formal degree to which the claim holds true that dynamical principles of movement coordination apply quite generally, regardless of their material implementation. Third, the formal identification of coupling functions may help to provide insight into the neural mechanisms underlying these patterns and thus promote our understanding of the relation between brain and behavior. Therefore, the behavioral predictions of the two coupling functions proposed by Haken et al. (1985), which are described below, were tested empirically in the current experiment.

Although both derivations presented by Haken et al. (1985) lead to the required coordination dynamics, the resulting order parameter equations are not identical. For a full discussion of the two derivations, the reader is referred to Haken et al. (1985) and Peper and Beek (1998). For our present purpose, it is sufficient to focus on the differences between the two versions of the model with respect to the resulting order parameter equations. In the prevailing version of the model of coupled differential equations, the coupling between the two oscillators was modeled using time derivatives (Haken et al. 1985; see also Peper and Beek 1998). This derivation resulted in the order parameter equation

$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = (\alpha + 2\beta r^2)\sin\phi - \beta r^2 \sin(2\phi) \tag{5}$$

where r is the real amplitude of the oscillations and α and β are two adjustable but then fixed parameters (i.e., α and β are assumed to be constant during an experimental run). Equation (5) is identical to (4) if $\alpha + 2\beta r^2 = -a$ and $\beta r^2 = 2b$. This implies that the transition from antiphase to inphase, which occurs at $b/a = 0.25$ in (4), takes place at the critical amplitude $r = \sqrt{-\alpha/4\beta}$, $\alpha < 0$. In other words, according to this version of the model, movement frequency does not affect the stability of the coordination patterns directly, but its influence is mediated entirely by the associated drop in amplitude (modeled by means of the Rayleigh damping term in the component oscillators).

In an alternative formulation of the model, the coupling between the limbs was assumed to depend on their positions at earlier moments in time, which was formalized by incorporating a time delay function (Haken et al. 1985; see also Peper and Beek 1998). The resulting order parameter equation

$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = -\frac{1}{\omega^2}\left[(\alpha + 6\beta r^2)\sin\phi - 3\beta r^2 \sin(2\phi)\right] \tag{6}$$

reveals that in this version of the model, pattern stability not only depends on the parameters α and β and amplitude r, but also directly on the movement frequency ω itself. Although this implies that an increase in ω results in an overall decrease in pattern stability, the attractor for antiphase coordination will not be annihilated, because both sine terms are equally affected by this parameter. Therefore, also for this version of the model, the vanishing of the attractor for antiphase coordination is explained on the basis of the drop in amplitude that is associated with an increase in frequency and occurs at the critical amplitude $r = \sqrt{-\alpha/12\beta}$, $\alpha < 0$.

In summary, in both versions of the HKB model, annihilation of the attractor for antiphase coordination is based on the inverse relation between movement frequency and amplitude, which is accounted for by the Rayleigh damping term in the component oscillators. Whereas the basic transition mechanism is the same, the two versions of the model differ with respect to the influence of movement frequency: While in the time derivatives version of the model the effect of movement frequency is fully mediated by the associated changes in amplitude, the time delays version shows an additional inverse dependence of pattern stability on movement frequency itself.

The HKB model was originally developed to explain the empirically observed frequency-induced transition from antiphase to inphase coordination. Because both versions of the model of coupled oscillators can account for this transition, the functional form of the coupling between the oscillators has so far not been evaluated. Yet the coupling function featuring in the time

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derivatives version of the model has been used in modeling the space-time properties of bimanual rhythmic movements (Kay et al. 1987), and it has been called a "fundamental biophysical coupling" (Kelso 1994, p. 401; see also Jirsa et al. 1994). In addition, the proposed amplitude-mediated transition mechanism has been generalized to account for frequency-induced transitions in multi-frequency coordination (Haken et al. 1996). Because the choice for this particular coupling function has not been based on direct empirical support but only on its formal expediency in accounting for phase transitions, the present study aims at a 'head-on' empirical evaluation of the functional form of the coupling between the limbs. This will be helpful in determining whether the coupling function derived for the time derivatives version of the model is indeed correct, or whether another coupling function (for instance, the one that was used in the time delays version of the model) would be more adequate.

