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Relative phase dynamics in perturbed interlimb coordination: the effects of frequency and amplitude

A. A. Post, C. E. Peper, P. J. Beek

Institute for Fundamental and Clinical Human Movement Sciences, Faculty of Human Movement Sciences, Vrije Universiteit, Amsterdam, The Netherlands

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Abstract. Schöner [Schöner G (1995) Ecol Psychol 7: 291–314] argued that the relative phase dynamics of rhythmic interlimb coordination may be attributed to the timing level in that the stability properties of the relative phase are largely independent of dynamical principles operating at the goal level, such as those related to the maintenance of a particular amplitude or target position. Yet, according to the coupling functions in the coupled oscillator model proposed by Haken et al. [Haken H, Kelso JAS, Bunz H (1985) Biol Cybern 51: 347–356], the effect of frequency on the stability properties of relative phase is either wholly or partially mediated by frequency-induced changes in amplitude, implying that the relative phase dynamics strongly depends on spatial factors. In order to distinguish between these contrasting interpretations of the organizational principles underwriting the phase dynamics of interlimb coordination, an experiment was conducted in which the effects of frequency and amplitude on the stability of relative phase were separated. Six subjects performed both in-phase and anti-phase coordination patterns at seven different frequencies and three different amplitudes. Two measures of pattern stability were used, the standard deviation of relative phase and the exponent of the relaxation process following phasic perturbations of relative phase. According to both measures, pattern stability decreased with increasing frequency, whereas the amplitude manipulation only had a significant effect on the standard deviation of relative phase. This result was interpreted to imply that the organizational principles at the (relative) timing level are affected only moderately by task constraints pertaining to the goal level, and that models of interlimb coordination in which amplitude coupling plays a partial or subordinate role should be preferred above models relying solely on amplitude coupling.

Correspondence to: A. A. Post
(e-mail: auke.post@fbw.vu.nl, Tel.: +31-20-4448454,
Fax: +31-20-4448509)

1 Introduction

A central and longstanding question in the study of motor control is: what variables are controlled by the central nervous system (cf. Stein 1982)? In this context, controlled variables are often defined as those variables that can take on new values independently of other controlled variables as conditions are changed (Latash 1993; cf. Schöner 1995). The assumption of mutual independence of controlled variables is essential in view of the fact that the human actor can perform a large variety of tasks in a multitude of manners: we can move to a particular location slowly or quickly, we can grasp an object firmly or gently, we can adopt a particular posture stably or unstably, and so on.

In extant models of motor control, these behavioral possibilities are accounted for by means of a small, but sufficiently large set of controlled variables that minimally allow for independent regulation of end point, speed and stiffness (tension). Two examples may serve to illustrate this point, the λ model of Feldman (1986) and Latash (1993), and the combined VITE-FLETE model of Bullock and Grossberg (1988, 1989). The λ model for (single-joint) motor control capitalizes on the "spring-like" properties of muscles instantiated by the tonic stretch reflex (Feldman 1980a,b; Latash 1993). According to this model, joint position is controlled by means of r commands, defining the intercept of the joint compliant characteristic, and joint stiffness by means of c commands defining the slope of the joint compliant characteristic, where the r and c commands are assumed to be controlled independently of each other. Movement speed is controlled indirectly by means of the time courses of the postulated r and c commands. In contrast to the λ model, which is based on the premise that the nervous system controls the threshold (λ) of the tonic stretch reflex, the combined VITE-FLETE model is built on the assumption that muscle length itself is a controlled variable. In addition, independent controls of movement speed and stiffness are postulated. Specifically, this model assumes a target position command for controlling the end position of the movement (in the

form of a multidimensional vector of muscle lengths), a GO-signal for controlling movement time (or speed), and a *P* command for controlling tension. In spite of the non-trivial differences between these two models, the independence of the variables allegedly controlled by the nervous system is postulated a priori in both models.

1.1 Levels in neural functioning

A different tack on the issue of controlled variables was proposed by Schöner (1995). He defined controlled variables as those measures of behavior that are stable against phasic (transient) perturbations, opening up the possibility of examining experimentally which variables are controlled by the nervous system. In this perspective, the term stability refers to the asymptotic stability of invariant solutions in dynamical systems, that is, after a phasic perturbation has driven the system away from an invariant solution, it will return to that solution after a certain relaxation time. For instance, if the relative phasing between two limbs moving rhythmically at the same frequency is perturbed mechanically (e.g., Scholz and Kelso 1989; Scholz et al. 1987), thus momentarily changing its value, it will return spontaneously to its pre-perturbation value. Likewise, if a goal-directed movement is perturbed by displacing the target, the end-effector will still reach the target (e.g., Georgopoulos et al. 1981; Prablanc and Martin 1992). Finally, in producing an isometric torque of an externally specified strength (i.e., target force level), small perturbations due to noise are known to lead to small initial errors that are counteracted by means of compensatory adjustments in the force trajectories (Gordon and Ghez 1987). Thus, in these examples, relative phase, target posture and target force are controlled variables in the sense that they are characterized by invariant solutions that are stable against brief, transient perturbations.

Schöner's definition (1995) of controlled variables is closely allied to his operationalization of levels in the behavioral analysis of neural functioning. A prerequisite for the identification of different levels of neural functioning is that behavioral components or dimensions associated with these levels are only weakly coupled. This may be assessed by means of perturbation techniques, as each level is deemed to stabilize a particular feature of behavior against a particular kind of perturbation. Schöner (1995) distinguished three such levels, the load level, the timing level and the goal level. The load level is defined as the set of dynamic variables that stabilizes against force perturbations, the timing level as the set of dynamic variables stabilizing against perturbations of (relative) timing, and the goal level as the level at which global properties of the movement trajectory, such as amplitude and target position, are stabilized. Each of these levels might be studied in isolation by experimental variations that minimally affect the two other levels. For example, in experiments on relative timing, a gradual increase of movement frequency has been shown to induce a differential loss of the stability of the in-phase and anti-phase modes of coordination (Kelso 1984; Schöner and Kelso 1988) without, however, affecting the load and the goal level. According to Schöner (1995), this can be inferred from the fact that the mechanical coupling between the moving fingers is negligible, while the relevant frequencies are all well within the range of frequencies attainable with ease and constant precision in single-limb movement. Thus, according to Schöner (1995), the observed coordination phenomena, including the loss of stability of the anti-phase pattern, could be attributed exclusively to the timing level.

The aforementioned conclusion seems quite justified in view of the fact that the relative timing experiments in question only involved the bimanual production of the in-phase and anti-phase coordination, while the amplitudes (i.e., the turning points) of the individual limb movements were free to vary. However, in these experiments, the gradual increase of movement frequency led to a systematic decrease of movement amplitude, suggesting that the relative phasing task involved an implicit adaptation of the global properties of the movement trajectories. In fact, this frequency-induced decrease in movement amplitude was modeled by Haken et al. (1985) as the 'formal mechanism' through which the differential loss of stability of the in-phase and anti-phase mode of coordination, including the loss of stability of the anti-phase mode, occurred (cf. Peper and Beek 1999). Thus, there is an interesting tension between the implications of the theoretical notions developed by Schöner (1995), which may be taken to imply that variations in target position (for discrete tasks) or amplitude (for cyclic tasks) would have no or little effect on the stability of relative phase, and the assumption of the Haken-Kelso-Bunz (HKB) model (Haken et al. 1985) that the effect of frequency on the stability of relative phase is mediated (fully or partially, see later) by movement amplitude.

In recognition of the importance of these contrasting interpretations for the issue of levels in the neural control of movement and their relative independence, we conducted a perturbation experiment that was designed to assess the differential effects of frequency and amplitude on the stability properties of relative phase. It follows from the preceding discussion that the goal of this experiment was twofold. It aimed to contribute to the theoretical framework proposed by Schöner (1995) by determining whether the organization of the stability properties of relative phase are indeed relatively independent of experimental manipulations referring to the goal level. Additionally, it aimed at a direct empirical test of the assumptions underlying the coupling functions proposed by Haken et al. (1985) in their (nonlinear) coupled oscillator model for bimanual rhythmic coordination. In view of this second goal, it is necessary to explain the HKB model in some detail and to briefly summarize previous research on the effects of frequency and amplitude on the stability of coordination.

