Psychological Research (2008) 72:123–137
DOI 10.1007/s00426-006-0096-9

ORIGINAL ARTICLE

Laterally focused attention modulates asymmetric coupling in rhythmic interlimb coordination

Harjo J. de Poel · C. (Lieke) E. Peper · Peter J. Beek

Received: 13 April 2006 / Accepted: 24 August 2006 / Published online: 5 October 2006

Abstract Peters (J Motor Behav 21:151–155, 1989; Interlimb coordination: neural, dynamical and cognitive constraints, Academic, Orlando, pp 595–615, 1994) suggested that expressions of handedness in bimanual coordination may be reflections of an inherent attentional bias. Indeed, previous results indicated that focusing attention on one of the limbs affected the relative phasing between the limbs in a manner comparable to the effects of hand dominance. The present study extended the comparison between the effects of attentional focus and handedness by testing their impact on the interactions between the limbs. Both left-handed and right-handed participants performed rhythmic bimanual coordination tasks (in-phase and antiphase coordination), while directing attention to either limb. Using brief mechanical perturbations, the degree to which the limbs were influenced by each other was determined. The results revealed that the non-dominant limb was more strongly affected by the dominant limb than vice versa and that, in line with Peters' proposition, this handedness-related asymmetry in coupling strength was reduced when attention was focused on the non-dominant limb, thereby highlighting the potential relation between inherent (handedness-related) asymmetries and voluntary attentional asymmetries. In contrast to previous findings, the (commonly observed) phase lead of the dominant limb was attenuated (rather than accrued) when attention was focused on this limb. This unexpected result was explained in terms of the observed attention-related difference in amplitude between the limbs.

Introduction

In bimanual task performance, the two upper limbs cooperate to achieve functionally coordinated bimanual behavior. Although bimanual coordination implies that the two hands work together as a synergy, their roles are not identical. Asymmetries due to hand dominance can be observed for the performance of everyday discrete tasks (e.g., striking a match; Guiard, 1987; Peters, 1994) and rhythmic bimanual movements alike (e.g., Byblow, Bysouth-Young, Summers, & Carson, 1998; Peters & Schwartz, 1989; Summers, Davis, & Byblow, 2002; Treffner & Turvey, 1995). Hand dominance (or handedness) is typically related to neurophysiological asymmetries such as hemispheric dominance (e.g., Haaland & Harrington, 1996; Sainburg, 2002; Serrien, Ivry, & Swinnen, 2006). In addition, its effects have been interpreted from a more psychological perspective. In particular, it has been proposed that, since the dominant hand typically executes the most demanding subtask (e.g., striking the match, rather than holding the matchbox) and, thus, receives most attention, the expressions of handedness in bimanual coordination

---

This research was made possible by Aspasia grant 015.001.040 of the Netherlands Organization for Scientific Research (NWO) awarded to Lieke Peper.

H. J. de Poel · C. (Lieke) E. Peper ·
P. J. Beek
Institute for Fundamental and Clinical Human Movement
Sciences, Amsterdam/Nijmegen, The Netherlands

H. J. de Poel (✉) · C. (Lieke) E. Peper ·
P. J. Beek
Faculty of Human Movement Sciences, Vrije Universiteit,
Van der Boechorststraat 9, 1081 BT Amsterdam,
The Netherlands
e-mail: h.depoel@fbw.vu.nl

are reflections of an inherent attentional bias (Peters, 1989, 1994). This suggested relation between handedness and attentional focus motivated the present study, which examined whether focusing attention on either limb influenced the handedness-related asymmetry in the strength of interlimb interactions during bimanual coordination (e.g., Byblow, Carson, & Goodman, 1994; De Poel, Peper, & Beek, 2006, in press).

Asymmetries in interlimb coupling strength

Bimanual isofrequency coordination constitutes an interesting model task for examining the effects of hand dominance on bimanual performance since in this type of coordination the subtasks of the two limbs are identical (viz., they oscillate at identical frequencies; cf. Carson, 1993). Key characteristics of such rhythmic coordination stem from the interactions between the moving limbs, due to which only two coordination patterns can be stably performed without training (e.g., Yamanishi, Kawato, & Suzuki, 1979; Zanone & Kelso, 1992): the in-phase pattern (i.e., the limbs oscillate symmetrically; relative phase ϕ = 0°) and the antiphase pattern (i.e., the limbs oscillate in an alternating fashion; ϕ = 180°). The stability properties of these two-phase relations have been successfully accounted for by the well-known HKB model (Haken, Kelso, & Bunz, 1985). Empirically, however, the phase relation between the limbs has been demonstrated to be affected by hand dominance. Typically, for right-handed (RH) participants the right hand is, on average, slightly leading in time, whereas the opposite is true for left-handed (LH) individuals (e.g., De Poel et al., in press; Semjen, Summers, & Cattaert, 1995; Stucchi & Viviani, 1993; Swinnen, Jardin, & Meulenbroek, 1996; Treffner & Turvey, 1995, 1996). For one-dimensional oscillatory movements this implies small but significant deviations (i.e., phase shifts) from the intended relative phases of 0° and 180°. With relative phase defined as the phase difference between the left and right limb ($\phi = \theta_L - \theta_R$) this implies that, for in-phase coordination, $\phi > 0°$ for left-handers and $\phi < 0°$ for right-handers. (Note that in the present analyses an alternative definition of ϕ was adopted, see Data reduction.)