Although the time derivatives version of the HKB model is more commonly used in the literature (e.g., Fuchs and Kelso 1994; Jirsa et al. 1994; Kay et al. 1987; Kelso 1994; Kelso et al. 1987), it may be argued that the time delays version is more plausible, because the incorporated time delays may reflect delays associated with underlying neurophysiological processes, for instance the use of afferent signals (cf. Haken 1996; Peper and Beek 1998). Moreover, in multifrequency coordination, coupling strength has been demonstrated to be inversely related to movement frequency, whereas no dependence on the amplitude of oscillation was observed (Peper and Beek 1998). Because the generalized version of the HKB model (Haken et al. 1996), which accounts for the coordination of multifrequency relations, is derived along similar lines as the HKB model, an empirically motivated choice between the two versions of the model could be made on the basis of these results: The strong inverse relation to movement frequency per se indicated that the coupling between the limbs was more adequately modeled when the time delay function was incorporated in the derivation (Peper and Beek 1998).

In the study by Peper and Beek (1998), the tempo of performance remained constant during each experimental run. Therefore, the model prediction that frequency-induced transitions are mediated by the inverse relation between movement frequency and amplitude could not be tested. This aspect of the model was examined in the present experiment. By instructing the subjects to maintain a fixed amplitude while increasing the frequency of oscillation, (the effect of) the Rayleigh damping term was eliminated from the component oscillators. If an increase in movement frequency is not accompanied by a drop in amplitude, neither version of the model of coupled oscillators predicts annihilation of the attractor for the antiphase pattern. According to the time derivatives version of the model, in which pattern stability varies solely as a function of movement amplitude, no transitions to the inphase pattern are expected to occur. According to the time delays version of the model, however, the dependence on movement frequency itself leads to an overall decrease in pattern stability. Therefore, transi-

tions to the inphase pattern might occur if the stability of the antiphase pattern becomes too small to resist stochastic fluctuations (cf. Schöner et al. 1986). The additional dependence on movement amplitude was examined by studying the behavior for different amplitude conditions. If a larger amplitude of oscillation indeed results in more stable coordination, the transition from antiphase to inphase coordination is expected to occur at a higher critical frequency.

2 Experiment

To be able to prescribe the required amplitude of oscillation effectively, the amplitude-based transition mechanism of both versions of the HKB model was examined using a rhythmic tracking task. Frequency-induced transitions have been demonstrated in the context of rhythmic tracking and have been interpreted on the basis of the HKB model (Wimmers et al. 1992). Although this task involves a purely unidirectional coupling between a visual stimulus and an oscillating limb, the order parameter dynamics predicted by the HKB model are qualitatively the same as those predicted for bidirectionally coupled systems.[1]

2.1 Method

Subjects. Potential subjects were screened before they were invited to participate in the experiment. During this screening, the required coordination patterns were practised under all amplitude conditions in a session that lasted about 30 min. One potential subject did not meet the amplitude requirements (for specifications see Procedure), whereas another one was unable to perform the antiphase coordination pattern. The other eight subjects (one woman and seven men) were invited to take part in the experiment. They were all self-professed right-handers (mean age 27.3 years, range 24–35 years). The subjects gave their informed consent prior to participating in the experiment. They were paid for their services.

Experimental set-up. A vertical manipulandum connected to a rotatable horizontal lever that rested on a vertical axle was secured on a tabletop, with the vertical axis pointing downward through a hole in the tabletop surface (see Fig. 2). A DC potentiometer, connected to an A/D interface card (sampling rate 200 Hz, 12 bits/s, LabMaster) to a microcomputer (486 processor, 33

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[1] Note that if the stimulus frequency is not equal to the eigenfrequency of the oscillating limb (assuming it has one), a symmetry-breaking term ($\Delta\omega$: the difference in eigenfrequency of the two oscillating components) has to be incorporated in the potential function (e.g., Kelso et al. 1990). The resulting dynamics may include phase drift and phase wrapping. These phenomena are also observed for bidirectionally coupled systems with different eigenfrequencies (e.g., the coordination between an arm and a leg; Jeka and Kelso 1995).
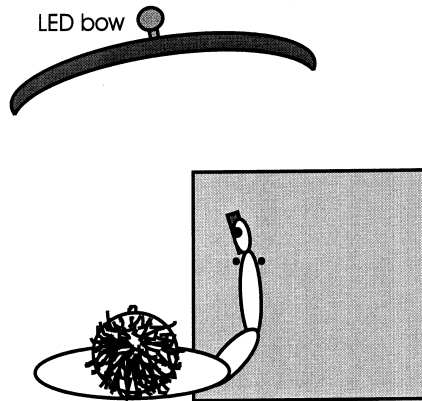
SIDE VIEW
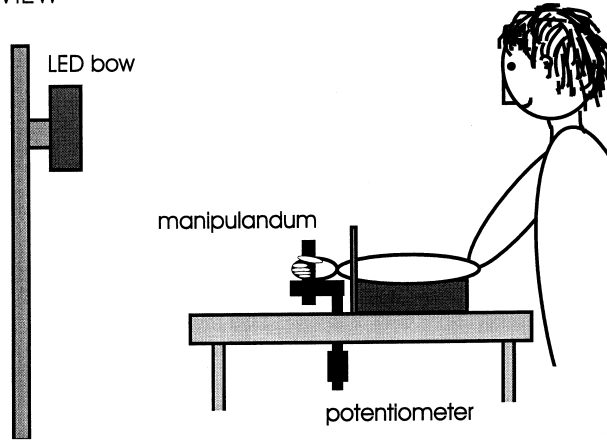
TOP VIEW