1.2 The HKB model: amplitude influences pattern stability

The HKB model (Haken et al. 1985), which was originally developed for bimanual 1:1 frequency coordination, consists of two parts, the level of the so-called potential and the level of coupled oscillators. The potential formalizes the stability properties of the relative phase ϕ between the limbs (the variable capturing the coordination phenomena of interest) in terms of a two-well potential landscape that is deformable as a function of the parameters a and b

$$V(\phi) = -a\cos\phi - b\cos 2\phi \ . \quad (1)$$

The minima of this potential represent the coordination modes to which the behavior is attracted, implying that the in-phase ($\phi = 0°$) and anti-phase ($\phi = 180°$) coordination patterns are stable. Extensions of this model have been formulated, incorporating the impact of frequency differences between the oscillating components and the influence of stochastic forces. When the dynamics of the relative phase is expressed in terms of the corresponding order parameter equation [with $\mathrm{d}\phi/\mathrm{d}t = -\mathrm{d}V(\phi)/\mathrm{d}\phi$], the additional influences of noise can be incorporated (Schöner et al. 1986)

$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = -a\sin\phi - 2b\sin 2\phi + \sqrt{Q}\xi \ . \quad (2)$$

This fundamental coordination equation has provided the theoretical framework and motivation for a large number of experimental studies focusing on the effect of frequency on the stability properties of relative phase (as mediated by the ratio between the parameters b and a in Eq. 2). Virtually all studies involving stationary performance employ the standard deviation of relative phase (or its circular equivalent) as a measure of stability. However, a more direct measure for stability can be obtained by perturbing the steady state, yielding an estimate of the strength of the relaxation process of relative phase (Schöner et al. 1986). This method has been applied successfully by Post et al. (in press), who compared these two stability measures and estimated the parameters a, b and Q of the stochastic version of the HKB model.

In contrast to the level of the potential, the level of coupled oscillators has received only limited attention. At this level, the full kinematics of the oscillating limbs and their interactions are modeled as a system of nonlinearly coupled nonlinear oscillators. Two elementary coupling functions have been formulated, namely the time derivatives and time delay version (see Sect. 2.5 for details), which differ with respect to the way in which the oscillators are supposed to be coupled. Although, in both versions, frequency-induced transitions from anti-phase to in-phase coordination are mediated by a frequency-induced drop in amplitude in the component oscillators, the predicted effects of frequency and amplitude on pattern stability are not identical. According to the time derivatives version, the stability properties of relative phase depend solely on amplitude, whereas the time delay version implies that these properties are affected by both frequency and amplitude.

To date, these predictions have never been tested in the context of a bimanual 1:1 frequency coordination task. They have been investigated, however, in the context of a unimanual rhythmic tracking task (Peper and Beek 1998a) and in the context of a bimanual multifrequency coordination task (Peper and Beek 1998b). By dissociating frequency and amplitude through experimental manipulation, these two studies sought to test the predicted effects of these variables on pattern stability in a different task domain. In the unimanual coordination experiment, arm-stimulus coupling was investigated on the basis of transition trials, using both the critical frequency and the standard deviation of relative phase as stability measures. In the bimanual coordination experiment, involving a multifrequency tapping task, Peper and Beek (1998b) used the degree of harmonicity of the movement trajectories in steady-state trials as an index of coupling strength (i.e., pattern stability). Whereas both experiments showed an inverse relationship between movement frequency and the stability-related measures, the predicted relation between movement amplitude and stability was not supported. In order to establish the generalizability of these studies, further experiments are required. Moreover, a motivated choice between (or against) the coupling functions formulated by Haken et al. (1985) calls for an experiment on 1:1 bimanual coordination for which the model was originally formulated. The present perturbation experiment allowed for testing the effects of amplitude and frequency on pattern stability using the strength of the relaxation process after perturbation as a direct measure of stability. Additional in-depth analyses with regard to specific model predictions were conducted on the basis of estimated values of the coupling parameters α and β.

1.3 Experiment

In the present experiment, the effects of frequency and amplitude on the stability of relative phase were tested in separate conditions by applying phasic mechanical perturbations. These effects were assessed using two measures of pattern stability: the standard deviation of relative phase SD(ϕ) and the decay parameter λ.[1] On the basis of Schöner's analysis (1995) of neural functioning, it was expected that the timing level would remain only weakly coupled to the goal level and that therefore the stability properties of variables pertaining to the timing level would be relatively insensitive to experimental manipulations referring to the goal level; more specifically, amplitude manipulation would have little or no effect on the stability of relative phase, whereas frequency as such would be inversely related to pattern stability. With regard to the second objective of the study, qualitative predictions pertaining to the effects of

[1] For denoting the decay parameter, we used λ instead of β (cf. Beek et al. 1995; Post et al. in press) as, following Haken et al. (1985), the latter was reserved to denote one of the coupling parameters.

frequency and amplitude on the coupling parameters followed from the time derivatives and the time delay coupling version of the HKB model, respectively. Contrary to the expectation formulated above, a positive relation between amplitude and pattern stability [i.e., larger amplitudes are associated with smaller SD(ϕ) and larger λ] was expected from the time derivatives version, whereas frequency as such was predicted to have no effect on stability. On the basis of the time delay version, however, the stability of performance was expected to depend on both amplitude (positively related) and frequency (inversely related). In addition to testing these predictions qualitatively, the parameters of the HKB model were estimated, both at the level of coupled oscillators and at the level of the order parameter equation (for specific predictions see Sect. 2.5).

2 Method

2.1 Subjects

Six healthy female volunteers (aged 20–27 years) participated in the experiment after having given their informed consent. They were all right-handed according to their scores on a Dutch version of the Edinburgh handedness inventory (Oldfield 1971). The subjects were selected on the basis of their ability to perform in-phase and anti-phase movements successfully in the experimental amplitude and frequency ranges. Successful performance was operationalized as the completion of an unperturbed pilot trial at a given combination of amplitude and frequency without loss of coordination. A maximum of five attempts per amplitude/frequency level was allowed.

2.2 Apparatus

Subjects were seated in a modified chair. Each forearm rested comfortably in a premolded carbon fiber splint mounted on a vertical axis, which was fitted into a slider to permit placement of the *epicondilus medialis* of the subject's elbow above the center of rotation. The arm rests were vertically adjustable. The splints allowed for flexion and extension around the elbow in the horizontal plane only, in a range of approximately 120°. The angular position of each axis was measured with a hybrid potentiometer (22HHPS-10, Sakae). A Digital Actuator Controller (developed by Fokker Aerospace) yielded positional data with an accuracy of 0.2°. A sampling rate of 300 Hz was used in all trials. In the frequency-paced conditions, computer-generated auditory stimuli (50 ms, pitch 440 Hz) were presented by means of two speakers. In the prescribed-amplitude conditions, two target light-emitting diodes (LEDs) were presented on two LED bows (one for each arm), defining the targets for maximal excursion of the manipulanda. Each LED bow consisted of two curved displays (30° segments of a circle with a radius of 2 m) on which a horizontal series of light-emitting diodes was mounted. Subjects received continuous feedback on amplitude by means of two laser diodes (5 mV) that were attached to the splints and projected the position of the manipulandum onto the LED bow. Data were stored for further analysis.

2.3 Procedure

Each subject was trained in session 1 and subsequently tested in sessions 2–5. Three factors were manipulated: coordination mode (in-phase and anti-phase), frequency [unpaced and paced (seven conditions, ranging over 0.75–2.25 Hz, in steps of 0.25 Hz)], and amplitude[2] [preferred and prescribed (three conditions: 0.1, 0.2 and 0.3 rad, further referred to as small, medium and large)]. Subjects were required to flex both forearms simultaneously with the tones of the pacing signal in the in-phase trials. In the anti-phase trials, they were instructed to flex the right arm and extend the left arm on each tone. In the training session, subjects performed unperturbed trials for each prescribed amplitude level with all frequency pacing levels nested within it in ascending order. This procedure was followed first for in-phase, then for anti-phase coordination. Training in a given condition was continued until certain amplitude requirements were met (mean absolute error of amplitude ≤ 0.025 rad; number of cycles with absolute amplitude error larger than 0.05 rad ≤ 2). The trial length was 15 cycles in all conditions. As each subject performed a different number of trials in session 1, depending on their learning rate, the duration of this session varied.