These effects of handedness on the relative phasing between the limbs and the associated stability characteristics have been accounted for by extending the HKB potential with additional handedness-related symmetry breaking terms (Treffner & Turvey, 1995). Converging theoretical and empirical results revealed that the identified effects of hand dominance on the coordination dynamics are related to an asymmetry in the strength of the coupling between the limbs. That is, the non-dominant (ND) limb is more strongly influenced by the dominant (D) limb than vice versa (De Poel et al., 2006, in press; Peper, Daffertshofer, & Beek, 2004a; see also Byblow et al., 1994; Carson, 1993). Empirically, this asymmetry in coupling strength was evidenced by demonstrations that both spontaneous, frequency-induced (Byblow et al., 1994; Byblow, Chua, & Goodman, 1995; De Poel et al., in press) and voluntary (Carson, Byblow, Abernethy, & Summers, 1996; De Poel et al., 2006) switches between coordination patterns were mediated predominantly by changes in the phasing of the ND limb and by the observation that the phasing of the ND limb was more strongly influenced by a mechanical perturbation of the contralateral (D) limb than the D limb's phasing was in response to a perturbation of the contralateral (ND) limb (De Poel et al., in press).[1]

Interestingly, previous studies revealed that the observed phase lead of the D limb could be modulated by means of attention: When attention was focused on the movements of the D (ND) limb, the phase lead of the D limb increased (decreased) (Amazeen, Amazeen, Treffner, & Turvey, 1997; Franz, 2004; Pellegrini, Andrade, & Teixeira, 2004; Riley, Amazeen, Amazeen, Treffner, & Turvey, 1997; Swinnen et al., 1996). Moreover, such an asymmetry in attentional focus affected the stability of bimanual performance, in that focusing on the D limb resulted in enhanced coordinative stability (Amazeen et al., 1997; Swinnen et al., 1996). These effects of attentional asymmetries on the bimanual coordination dynamics were similar to those obtained for handedness and were therefore consistent with the asymmetric potential proposed by Treffner and Turvey (1995; see Amazeen et al., 1997; Riley et al., 1997). Furthermore, this correspondence regarding the way in which hand dominance and attentional focus affected the relative phase dynamics was in agreement with Peters' (1989, 1994) suggestion that the effects of handedness during bimanual coordination are related to an attentional bias (see Amazeen et al., 1997). However, since in principle similar relative phase dynamics may result from distinct underlying system properties and

---

[1] Note that the handedness-related asymmetries in interlimb coupling strength may be altered when additional task-related differences between the limbs are introduced. For instance, it has been shown for non-mirror-symmetric bimanual circle drawing that the direction of circling determines which limb tends to lead (Franz, Rowse, & Ballentine, 2002) and that, when tapping two unequal rhythms, the faster tapping hand influences the slower hand more strongly than vice versa (e.g., Byblow et al., 1998; Peper, Beek, & Van Wieringen, 1995a; Summers et al., 2002), even though in the latter case handedness-related effects are still noticeable (Byblow et al., 1998; Summers et al., 2002).

processes (cf. Peper, Ridderikhoff, Daffertshofer, & Beek, 2004c), the observed association is not sufficient to draw definite conclusions in this regard. In order to uncover the origins of the coordinative asymmetries due to handedness and asymmetric attentional focus it is imperative to compare their effects on the relative strength of the interlimb interactions. That is, if Peters' proposition is correct, the effects of laterally focused attention should resemble those of hand dominance with respect to not only the relative phase dynamics, but also the asymmetry in interlimb coupling strength (De Poel et al., in press; Peper et al., 2004a). In other words, focusing attention on one of the limbs is expected to reduce the degree to which that limb is influenced by the movements of the contralateral (unattended) limb, whereas the coupling influences in the reverse direction are expected to increase. This leads to the hypothesis that the handedness-related asymmetry in interlimb coupling strength is smaller (or even reversed) when the ND limb is attended compared to when the D limb is attended. The present study was conducted to examine this hypothesis. Note that whereas confirmation of this hypothesis does not necessarily imply that handedness is indeed caused by an inherent asymmetry in attentional focus, falsification would speak against Peters' suggestion and render the proposed psychological correlate of handedness effects in bimanual coordination unlikely.