Fig. 2. Schematic representation of the experimental set-up

MHz), was attached to the lower end of the axle for registration of the angular position of the lever. A LED bow, on which an oscillating signal with adjustable amplitude and frequency could be presented, was positioned in front of the manipulandum at a distance of about 1 m. The setup was calibrated in such a way that the angular positions of the manipulandum matched those of the LED signal. Three amplitudes were used in the experiment: 5°, 15°, and 25°. (Note that the range of motion was twice the amplitude of oscillation.) These amplitudes were specified by means of static color-coded targets (width: ca. 1 cm) positioned just below the LED signal on the LED bow and by means of the LED signal itself.

Procedure. Subjects were seated in a chair close to the table on which the manipulandum was mounted, at a distance that fitted the individual body measures. They grasped the manipulandum with their right hand, and its position was adjusted in such a way that the wrist was located directly above the rotation point of the lever. The lower arm rested comfortably on an arm rest positioned on the table. To avoid sideward movements

of the wrist, the most distal part of the lower arm was secured between two vertical metal bars coated with foam-rubber. The position of these bars could be adjusted to fit each subject's wrist snugly.

The experiment consisted of two parts. In the first part, the preferred movement frequency was determined for each amplitude condition as well as for the preferred amplitude of oscillation. The four conditions (i.e., three prescribed amplitudes and the preferred amplitude) were presented blockwise (randomized order, five trials per block). The subjects were instructed to oscillate their hand at a comfortable frequency of oscillation while, for the prescribed amplitude conditions, the required amplitude was specified by the color-coded targets. Once a comfortable frequency was attained, the actual measurement (lasting 30 s) was started, during which the prescribed amplitude was also specified by means of two LEDs at the extremes of the required movement range. For each movement cycle, the amplitude of the hand movement was determined. If for a given trial more than 50% of the cycles were performed with an amplitude that differed by more than $\pm 5°$ from the required amplitude, the recorded data were deleted and the trial was rerun. Over subjects, the average number of rerun trials was 0.9 (range 0–2).

In the second part of the experiment, the LED signal oscillated (sine wave) in the horizontal plane. During a trial, its frequency was scaled from 1.0 to 2.8 Hz in 10 bins (0.2-Hz steps), consisting of 10 cycles each (trial duration 58.4 s). The subjects were instructed to oscillate their hand either in phase (same movement direction) or in antiphase (opposite movement direction) with this signal, while matching its amplitude. They were also told that they should not actively resist if the pattern changed during a trial (cf. Kelso 1995). The inphase and antiphase conditions were tested blockwise, counterbalanced over the subjects. Within these coordination mode blocks, the three amplitude conditions (5°, 15°, and 25°) were arranged in blocks (consisting of five trials each) which were presented in a random order. For each trial, the movement amplitudes were determined for each cycle and evaluated per frequency bin. If for any of the bins more than 50% of the movement amplitudes differed by more than $\pm 5°$ from the required amplitude, the data were deleted and the trial was rerun. Over subjects, the average number of rerun trials was 2.8 (inphase 3.1 [range 0–8]; antiphase 2.5 [range 0–4]).

Running the experiment took about 1.5–2 h. Between the first and the second part of the experiment and between the inphase and antiphase divisions of part 2, the subjects were allowed a rest period of approximately 10 min.

2.2 Analysis

The signals were low-pass filtered with a recursive second-order Butterworth filter, which was applied back and forth (cut-off frequency 15 Hz). A peak-finding algorithm was used to identify maximal extension and flexion for each cycle. Cycle frequency (in Hz) was

defined as the inverse of the period between two peak extensions; cycle amplitude (in degrees) was defined as the average of two adjacent extension-flexion, flexion-extension half-cycle excursions divided by 2.