Regarding the experimental sessions, preferred-amplitude trials were collected in session 2. Trials were grouped together in two 'coordination mode' blocks, which were presented in the same order to each subject (first in-phase, then anti-phase). Within each block, one unperturbed trial and five perturbed trials were presented for each of the eight frequency levels.[3] The trial order was fully randomized within a block. The six prescribed-amplitude blocks were presented in sessions 3–5 (two blocks/session). The three in-phase blocks were presented first to each subject in randomized order (session 3, first half of session 4), after which the anti-phase blocks followed in the same fashion (second half of session 4, session 5)[4]. Trial randomization within a block was realized in the same fashion as described for session 2.

A mechanical perturbation was applied close to a particular phase in the movement cycle (the moment of zero velocity at peak elbow extension), thus avoiding

[2] Amplitude was defined as range (peak-to-peak) divided by two. 0.1 rad = 5.7°, 0.2 rad = 11.5°, 0.3 rad = 17.2°.

[3] For this session, the subjects inadvertently received four perturbed trials for the preferred-frequency conditions. In all other conditions the subjects received five perturbed trials.

[4] In-phase and anti-phase conditions were presented in this order since subjects were not able to perform the more difficult (anti-phase) condition without being accustomed to the amplitude requirements.

large changes in kinetic energy. In view of the finding that the choice of a particular phase has no effect on the strength estimate of the relaxation process after mechanical perturbation of a limit cycle (cf. Kay et al. 1991), no other perturbation phases were considered. The perturbation was applied randomly between cycles 12 and 17 of the trial. The moment of perturbation onset was extrapolated on-line from the eight preceding movement cycles. The strength of perturbation was infinitely decelerative, resulting in a complete arm arrest, and had a duration of 0.25 of the cycle time (corresponding to 90°).

To insure that the amplitude requirements were met, the average amplitude during the pre-perturbation segment was evaluated upon completion of each trial. When the amplitude criteria (mean absolute error of amplitude ≤ 0.025 rad; number of cycles with absolute amplitude error larger than 0.05 rad ≤ 2) were not met, the trial was repeated once. The trial length was 32 cycles in all conditions (resulting in a variable trial duration in seconds) except in the preferred-frequency condition (fixed trial length of 48 s). Each experimental session lasted approximately 2 h, including breaks.

2.4 Data reduction

Angular position data were differentiated with a five-point approximation algorithm into angular velocity data, which were subsequently low-pass filtered (bi-directional second-order Butterworth filter, cutoff frequency 25 Hz). Peaks were extracted from the position and velocity time series for estimation of frequency, amplitude, and peak velocity. The position signal was normalized by multiplying it with the within-trial mean of angular frequency (cf. Beek and Beek 1988). After conversion to polar coordinates, the normalized continuous phase angle ϕ_i was determined for each hand, using $\phi_i = \arctan(\dot{x}_i/x_i^*)$, with x_i^* denoting normalized position, $\dot{x}_i$ denoting velocity, and i indicating sample index. The continuous relative phase (ϕ) was calculated as $\phi = \phi_{\text{right}} - \phi_{\text{left}}$. Three segments of each trial were selected for further analysis: a pre-perturbation segment (the eight cycles prior to perturbation onset), a perturbation return segment (3 s following perturbation offset), and a post-perturbation segment (the eight cycles following the perturbation return segment).

2.5 Analysis

2.5.1 Stationary performance. The steady-state behavior was evaluated on the basis of the mean values and coefficients of variation (CV) of frequency, amplitude and peak velocity, as well as the mean ϕ and its standard deviation [SD(ϕ)]. These measures were calculated separately for the pre-perturbation and post-perturbation segments. Frequency (in Hz) was defined as the inverse of the average time elapsed between positive peaks in the position signal; amplitude (in degrees) was defined as the average angular distance between peak flexion and extension divided by two.

2.5.2 Pattern stability. Two measures of stability were used: SD(ϕ) and the strength of the relaxation process following a perturbation (λ). SD(ϕ) was calculated as described previously. The strength of the relaxation process was determined in the following fashion. The return signal after perturbation (ϕ^*) was defined as the difference between the actual return trajectory of relative phase (ϕ_{return}) and the pre-perturbation average of relative phase ($\bar{\phi}_{\text{pre}}$):

$$\phi^* = \phi_{\text{return}} - \bar{\phi}_{\text{pre}} \ . \tag{3}$$

In general, the strength of attraction, which is inversely related to the relaxation time τ_{rel}, may be estimated by determining the exponential decay parameter λ,

$$\phi^*(t) = p + q\mathrm{e}^{-\lambda t} \ , \tag{4a}$$

where p is the offset and $q = \phi^*_{t=0} - p$. Large values of λ correspond to a rapid decay (cf. Schöner et al. 1986; Beek et al. 1995), and thus to short relaxation times. To allow for the application of the local linear approximation, according to which $\sin\phi \approx \phi$ (Schöner et al. 1986), the exponential fit had to be limited to the vicinity of the desired relative phase. This was operationalized by starting the fit (i.e., $t = 0$) at the point in the return segment at which ϕ^* reached 45°, on average resulting in removal of the first 9% of the return signal (mean 0.28 s, SD 0.14 s).

In line with previous findings (Post et al. in press), visual inspection of the return data revealed that the relaxation process was sometimes compromised by damped oscillations of the kind depicted in Fig. 1A and B. To accommodate the occurrence of oscillations in the obtained return signals, a modified version of the fitting procedure described by (4a) was applied:

$$\phi^*(t) = p + q\mathrm{e}^{-\lambda t}\cos(\omega_\phi t + \theta) \ , \tag{4b}$$

where ω_ϕ is the oscillation frequency of ϕ, and θ denotes the phase of this oscillation (see Post et al. in press). In this way, extreme sensitivity to the initial decrease of the return signal was avoided, as is illustrated in Fig. 1A and B. The procedure did not affect the fit of trials without such oscillations (see Fig. 1C and D).

Trials were excluded from analysis if one of the following criteria was met: (a) the initial coordination mode was not re-established after the perturbation ($|\bar{\phi}_{\text{pre}} - \bar{\phi}_{\text{post}}| > 90°$); (b) $\phi^* > 45°$ for the entire return signal, rendering the local approximation interpretation inadequate; (c) no stable pre- or post-perturbation behavior was established [SD($\phi_{\text{pre,post}}$) > 45°]; (d) the return signal was not a decay function within the observation interval ($\lambda < 0$); (e) the fit was unreliable [SE(λ) > median(λ)]. On the basis of these criteria, 403 of the 1908 perturbed trials (i.e., 21%) were excluded. The number of excluded trials did not differ significantly over coordination mode (anti-phase: 231, in-phase: 171), $\chi^2(1) = 2.39$, frequency (preferred: 41, 0.75 Hz: 30, 1.0 Hz: 47, 1.25 Hz: 51, 1.5 Hz: 55, 1.75 Hz: 54, 2.0 Hz: 60, 2.25 Hz: 64), $\chi^2(7) = 3.89$, or amplitude (preferred, 58; small, 123; medium, 108; large, 113), $\chi^2(3) = 4.28$.

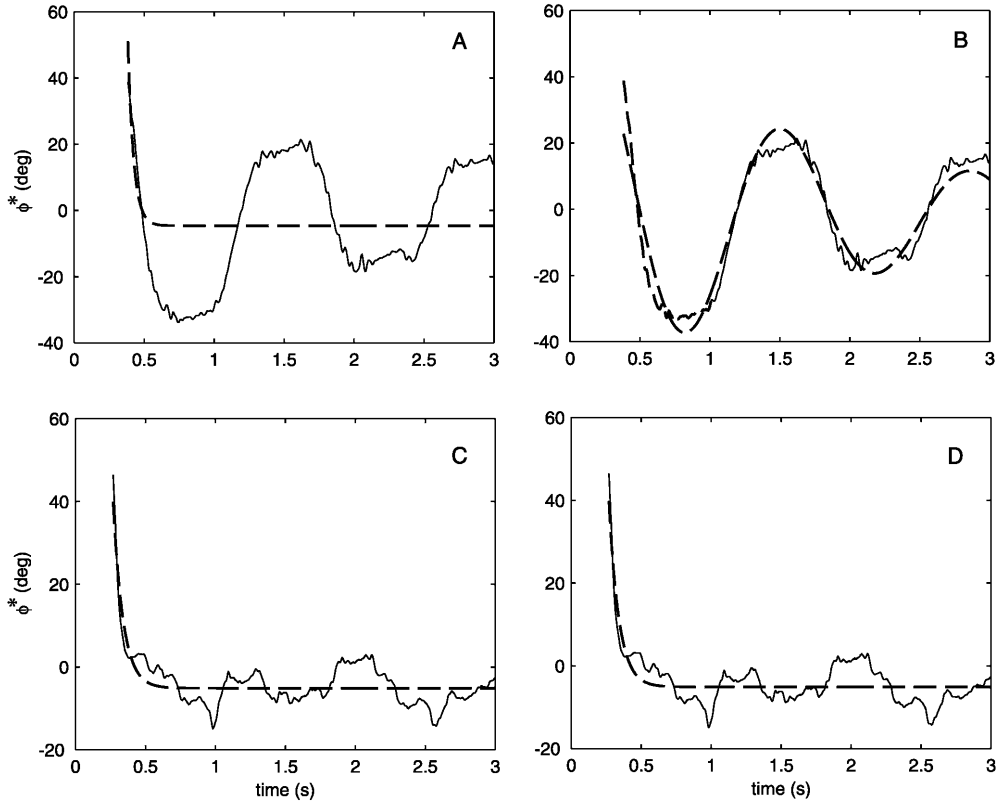

Fig. 1A–D. *Upper panels* Comparison between $\phi^*(t)$ (*solid line*) and model fit (*dashed line*) for a representative trail with oscillations in ϕ. **A** Using (4a) ($\lambda = 28.2$, $r^2 = 0.07$). **B** Using (4b) for the same trial ($\lambda = 1.1$, $r^2 = 0.83$, $\omega_\phi = 0.73$ Hz). *Lower panels* The same comparison for a trial without such regular oscillations: **C** Using (4a) ($\lambda = 14.0$, $r^2 = 0.63$). **D** Using Eq. (4b) for the same trial ($\lambda = 13.9$, $r^2 = 0.63$, $\omega_\phi = 0.0002$ Hz)

In 11 trials, a stable coordination mode was established after the perturbation, but not without a phase shift of 360° (i.e., one arm 'jumped' a full cycle ahead of the other). Since the fit procedure was based on a local approximation (i.e., $\phi^* < 45°$) these trials were not excluded from further analysis.

The fits were performed using the nonlinear Gauss–Newton algorithm with Levenberg–Marquardt modifications for global convergence (available in the Matlab statistics toolbox). To ensure that the fit did not depend on a local optimum in parameter space, each trial was fitted with four different initial values for λ (i.e., 1, 2, 5, 10). The fit with the highest r^2 was selected for further analysis. Median values[5] of λ were calculated for each experimental condition. Group values were derived by averaging the so-obtained values over subjects for each condition.

2.5.3 Coupling between limb and pacing signal. To verify that the response to the perturbation resulted from the coupling between the limbs rather than from a unilateral coupling between the perturbed limb and the pacing signal, the phase relations with the pacing signal before and after the perturbation were examined. In view of the discrete nature of the pacing stimuli, this analysis was based on point estimates of relative phase (cf. Beek et al. 1996). The point estimates of relative phase (θ_R and θ_L) between each individual arm and the pacing signal were calculated for the pre- and post-perturbation segments. To investigate whether a systematic offset between the pre-perturbation and the post-perturbation steady state occurred in the perturbed frequency-paced trials, the phase difference was calculated as $\Delta\theta_{R/L} = \bar{\theta}_{R/L,post} - \bar{\theta}_{R/L,pre}$.

To establish whether this phase relation indeed depended on the pacing signal rather than being the consequence of an endogenous 'clock', the phase development of each arm during the unprescribed perturbed trials was also examined. Since point estimates of relative phase (θ) are (by definition) not obtainable for these trials, right and left continuous phase (ϕ_R and ϕ_L) were used instead. ϕ_R and ϕ_L were calculated using the following procedure. The phase time series were unwrapped to convert them into a monotonically increasing series. Subsequently, the pre-perturbation segment, representing the steady-state behavior of the oscillating limb, was selected. The slope of this segment was calculated, and served as the basis for detrending the entire unwrapped phase time series. For each arm, the phase difference was then calculated as $\Delta\bar{\phi}_{R/L} = \bar{\phi}_{R/L,post} - \bar{\phi}_{R/L,pre}$.

2.5.4 Parameters a, b and Q (order parameter equation). Schöner et al. (1986) demonstrated that the parameters a and b in (2) can be estimated when the relative phase dynamics is linearized in the vicinity of the stable values of relative phase. The so-obtained local potentials (one for in-phase and one for anti-phase coordination) allow for the estimation of a and b when

[5] Throughout the analyses, median values were calculated instead of mean values in case the set of values for a given dependent variable was characterized by outliers.

the relaxation times for both coordination patterns are established at a fixed frequency of performance. An elegant feature of this method is that the estimations are based on the form of the potential well, which determines the swiftness of return. According to Schöner et al. (1986), the relative phase relaxation after perturbation [with ϕ for the in-phase mode, and $\varepsilon = (\phi - 180°)$ for the anti-phase mode] is characterized by

$$\phi(t) = \phi_0 e^{-(4b+a)t}, \quad \varepsilon(t) = \varepsilon_0 e^{-(4b-a)t} \ . \tag{5}$$

As the inverse of the exponential decay parameters can be equated with the local relaxation times (Schöner et al. 1986), this yields (using Eq. 4a)

$$\lambda_{in} = 1/\tau_{rel,in} = 4b + a, \quad \lambda_{anti} = 1/\tau_{rel,anti} = 4b - a \ . \tag{6}$$

Note that the inclusion of an oscillatory process (cf. Eq. 4b) does not affect the relation between λ and τ_{rel}. Equation (6) is easily solved for a and b:

$$a = \frac{\lambda_{in} - \lambda_{anti}}{2}, \quad b = \frac{\lambda_{in} + \lambda_{anti}}{8} \ . \tag{7}$$

Thus, the values of a and b were estimated per subject for each frequency level, using the median values of λ calculated for each condition. Group values were obtained by taking the median values of a and b over subjects for each frequency level.

Following Schöner et al. (1986) and Post et al. (in press), the noise level Q was estimated using λ and the absolute mean of ϕ ($\langle|\phi|\rangle_{stat}$) and its SD ($\sqrt{\sigma_{stat}}$), as determined for the pre-perturbation segment. For the in-phase mode, this was accomplished using

$$Q_{in} \approx 2\lambda_{in}\left(\sigma_{stat,in} + \langle|\phi|\rangle_{stat}^2\right) \ . \tag{8}$$

Similarly, for the anti-phase mode (with $\varepsilon = \phi - 180°$), the estimates were obtained using

$$Q_{anti} \approx 2\lambda_{anti}\left(\sigma_{stat,anti} + \langle|\varepsilon|\rangle_{stat}^2\right) \ . \tag{9}$$

Thus, Q was estimated for separate trials [using λ, mean ϕ, and SD(ϕ) as determined for each individual trial]. Group values were obtained by averaging the values of Q over subjects for each experimental condition.

2.5.5 Parameters α and β (coupling function). In examining the validity of the proposed coupling functions, it is useful to estimate the corresponding parameter values. To date, few (successful) efforts have been made to estimate the values of the coupling parameters α and β. The attempt of Beek et al. (1996) to estimate these parameters[6] from the level of coupled oscillators led to unreliable results due to a concatenation of estimation errors. In the current context, however, the coupling parameters α and β could be readily obtained on the basis of the estimated exponential decay parameters.