For the frequency-scaled trials, point estimates of relative phase were determined using the maximal excursions in the visual signal (V) and in the recorded wrist movements (W). Relative phase (ϕ) was determined for every peak in the visual signal, resulting in two estimates of relative phase for each movement cycle. These were defined as $(t(V_n) - t(W_m))/(t(W_{m+1}) - t(W_m))\pi$, where t refers to the moment in time at which a given peak was attained and m and $m + 1$ refer to the indices of the two peaks in the wrist signal between which the considered peak in the visual signal (indexed by n) was situated in time.

For each bin in the frequency-scaled trials, the mean direction of relative phase, a measure of central tendency, was calculated following Mardia (1972; see also Batschelet 1981). In addition, the 'uniformity', of relative phase, which is a measure of variability for circular data, was determined. Uniformity takes values on the unit interval [0, 1], but can be transformed to the range of 0–∞ using:

$$s_0 = -2\ln(\sqrt{1 - S_0}) \tag{7}$$

where S_0 denotes the measure of uniformity on the unit interval [0, 1] and s_0 is the transformed uniformity measure. This measure is somewhat analogous to the sample standard deviation and permits the use of inferential tests based on standard normal theory (Mardia 1972). Note that larger values for transformed uniformity correspond to smaller variability.

On the basis of the transformed uniformity of relative phase, each bin was categorized as showing either stable or unstable behavior: A bin was considered to be performed in a stable fashion if the transformed uniformity was larger than 2.25. This criterion was chosen on the basis of detailed inspection of the data. To determine whether the correct phase relation was performed, a tolerance range of ±30° was used. As described in the Results section (Mean direction of initial relative phase), the subjects tended to perform both coordination patterns with a considerable offset, which probably resulted from the asymmetry in the experimental setup (see footnote 1). To deal with these phase shifts, the analyses not only included a tolerance range around the required frequency range, but also one centered around the mean direction of relative phase that was performed in the first bin. If, for a specific frequency bin, the performance was considered to be stable (i.e., transformed uniformity > 2.25), and the mean direction of relative phase was situated in either tolerance range, the performance was categorized as 'stable performance of the required coordination pattern'. The frequency that was performed in the first frequency bin for which these requirements were no longer met was adopted as the critical frequency (i.e., regardless of whether or not a transition to another phase relation occurred). In case the stability of the required phase relation was not lost, the maximal required frequency (2.8 Hz) was taken as the critical frequency.

3 Results

3.1 Part 1: Control trials

Amplitude. A one-way repeated measures ANOVA with the factor Amplitude (4 levels: small, middle, large, and preferred amplitude) performed on the amplitude of the hand movements revealed a significant effect (small 5.2°; middle 14.7°; large 25.4°; preferred amplitude 20.0°), $F(3, 21) = 118.4$, $P < .0001$. Post-hoc analysis (Newman-Keuls, $P < .05$) showed that all conditions resulted in significantly different movement amplitudes.

Preferred frequency. Although there was a tendency for the preferred frequencies to decrease with movement amplitude (small 1.56 Hz; middle 1.53 Hz; large 1.32 Hz; preferred amplitude 1.49 Hz), a one-way repeated measures ANOVA testing the effect of amplitude on preferred movement frequency revealed that these differences were not significant.

3.2 Part 2: Frequency-scaled trials

Accuracy of frequency tracking. To establish whether the subjects were adequately tracking the frequency of the visual signal across the frequency bins (1–2.8 Hz), Pearson's product-moment correlations were determined between the required and the actually performed frequencies for each of the 240 trials (30 trials per subject). For all subjects and conditions, the values of r were in the range from .97 to 1.00. In addition, the mean constant error in frequency (observed frequency − target frequency), averaged over frequency bins and amplitude conditions, was small (inphase 0.01 Hz; antiphase 0.02 Hz).