According to the time derivatives version, the stability of relative phase varies solely as a function of movement amplitude, that is, the effect of frequency on pattern stability is fully mediated by amplitude. As frequency increases amplitude drops, resulting in a differential loss of stability of the in-phase and anti-phase solutions of relative phase described by

$$\frac{d\phi}{dt} = (\alpha + 2\beta r^2)\sin\phi - \beta r^2 \sin 2\phi \ , \tag{10}$$

where $\alpha + 2\beta r^2 = -a$ and $\beta r^2 = 2b$ (cf. Eq. 2). The parameters α and β are coupling parameters (and are assumed to be constant within a trial), and r is the amplitude of oscillation. Thus, the time derivatives coupling parameters can be expressed as $\alpha = -a - 4b$ and $\beta = 2b/r^2$, which (using Eq. 6) can be rewritten into

$$-\alpha = \lambda_{in}, \ \beta = \frac{\lambda_{in} + \lambda_{anti}}{4r^2} \ . \tag{11a, b}$$

According to the time delay version, the stability of relative phase not only depends on amplitude but also on the inverse of movement frequency squared, as can be appreciated from the order parameter equation

$$\frac{d\phi}{dt} = -\frac{1}{\omega^2}\left[(\alpha + 6\beta r^2)\sin\phi - 3\beta r^2 \sin 2\phi\right] \ , \tag{12}$$

where $(\alpha + 6\beta r^2)/\omega^2 = a$ and $3\beta r^2/\omega^2 = -2b$ (cf. Eq. 2). The time delay coupling parameters then read $\alpha = \omega^2(a + 4b)$ and $\beta = -\omega^2(2b/3r^2)$. Using (6) again, we find

$$\alpha = \omega^2\lambda_{in}, \beta = -\frac{\omega^2(\lambda_{in} + \lambda_{anti})}{12r^2} \ . \tag{13a, b}$$

The estimations were calculated by entering the averages per experimental condition of the actual performance values of frequency (ω) and amplitude (r) into the equations.

A central assumption of the HKB model is that, during the performance of a transition trial (i.e., a trial in which movement frequency is gradually increased), the coupling parameters α and β remain fixed. In the present experiment, movement frequency was not varied within a trial. Determination of α and β (for each version of the model) allows for testing the natural default assumption that, also in this situation, these parameters were fixed over the different frequency and amplitude conditions.

3 Results

3.1 Steady-state task performance: frequency, amplitude and relative phase

Figure 2 summarizes the observed frequency-amplitude relations, averaged over subjects and trials. The subjects performed the required coordination pattern at the prescribed tempo within rather small margins of within-

[6] In Beek et al. (1996), the coupling function parameters were defined as a and b (they reserved α and β for oscillator equation parameters). Haken et al. (1985) defined the coupling function parameters as α and β (parameters a and b were used for the potential). We follow the convention of Haken et al. (1985) here.

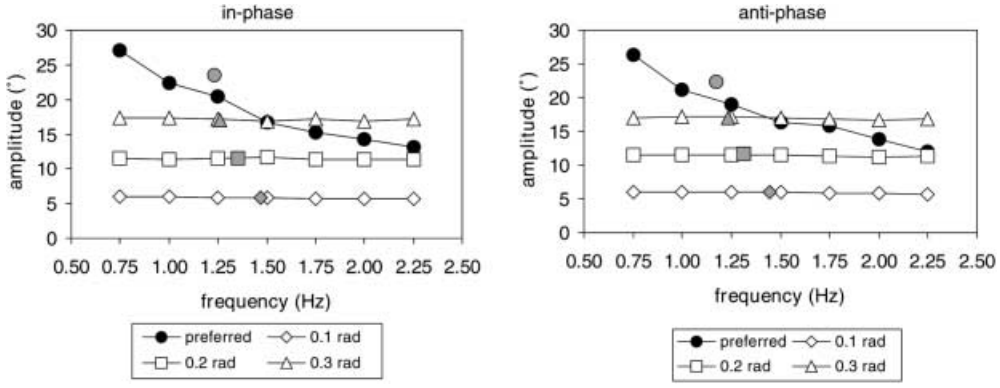

Fig. 2. Movement amplitude as a function of pacing frequency. *Gray symbols* represent values obtained for performance at the preferred frequency

trial movement frequency error and variability (mean absolute error < 0.02 Hz, mean CV < 3%; values averaged over all subjects and trials). The mean movement frequency in the unprescribed trials (Fig. 2) was 1.23 Hz in the in-phase condition and 1.16 Hz in the anti-phase coordination mode, with mean CVs of 2.2% and 2.3%, respectively. This indicates that the obtained values of mean and CV of the unprescribed in-phase and anti-phase trials were sufficiently similar to permit direct comparison of these trials. For the prescribed-amplitude trials, the mean values of preferred frequency decreased over the amplitude conditions (small to large) from 1.47 Hz to 1.23 Hz (Fig. 2). The mean CV of preferred frequency decreased with prescribed amplitude from 3.0% to 2.0%. The actual excursion of the limbs matched the prescribed amplitude values quite closely (mean absolute amplitude error < 0.01 rad, mean CV < 6%; values averaged over subjects and trials; see Fig. 2). Conform to the instructions, movement frequency did not have a profound effect on movement amplitude in these conditions. For the preferred-amplitude conditions, however, a clear decrease with increasing frequency was observed (Fig. 2). In these conditions, the mean CV of amplitude increased with pacing frequency from 4% to 7%. Together, these values indicate that subjects moved their arms in a rather consistent fashion in all conditions.

3.2 Pattern stability

3.2.1 Variability of ϕ. A paired-samples *t*-test was performed on the mean SD(ϕ) values obtained for the unprescribed trials (i.e., preferred-amplitude, preferred-frequency trials), which revealed that the effect of mode tended toward significance [$t(5) = 2.33$, $P = 0.068$]. The mean SD(ϕ) was 9.4° for the anti-phase mode, and 6.1° for the in-phase mode.

The mean SD(ϕ) values of the prescribed-amplitude, preferred-frequency trials were tested in a 2 × 3 repeated measures ANOVA[7] with the factors mode (in-phase, anti-phase) and prescribed amplitude (small, medium, large). Significant main effects of mode ($F(1, 5) = 8.55$, $P < 0.05$) and prescribed amplitude ($F(2, 10) = 16.26$, $P < 0.005$) were found. Mean SD(ϕ) was higher in the antiphase mode (9.5°) than in the in-phase mode (8.1°), and was higher in the small prescribed amplitude condition (10.3°) than in the larger amplitude conditions (medium: 8.5°, large: 7.5°) (Tukey HSD, $P < 0.05$).

A 2 × 7 repeated measures ANOVA with the factors mode (in-phase, anti-phase) and pacing frequency (0.75, 1.00, 1.25, 1.50, 1.75, 2.00, 2.25 Hz) was used to test the mean SD(ϕ) values of the preferred-amplitude, prescribed-frequency trials. Significant effects of mode [$F(1, 5) = 124.22$, $P < 0.005$] and pacing frequency [$F(4, 20) = 14.91$, $P < 0.001$] were found. The mode × pacing frequency interaction tended toward significance [$F(4, 19) = 2.87$, $P = 0.055$]. Again, the mean SD(ϕ) was higher in the anti-phase mode (10.4°) than in the in-phase mode (6.8°). Furthermore, SD(ϕ) was a function of the pacing frequency, with frequencies higher than 1.5 Hz resulting in significantly larger SDs than frequencies below 1.5 Hz (Tukey HSD, $P < 0.01$).

The mean SD(ϕ) values of the fully prescribed trials were subjected to a 2 × 3 × 7 repeated measures ANOVA with the factors mode (in-phase, anti-phase), prescribed amplitude (small, medium, large) and pacing frequency (0.75, 1.00, 1.25, 1.50, 1.75, 2.00, 2.25 Hz). This analysis yielded significant main effects of mode [$F(1, 5) = 363.36$, $P < 0.001$], prescribed amplitude [$F(2, 8) = 17.73$, $P < 0.005$] and pacing frequency [$F(4, 18) = 10.38$, $P < 0.001$]. A significant effect of the mode × pacing frequency interaction was also observed [$F(6, 29) = 12.91$, $P < 0.001$]. The mean SD(ϕ) was larger in the anti-phase mode than in the in-phase mode (10.7° and 7.9°, respectively), as well as for small prescribed amplitudes (10.6°) compared to medium (8.9°) or large amplitudes (8.4°) (Tukey HSD, $P < 0.01$). Furthermore, SD(ϕ) depended on pacing frequency, with frequencies higher than 1.75 Hz resulting in significantly larger SDs than frequencies below 1.75 Hz (Tukey HSD, $P < 0.01$). The interaction effect revealed a differential effect of pacing frequency on the SDs obtained for the two modes: SD(ϕ) in the anti-phase mode increased at higher pacing frequencies, whereas SD(ϕ) remained virtually constant for the in-phase mode (see Fig. 3).

[7] In all repeated measures ANOVAs performed, the Huynh-Feldt ε adjustment was applied in order to correct degrees of freedom, *F* and *p* values for violation of the sphericity assumption.

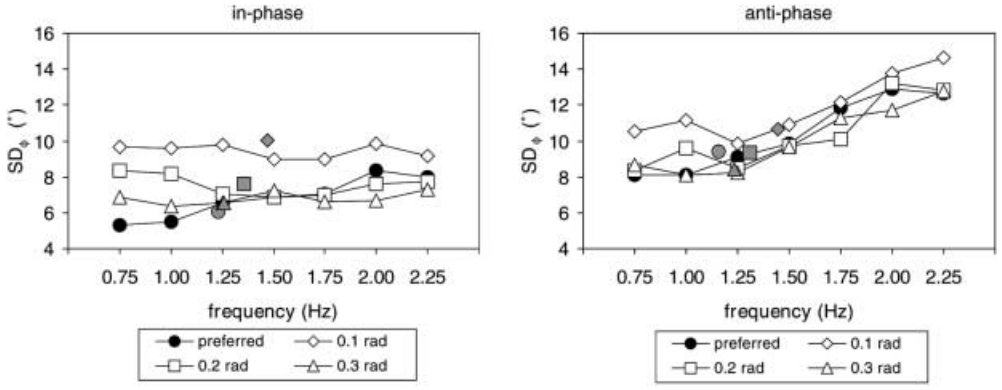

Fig. 3. SD (ϕ) as a function of pacing frequency for different prescribed amplitudes. *Gray symbols* represent values obtained for performance at the preferred frequency

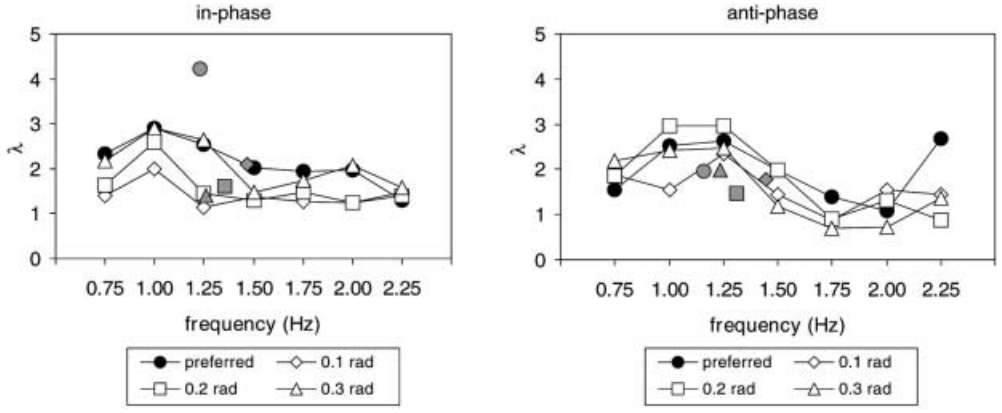

Fig. 4. λ as a function of pacing frequency for different prescribed amplitudes. *Gray symbols* represent values obtained for performance at the preferred frequency

3.2.2 Decay parameter λ. The group-averaged median values of λ that were obtained by fitting the decay process according to (4b) are presented in Fig. 4. Note that high values of λ (i.e., fast decay) reflect high pattern stability. Statistical tests were performed in the same fashion as described for SD(ϕ). For the unprescribed trials, a paired-samples t-test on the factor mode (anti-phase, in-phase) yielded no significant effect. The prescribed-amplitude trials were tested in a 2 (mode) × 3 (amplitude) repeated measures ANOVA, which produced no significant effects. Furthermore, the prescribed-frequency trials were subjected to a 2 (mode) × 7 (frequency) repeated measures ANOVA. Again, no significant effects were observed. Finally, the fully prescribed trials were subjected to a 2 × 3 × 7 repeated measures ANOVA with the factors mode, amplitude and frequency. In this case, a main effect was found for pacing frequency [$F(3, 17) = 8.08$, $P < 0.005$], while prescribed amplitude tended toward significance [$F(2, 8) = 3.33$, $P = 0.097$]. A Tukey HSD test ($P < 0.05$) showed that λ was significantly larger at 1 Hz and 1.25 Hz than at the higher frequencies (≥ 1.5Hz).

Since SD(ϕ) and λ are both considered to be indices of the stability of relative phase, they should produce comparable statistical effects, albeit in opposite directions. Since the results reported show that this is not the case, we decided to investigate whether the expected inverse relation between SD(ϕ) and λ was indeed present. The SD(ϕ) and λ values used in the ANOVA were therefore subjected to a non-parametric correlation test (Spearman rank correlation, $n = 384$). The measures were significantly negatively correlated (Spearman's $\rho = -0.265$, $P < 0.0005$), confirming the existence of the expected relation between SD(ϕ) and λ.

3.2.3 Coupling between limb and pacing signal. The mean value of θ (averaged over all trials, subjects and arms) was −71° (SD = 28°), indicating the presence of a considerable phase lag between the arm movements and the stimulus, which was not in agreement with the task requirement of phase locking at $\theta = 0°$. For each arm, the offsets obtained for the pre-perturbation and post-perturbation segments of each individual trial were subjected to a paired-samples t-test.

Only perturbed, frequency-paced trials were included in the first analysis ($n = 1318$). For the right (perturbed) arm, a systematic difference between the pre- and post-perturbation segments was observed [$t(1317) = 7.36$, $P < 0.005$]; $\Delta\bar{\theta}_R = -3.9°$. For the left (unperturbed) arm, a similar effect occurred [$t(1317) = 9.33$, $P < 0.005$]; $\Delta\bar{\theta}_L = -5.0°$. This implies that the phase lag of each arm relative to the pacing signal increased, that is, the arm movements did not completely recover from the 90° perturbation. To compare the phasing of the arms relative to the stimulus (θ) with the phasing of the arms relative to each other (ϕ), a paired-samples t-test was performed in which the pre-perturbation and post-perturbation means of ϕ were entered for the same trials. A small but significant offset of 1.3° was found [$t(1317) = 7.41$, $P < 0.005$], which corresponds well with $|\Delta\bar{\theta}_R - \Delta\bar{\theta}_L| = 1.1°$. Note that the small difference of 0.2° was due to the manner in which relative phase

was determined (point estimate versus continuous estimate).

The second offset analysis was performed for the unpaced trials ($n = 187$), which revealed the existence of a highly significant change in the phase of oscillation of both arms: $\Delta\bar{\phi}_R = 52.8°$ [$t(186) = 17.60$, $P < 0.005$]; $\Delta\bar{\phi}_L = 51.0°$ [$t(186) = 16.99$, $P < 0.005$]. The changes in phase were comparable for the two arms ($|\Delta\bar{\phi}_R - \Delta\bar{\phi}_L = 1.8°$), which implies that subjects succeeded in maintaining the required phase difference between them.

3.3 Parameter estimation

3.3.1 Parameters a, b and Q (order parameter equation). The estimated values of a and b (averaged over subjects) are presented in Fig. 5. To test the model prediction that the values of both parameters scale positively with movement amplitude (as predicted by both versions of the HKB model) and decrease with increasing frequency for the estimates based on the time delay version, a and b were separately subjected to repeated measures ANOVAs. The tests regarding prescribed-amplitude trials and prescribed-frequency trials yielded no significant effects. For the fully prescribed trials, however, a significant main effect of frequency on b was obtained [$F(3, 17) = 8.08$, $P < 0.005$]. A Tukey HSD test ($P < 0.05$) showed that b was significantly higher at 1.0 and 1.25 Hz than at the higher frequencies (≥ 1.5 Hz).

The group-averaged estimates of noise strength Q are plotted as a function of pacing frequency in Fig. 6. To investigate whether Q was affected by the experimental manipulations, a $2 \times 3 \times 7$ repeated measures ANOVA with the previously described factors mode, prescribed amplitude, and pacing frequency was applied to the paced trials. A significant main effect was found for frequency [$F(6, 30) = 3.74$, $P < 0.01$]. A post-hoc test (Tukey HSD, $P < 0.05$) revealed that Q did not change monotonically with pacing frequency, but that its values were significantly higher at 1.0 Hz and 1.25 Hz than at 1.75 Hz (see Fig. 6).