Movement amplitude. Movement amplitude was examined in a $2 \times 3 \times 10$ ANOVA, with the factors Coordination Mode, Amplitude, and Tempo. The effect of amplitude was significant (small 6.4°; middle 15.6°; large 25.1°), $F(2, 14) = 1702.8$, $P < .0001$. Post-hoc analysis (Newman-Keuls, $P < .05$) revealed that all three amplitude conditions resulted in significantly different movement amplitudes. The main effect of tempo was also significant, $F(9, 63) = 12.9$, $P < .0001$, resulting from decreasing amplitude with increasing tempo (Newman-Keuls post-hoc analysis, $P < .05$). In addition, the two-way interaction effects between Coordination Mode and Tempo and between Amplitude and Tempo were significant, $F(9, 63) = 9.2$, $P < .0001$ and $F(18, 126) = 3.7$, $P < .0001$, respectively, as well as the three-way interaction between Coordination Mode, Amplitude, and Tempo, $F(18, 126) = 4.0$, $P < .0001$. Post-hoc comparisons (Newman-Keuls, $P < .05$) revealed that the effect of tempo was stronger for the
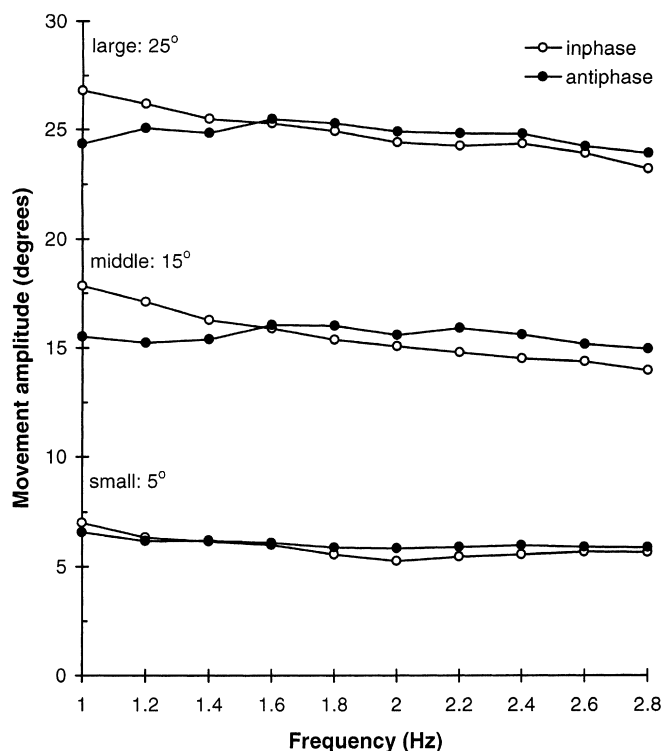
Fig. 3. Movement amplitude (averaged over subjects) as obtained for each amplitude condition, presented per frequency bin

inphase conditions than for the antiphase conditions, and that the decrease in amplitude with increasing tempo was more pronounced for larger required amplitudes (see Fig. 3). Interestingly, according to the post-hoc tests, no significant decrease in amplitude occurred in the antiphase trials for the small amplitude. For the middle amplitude, the antiphase trials showed only a significant difference between the first bin (1 Hz) and the last two bins (2.6 and 2.8 Hz).

Mean direction of initial relative phase. In a large number of trials, the subjects started off performing the required phase relation with a substantial phase shift in the first frequency bin (inphase $-38.1°$, SD $= 21.1°$; antiphase $-44.4°$, SD $= 21.4°$): In 99% of the trials, the wrist oscillations were leading the visual signal in time. The observed phase shift never exceeded $\pm 90°$, implying that the performed phase relation in the first frequency bin was always closer to the required phase relation (i.e., $0°$ or $180°$) than to the other coordination pattern (i.e., $180°$ or $0°$, respectively). This phase shift may have resulted from the asymmetry in the experimental setup, involving the coordination between a hand and an oscillating visual signal. A difference in eigenfrequency between two oscillating components has been demonstrated to lead to shifts in equilibrium phase (e.g., Schmidt et al. 1993; Sternad et al. 1992), which is in agreement with the extended version of the HKB model in which the difference in eigenfrequency ($\Delta\omega$) has been incorporated as a symmetry-breaking term (Kelso et al. 1990; see also footnote 1).

Variability of relative phase. A 2 (Coordination Mode) × 3 (Amplitude) × 10 (Tempo) repeated measures ANOVA on the transformed uniformity of relative phase revealed that performance was less variable (higher values for transformed uniformity) during the inphase trials (inphase 2.48; antiphase 2.14), $F(1, 7) = 73.9$, $P < .0005$. The effect of Tempo was also significant, revealing that with increasing movement frequency the variability of relative phase increased, $F(9, 63) = 10.74$, $P < .0001$. The effect of amplitude tended towards significance (small 2.22; middle 2.40; large 2.30), $F(2, 14) = 3.5$, $P < .1$. In addition, the interaction between Coordination Mode and Tempo resulted in a significant effect, $F(9, 63) = 3.7$, $P < .005$. Post-hoc analysis (Newman-Keuls, $P < .05$) revealed that for inphase coordination, the transformed uniformity decreased steadily over the frequency bins, indicating increasing variability. The decrease in transformed uniformity in the first four bins was stronger in the antiphase trials than in the inphase trials. Following a brief increase (see Fig. 4), the transformed uniformity obtained for the antiphase trials in the last four bins was not significantly different from the corresponding values obtained for the inphase trials.