3.3.2 Parameters α and β (coupling function). Figure 7 depicts the group-averaged estimates of α and β as a function of frequency. To examine the impact of the experimental manipulations on these parameters, the estimates of α and β were tested in a 3×7 repeated measures ANOVA with factors prescribed amplitude (0.1, 0.2, 0.3 rad) and pacing frequency (0.75, 1.0, 1.25, 1.5, 1.75, 2.0, 2.25 Hz). Separate tests were performed for the parameter estimates obtained for the time derivatives and for the time delay version. In this way, the first-order assumption that α and β do not vary over the frequency and amplitude manipulations was tested.

3.3.3 Time derivatives version. Parameter α was significantly affected by both amplitude [$F(2, 10) = 4.61$, $P < 0.05$] and frequency [$F(4, 20) = 3.04$, $P < 0.05$]. Post-hoc analysis (Tukey HSD) revealed that α was more strongly negative in the small amplitude condition than in the large amplitude condition ($P < 0.05$), and

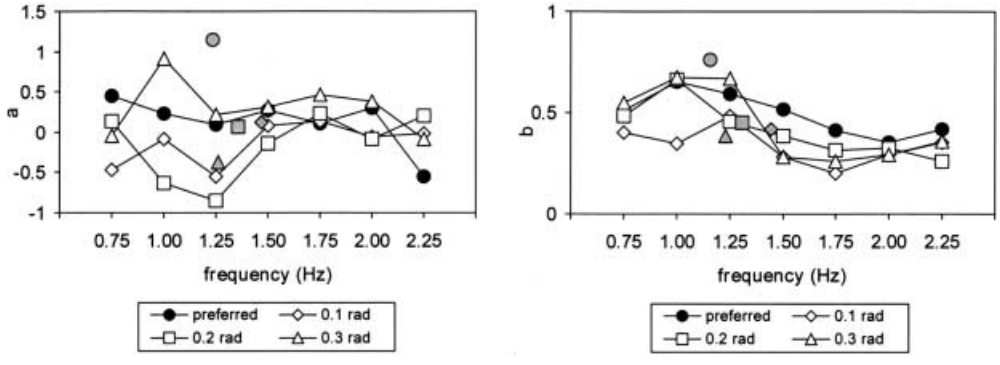

Fig. 5. a and b as a function of pacing frequency for different prescribed amplitudes. *Gray symbols* represent values obtained for performance at the preferred frequency

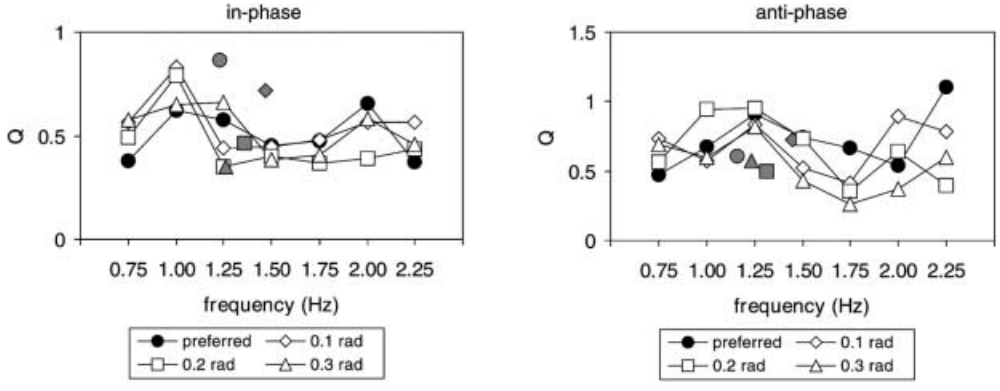

Fig. 6. Q as a function of pacing frequency for different prescribed amplitudes. *Gray symbols* represent values obtained for performance at the preferred frequency

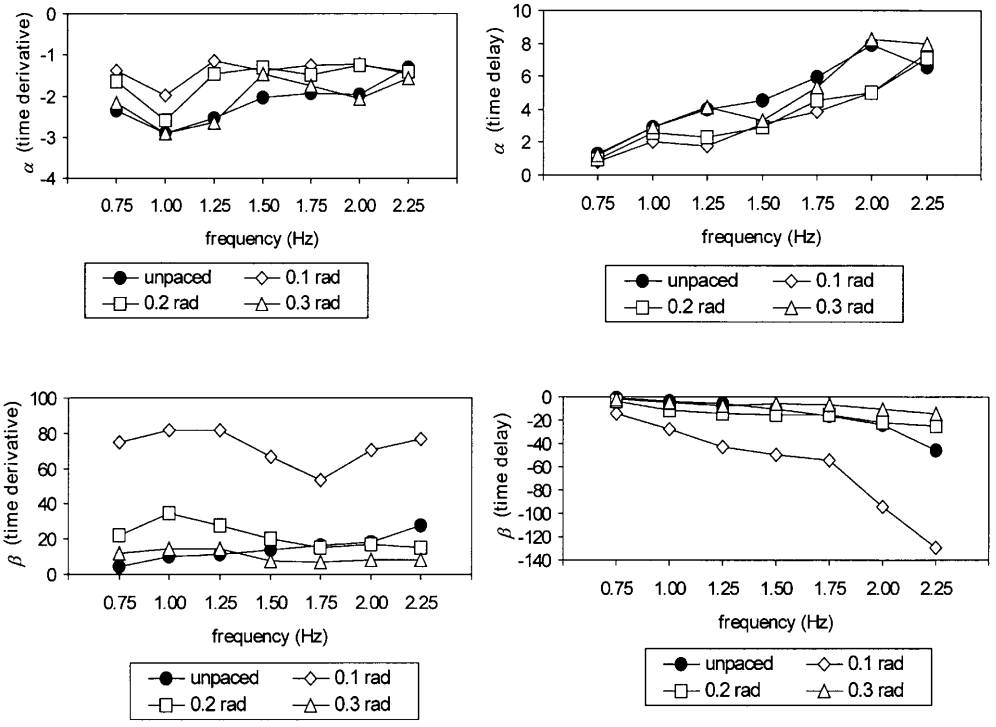

Fig. 7. Coupling function parameters α and β as a function of pacing frequency for different prescribed amplitudes. *Left panels* Estimates obtained for the time-derivatives version of the HKB model; *Right panels* Estimates obtained for the time-delay version

that its value was significantly smaller at 1.0 Hz than at frequencies of 1.5 Hz and higher ($P < 0.05$). For parameter β, a significant effect of amplitude was found [$F(1, 6) = 124.28$, $P < 0.005$], resulting from the fact that β was much larger in the small amplitude condition than in the medium and large amplitude conditions (Tukey HSD, $P < 0.01$).

3.3.4 Time delay version. Parameter α was significantly affected by frequency [$F(5, 23) = 26.86$, $P < 0.005$]. A Tukey HSD test ($P < 0.01$) showed that the estimates were significantly larger at frequencies of 2.0 Hz and higher than the estimates at frequencies of 1.5 Hz and lower. Parameter β was significantly affected by both amplitude [$F(1, 5) = 64.13$, $P < 0.005$] and frequency [$F(4, 19) = 16.19$, $P < 0.005$], as well as by the interaction between these two variables [$F(5, 25) = 9.72$, $P < 0.005$]. The amplitude effect was due to the fact that β was more negative in the small amplitude condition than in the medium or large amplitude conditions (Tukey HSD, $P < 0.01$). The post-hoc test for frequency revealed that the estimates at the higher frequencies were significantly more negative than the estimates at the lower frequencies ($P < 0.01$). The interaction effect revealed that the frequency manipulation had a stronger effect on the estimated β values in the small amplitude condition than in the medium or large amplitude conditions.

4 Discussion

The goal of the present experiment was twofold. The first, general goal was to develop empirically Schöner's analysis (1995) of neural functioning in terms of distinguishable levels or behavioral components. This was accomplished by means of an experiment on the stability properties of relative phase that was not designed to isolate the timing level as much as possible, as in the original experiments of Kelso (1984), but rather to deliberately add experimental constraints, in the form of prescribed amplitudes (i.e., turning points), that referred explicitly to the goal level. In so doing, we could examine to what degree the timing and the goal level remained independent. The second, more specific goal was to use the empirical findings to evaluate the coupling functions proposed by Haken et al. (1985) to account for the dynamics of rhythmic interlimb coordination and their underlying assumptions. Specifically, the predictions from two coupling functions were tested. According to the time derivatives version, only amplitude would affect the stability of relative phase, whereas according to the time delay version, both amplitude and frequency would have an impact on stability. The employed method involved the independent prescription of frequency and amplitude in an experimental design allowing for the estimation of two measures of pattern stability, the variability of relative phase [SD(ϕ)] and the exponent of the relaxation process following a phasic perturbation of relative phase (λ).

Before discussing the experimental results in view of the general and specific goals of the study, it is useful to briefly summarize the results with regard to the validity of the applied method. This examination concentrated on bimanual coupling effects (versus unilateral coupling with a pacing signal) and the question of constancy of noise level Q [a necessary prerequisite for the use of SD(ϕ) as a measure of stability]. Comparison of the phase relations before and after perturbation for both ϕ and θ revealed that the phase of both arms (rather

than the phase of the perturbed arm only) was adjusted in order to satisfy the required phase relation. This indicated that the return characteristics were due to the coupling between the limbs. An analysis in terms of the stability of interlimb coupling was therefore deemed adequate. In the present experiment, noise did not vary systematically with frequency; Q was elevated at only two intermediate frequency levels. Therefore, we regarded the noise level as being sufficiently constant to justify a stability analysis based on SD(ϕ).

4.1 Independence of levels

To examine Schöner's hypothesis (1995) that the relative phase dynamics of interlimb coordination reside predominantly at the timing level and are relatively independent of the goal level, we explicitly introduced task constraints referring to the goal level in the form of amplitude (i.e., turning point) requirements. If the timing level and the goal level are indeed separately identifiable, that is, weakly coupled levels of neural functioning, then the introduction of spatial targets in the relative timing of interest would be expected to have only a small effect on the stability properties of relative phase.

To evaluate this expectation, it is important to realize that, in the present experiment, it was not attempted to isolate the timing level as much as possible. Instead, the experimental variations referring to the timing level were deliberately supplemented with task constraints referring to the goal level. It should be noted that this situation deviates from that in the original experiment of Kelso (1994) in which amplitude was free to vary. Nevertheless, we found some but no strong effect of the introduced spatial constraints on the stability properties of relative phase. This implies that even if the two levels are mixed as in our experiment, the expected independence of the timing level is largely preserved. This is not to say that the coordination was totally immune for the introduced task constraint. Coordination stability expressed as the variability of relative phase was significantly lower in the smallest amplitude condition than in the other two amplitude conditions. This effect was roughly additive to the effect of the tempo (cf. Fig. 3). When stability was expressed as the exponent of the relaxation process, the lower coordination stability in the small amplitude condition was still visible (cf. Fig. 4), but no longer statistically significant. Thus, to the extent that manipulation at the goal level (i.e., invoking spatial requirements) had any effect, confining them to small values was most effective in influencing the timing level.

The conclusion that the relation between these levels of neural organization depended on the prevailing task constraints is in agreement with Schöner's notion (1995) that the nervous system is organized in a task-dependent manner. The behavioral space of the nervous system can be restructured as a function of task constraints through their impact upon the stability properties of the performed pattern. Such restructuring can lead from virtually no interaction between levels (as in experimental setups designed to isolate a particular level and to study it in its 'pure' form) to stronger interactions between them (as has been demonstrated by the present experiment). Extending this line of reasoning, it is conceivable that even more demanding constraints at the goal level may not only reduce the stability of variables at the timing level, but ultimately compromise the coordination task itself.

4.2 Appropriateness of proposed coupling functions

If stability was expressed in terms of variability of steady-state relative phase, an effect of amplitude was observed. However, when stability was expressed in terms of a more direct measure (attractor strength, i.e., inverse of relaxation time), only a tendency toward significance of amplitude was found. Nevertheless, the significant Spearman correlation between these measures reassured us that these two key quantities were in fact related to pattern stability. A significant effect of tempo was revealed in both measures. The SD(ϕ) results do not fully corroborate the relative phase variability results of Peper and Beek (1998a), who found a nonsignificant tendency for variability to be lower in their medium amplitude condition than for a small or large amplitude. Their experiment involved paced unimanual tracking of a continuously oscillating stimulus within a transition protocol. The critical frequency at which the transition from anti-phase to in-phase coordination occurred was not influenced by the amplitude of the movements, which indicated that neither version of the HKB coupling function could adequately account for their results. In the present experiment, involving paced bimanual trials and a discrete stimulus within a perturbation protocol, significant effects of frequency [on both λ and SD(ϕ)] and an effect of amplitude [on SD(ϕ)] were found. Therefore, we conclude that the assumption underlying the time derivatives coupling function, namely that the degree of interaction between the limb movements is determined solely by their amplitudes, has to be rejected.

The two coupling parameters, α and β, turned out to vary with both amplitude and frequency. This may indicate that they were adjustable between trials (e.g., due to intention; see Post et al. in press; Schmidt et al. 1998). Presumably, such adjustments served the purpose of preserving the stability of performance in the face of the task requirements at hand. In the current context, the results obtained for the time delay version of the coupling function might reflect adjustments in α and β counteracting a reduction of stability (i.e., smaller values of λ; cf. Eq. 13a and b) due to the amplitude and frequency manipulations. Also for the time derivatives version, significant effects of amplitude and frequency were obtained. Since the latter variable does not influence the coupling parameters in this version of the model (cf. Eq. 11a and b), its influence can only be understood indirectly (namely through the effect of frequency on the values of λ obtained for the in-phase condition; cf. Eq. 11a). As such, the analysis of the estimated coupling parameters seems to support the time delay version of

the model and renders the time derivatives version less likely.

Thus, if a choice has to be made between the proposed coupling functions, the delay version has to be preferred in view of the current data since, in this case, the coupling is determined both by amplitude and frequency. This conclusion was supported by the estimated values of the coupling function parameters α and β. Note that the effects of frequency and amplitude observed in the present study and those observed by Peper and Beek (1998a) were not the same. This suggests that the functional form of the coupling was quite different in these two experimental tasks (bimanual coupling versus visual-unimanual coupling). With respect to a comparison between the present experiment and the study of Peper and Beek (1998b), a similar conclusion can be drawn. Although both tasks were bimanual coordination tasks, the differences in coupling type [1:1 forearm oscillations in the present experiment versus 2:3 hand tapping in the experiment of Peper and Beek (1998b)] make it quite conceivable that the functional form of the coupling in these experiments differed.

Our overall conclusion regarding the HKB model is that, although the HKB potential is broadly applicable and as such reflects generic coordination principles (accounting for phenomena such as bistability and loss of stability), the adequacy of the accompanying analysis in terms of coupled oscillators is questionable (cf. Peper and Beek 1998a, 1999). This discrepancy can be understood logically in that the HKB potential represents a more general formulation of the observed coordination dynamics than the accompanying effort to model the individual limb movements and the nature of their interaction in terms of coupled oscillators. It could well be that such an effort is hampered by the fact that the human movement system has the ability to restructure its behavioral components and their interactions to satisfy a specific set of task constraints. In the light of this ability, it seems highly unlikely that a single 'fundamental biophysical coupling' can be derived that applies generically to all possible sets of task constraints, as has been suggested by Jirsa et al. (1994) (see also Kelso 1994).

Therefore, if the researcher's objective is to identify general principles, it seems more useful to look for general principles in the manner in which behavioral components are structured and restructured as a function of task constraints, instead of embarking on a research program aimed at constructing a large, potentially infinite number of context-specific coupling functions. If the researcher's objective is to gain deeper knowledge about a particular type of behavior, it remains a perfectly valid enterprise to search for the coupling function which specifically applies to the studied phenomenon. As pointed out, for instance, by Peper and Carson (1999), coordinative phenomena may be contingent upon sensory feedback and bilateral motor activation processes. In both the identified scenarios, the question remains how coordination principles at the behavioral level correspond to the functional organization of the nervous system.

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