Critical frequency. In all antiphase trials stability was eventually lost, whereas in 18% of the inphase trials (i.e., 22 trials) the required pattern was performed stably throughout the trial. A 2 × 3 repeated measures ANOVA with the factors Coordination Mode and Amplitude revealed that the critical frequencies obtained for the inphase trials (mean 2.37 Hz) were significantly higher than those obtained for the antiphase trials (mean 1.57 Hz), $F(1, 7) = 64.2$, $P < .0005$. In addition, the difference between the amplitude conditions was significant: The critical frequencies obtained for the small and large amplitudes (1.93 Hz and 1.94 Hz, respectively) were significantly lower than those obtained for the middle amplitude (2.04 Hz), $F(2, 14) = 4.2$, $P < .05$. However, if, for each individual subject, the critical frequencies were scaled to the mean preferred frequencies (f_{pref}) determined for each amplitude condition, a
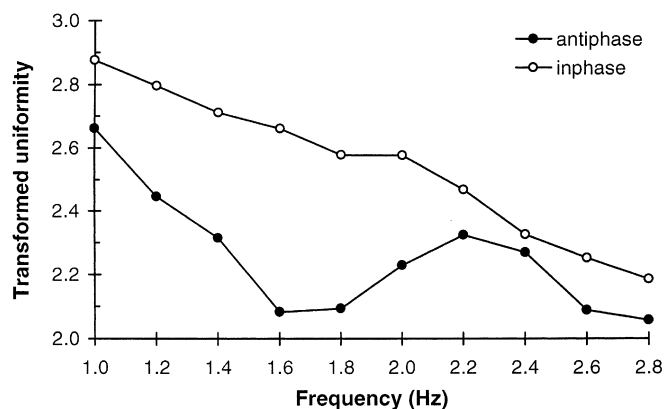

Fig. 4. Transformed uniformity of relative phase, averaged over subjects and amplitude conditions, presented for each frequency bin. Larger values reflect smaller variability

similar ANOVA revealed that only the difference between the two coordination modes (inphase $2.0 \times f_{pref}$; antiphase $1.3 \times f_{pref}$) was significant, $F(1, 7) = 36.6$, $P < .001$.

Transitions. As mentioned above, stability of performance of the required pattern was lost in all antiphase trials. In a subsequent analysis, it was determined whether this loss of stability of the required phase relation was followed by a transition to the inphase coordination pattern. Such a transition was deemed to have occurred if for at least two adjacent bins the mean direction of relative phase fell within the range of $-30°$ to $30°$ or, taking the initial phase shift into account, within the same tolerance range around the mean direction of relative phase performed in the first bin shifted by $180°$. In addition, these bins had to meet the criterion for stable performance (i.e., transformed uniformity of relative phase > 2.25). According to this analysis, loss of stability of the required coordination mode was in 57.5% of the antiphase trials (i.e., 69 trials) followed by a transition to the inphase pattern (see Fig. 5). The number of trials in which a transition occurred did not differ significantly over the amplitude conditions (small 55.0%; middle 62.5%; large 55.0%), $\chi^2(2) = 2.3$. A similar analysis performed on the inphase trials revealed that transitions to the antiphase pattern never occurred.

To examine whether loss of stability of the antiphase pattern was associated with the slight decreases in amplitude over the frequency bins that had occurred despite the task instructions (see Fig. 3), the mean amplitude in the transition bin was determined for each antiphase trial. This amplitude was compared with the mean amplitude attained in the first bin of the same trial to determine whether loss of stability of the antiphase pattern was associated with either a decrease or an increase in amplitude. Although the number of trials in which movement amplitude had decreased (68 trials; mean decrease $= -1.9°$; SD $= 1.8°$) was larger than the number of trials in which an increase was observed (52 trials;

mean increase $= 1.6°$; SD $= 1.3°$), this difference was not significant, $\chi^2(1) = 2.13$. The same analysis was performed on the subset of 69 antiphase trials in which a transition to the inphase coordination mode was observed. Again, the difference in the number of occurrences of either a decrease (37) or an increase (32) was not significant, $\chi^2(1) = 0.33$. For this subset of trials, the mean decrease in amplitude was $-1.6°$ (SD $= 1.5°$) and the mean increase was $1.7°$ (SD $= 1.5°$).

4 Discussion

The current formulations of the HKB model of coupled oscillators explain frequency-induced transitions from antiphase to inphase coordination on the basis of the inverse relation between movement frequency and amplitude. In the present study, using a unimanual tracking task, the frequency-amplitude relation was altered by means of the instruction to maintain a fixed amplitude while the movement frequency was increased. According to both the time derivatives and the time delays versions of the HKB model, an increase in movement frequency does not result in annihilation of the attractor for antiphase coordination when movement amplitude is constant. This prediction as well as related predictions regarding the effects of frequency and amplitude on pattern stability were examined by studying the behavior for three constant amplitude conditions.

The results revealed that for all amplitude conditions, transitions from antiphase to inphase coordination occurred in the majority of antiphase trials, even if the movement amplitude increased slightly during the trial. In addition, the variability of relative phase (a measure of pattern stability) was shown to be inversely related to the frequency of the oscillations, whereas no significant differences were obtained between the three amplitude conditions. These results indicate that, at least in the rhythmic tracking task examined, the effect of movement frequency on pattern stability is not, or at least not necessarily, mediated by a drop in movement amplitude. As such, they undermine an essential property of both the time derivatives and the time delays versions of the model, albeit that their implications are more damaging for the former than for the latter. The obtained results cannot be accounted for by the prevailing time derivatives version, because in this version of the model, the effect of movement frequency on pattern stability depends solely on the associated drop in amplitude. The occurrence of transitions despite constant or even slightly increasing movement amplitudes, however, can still be reconciled with the time delays version of the model, where movement frequency itself is associated with an overall decrease in pattern stability. Although also for this version of the model the deterministic aspect of the transition (annihilation of the attractor for antiphase coordination) depends on a drop in amplitude, frequency-induced transitions to inphase coordination may be argued to occur if the pattern stability becomes too small to resist the stochastic fluctuations in the
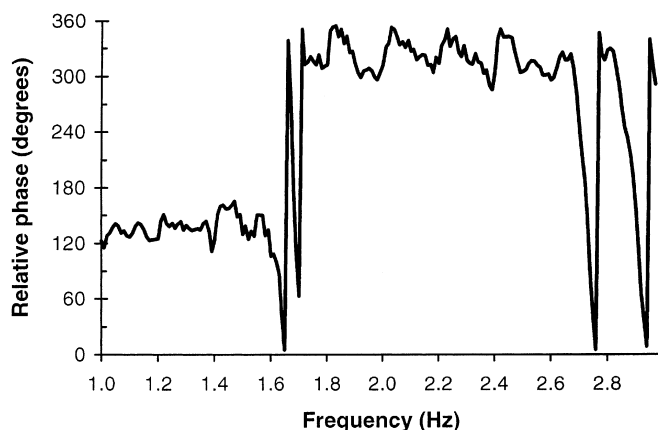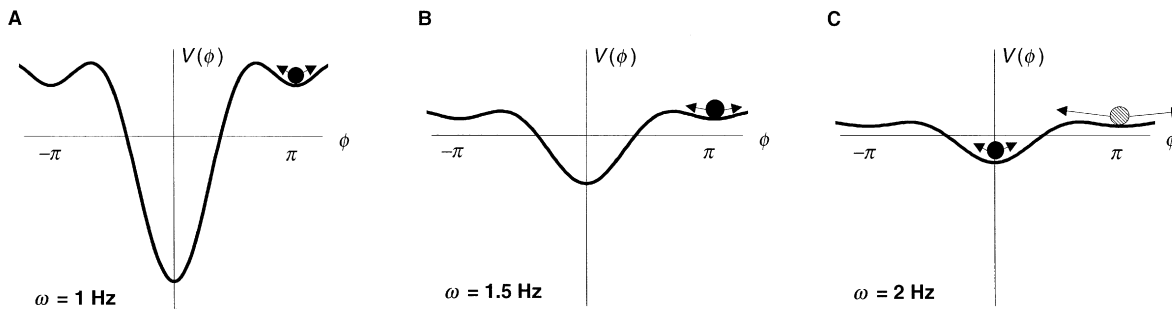

Fig. 5. A typical transition from antiphase to inphase coordination, as obtained for a single trial in the 'middle' amplitude condition. The start of each frequency bin is indicated on the *horizontal axis*

Fig. 6. The potential $V(\phi)$ for the time delays version of the HKB model with fixed parameters ($\alpha = -1$, $\beta = 0.11$) and constant amplitude ($r = 1$), presented for three different frequencies (ω). The effect of noise is schematically represented by the arrows. When frequency is increased, both attractors become less stable. As a result a noise-induced transition from antiphase to inphase coordination may occur when the antiphase attractor has become sufficiently unstable (grey instead of black ball in panel C)

system (cf. Schöner et al. 1986). Figure 6 indicates how even in case the amplitude remains constant, an increase in the movement frequency may result in a transition from antiphase to inphase coordination.

Although the occurrence of frequency-induced transitions can be understood, in line with Peper and Beek (1998), on the basis of the time delays version of the HKB model, the absence of systematic effects of movement amplitude on the number of transitions, pattern stability, and critical frequency seems to be at odds with both versions of the model. It may be, however, that pattern stability does not depend on the absolute amplitude of the movements, but rather on relative changes therein (with r being, for instance, normalized to the initial amplitude of oscillation). On the other hand, the absence of the predicted effects of movement amplitude on the stability of coordination may indicate that the spatial and temporal aspects of movement coordination were controlled relatively independently of each other. In this respect, the data are consistent with motor control models that assume that target position and movement speed are factorized, such as the VITE model for goal-directed arm movements (Bullock and Grossberg 1988).

In interpreting the results of the present study as well as those of Peper and Beek (1998), it is important to realize that they were obtained using specific experimental settings (unimanual tracking and multifrequency tapping, respectively), while movement amplitude was constrained by means of instruction. Whereas the current results indicate that transitions are not necessarily mediated by a drop in amplitude, this does not rule out the possibility that in rhythmic coordination without such spatial constraints, the drop in amplitude does play an instrumental role in inducing transitions from antiphase to inphase coordination. Therefore, it would be worthwhile to examine the relation between movement amplitude and pattern stability also for rhythmic performance without restrictions on the amplitude of oscillation. This may be accomplished by estimating the parameters a and b in (1) and by relating these estimated parameters to the frequency and amplitude of the movements (Peper and Beek 1998).

In principle, the parameters a and b can be estimated on the basis of the relaxation time (i.e., the time needed

to return to the original coordination pattern following a brief mechanical perturbation) as obtained for both antiphase and inphase coordination (Schöner et al. 1986) or on the basis of the stochastic properties of the otherwise unperturbed time evolution of relative phase. The latter possibility was recently pursued by Molenaar and Newell (1997), who estimated the evolution of the parameters a and b during experimental runs using a recursive fit procedure. Their estimations were based on the time series of ϕ during phase transitions that were obtained for rhythmic coordination between the two index fingers (i.e., the task for which the HKB model was originally formulated). Their results showed that although the ratio b/a indeed decreased when the frequency was scaled up, this decrease did not involve a differential decrease of the two parameters. On the contrary, whereas b gradually decreased, a was demonstrated to increase with increasing frequency. This finding challenges both versions of the model which predict that an increase in frequency is associated with decreasing values for both b and a, given the dependence on amplitude and, for the time delays version, movement frequency itself.

Whereas in many instances the dynamics of relative phase has been demonstrated to adhere to the HKB model or one of its more recent extensions (e.g., Kelso et al. 1990; Treffner and Turvey 1996), the current results, as well as those of Peper and Beek (1998) and Molenaar and Newell (1997), suggest that the HKB potential function, the validity of which has been well corroborated, is not yet accompanied by an equally well-validated system of coupled differential equations. Although the proposed versions of the coupled oscillator model result in the required order parameter dynamics and as such are consistent with the HKB potential function, the predicted relations between pattern stability and movement kinematics have not been fully corroborated. If the predicted relation between pattern stability and movement amplitude is not supported in future experiments either, the functional form of the coupling between the oscillators may have to be reformulated. This should be done in such a way that pattern stability is inversely related to movement frequency but remains unaffected by the associated changes in amplitude of oscillation.

Although various modeling strategies may be pursued, one possibility would be that frequency-induced changes in the kinematics of the oscillating limb(s), such as the drop in amplitude with increasing frequency (cf. Beek et al. 1996; Kay et al. 1987), result from biomechanical properties of the end effector(s) and do not play a role in the neural coupling underlying the coordination between limb movements. If this is the case, a two-tiered rather than a single-level model has to be developed in which a system of neural oscillators interacts with the dynamical properties of the end effector(s). Such a two-tiered model will have the additional advantage that it may account for the negative lag-1 autocorrelations that are typically obtained for unimanual rhythmic tapping (cf. Wing and Kristofferson 1973), given the fact that a dynamical model of two coupled oscillating components with an additional noise source has been shown to produce this characteristic aspect of the temporal variability of performance (Daffertshofer 1998).

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