Experimental manipulations and predictions

In previous studies, two basic strategies have been employed to address the effects of laterally focused attention on bimanual coordination. One involved manipulation of attention by superimposing an additional task to (one of) the limbs, involving additional spatial (accuracy) requirements (Amazeen et al., 1997; Amazeen, Ringenbach, & Amazeen, 2005; Pellegrini et al., 2004; Riley et al., 1997). In this way, attention was (presumed to be) focused primarily on the limb that had to perform the most difficult subtask, without any explicit instruction to this effect. An advantage of this manipulation is that, by varying the stringency of the two required subtasks, graded variations in the degree of attentional asymmetry may be induced. However, a considerable disadvantage is that the associated spatial demands may alter the limb's component dynamics [e.g., influencing the (non-linear) stiffness of the component oscillator, see Mottet & Bootsma, 1999]. Theoretically, such differences in component dynamics may affect the relative phase dynamics as well (Daffertshofer, Van Den Berg, & Beek, 1999; Fuchs, Jirsa, Haken, & Kelso, 1996). Indeed, Amazeen et al. (2005) recently demonstrated empirically that manipulation of the direction of attention by means of asymmetric spatial requirements altered the characteristics of the individual limb movements to such an extent that changes in the relative phasing between the limbs could be mainly attributed to these task demands (i.e., a difference in amplitude), rather than to the asymmetry in attentional focus. In other words, this type of manipulation may introduce a confounder in the examination of the relation between lateral attentional focus and the relative phase dynamics by invoking differences between the coordinated components.

In other studies, attention was manipulated by instructing the participants to look at and concentrate on the movements of one of the limbs (e.g., Franz, 2004; Swinnen et al., 1996; Wuyts, Summers, Carson, Byblow, & Semjen, 1996), while Franz (2004) also examined instructionally directed non-visual attention (see also Sherwood & Rios, 2001). Although, in contrast to the previous paradigm, this instructional manipulation does not readily allow for graded variations in the attentional asymmetry, it does not introduce or impose a difference in performance requirements between the two subtasks. As such, this method reduces the chance of introducing confounding factors into the experimental design. For this reason, and because manipulation of attentional focus by means of instruction led to similar results regarding the lead–lag relation between the limbs (Franz, 2004; Swinnen et al., 1996; Wuyts et al., 1996), the latter strategy was applied in the present experiment.

To determine the (asymmetry in) interlimb coupling strength, the experiment focused on the transient stage following mechanical perturbation of the interlimb coordination pattern (cf. Court, Bennett, Williams, & Davids, 2002; De Poel et al., in press; Post, Peper, & Beek, 2000a; Post, Peper, Daffertshofer, & Beek, 2000b; Scholz, Kelso, & Schöner, 1987). After perturbation of a bimanual coordination pattern the original pattern is typically restored, reflecting the stability properties of bimanual coordination (cf. Post et al., 2000a; Post et al., 2000b; Scholz et al., 1987). In the present study, the bimanual pattern was perturbed by suddenly arresting and subsequently releasing one of the limbs (thereby inducing an abrupt change in relative phase). De Poel et al. (in press) recently demonstrated that the relaxation back to the original pattern was typically mediated not solely by the limb that was actually perturbed, but also by phase adaptations in the contralateral, unperturbed limb. That is, the phase of the unperturbed limb was attracted towards the phase of the perturbed limb, as a consequence of the interactions between the limbs. More specifically, it was found that the contribution of the unperturbed limb to this process was more pronounced when the D limb was perturbed than when the ND limb was perturbed. This revealed that, as expected, the movements of the ND limb were more strongly influenced by (an imposed change in) the movements of the D limb than vice versa, demonstrating a handedness-related asymmetry in coupling strength.

In the present experiment, both RH and LH individuals participated (allowing for a systematic examination of the effects of attentional asymmetry in relation to hand dominance) and the direction of attention (to either limb) was manipulated by means of instruction. Given the predicted asymmetry in coupling strength, the specific hypotheses were as follows: (1) The adjustments made by the contralateral limb are larger when the D limb is perturbed than when the ND limb is perturbed (cf. De Poel et al., in press); (2) Based on the assumption that hand dominance results from a lateral attentional bias (Peters, 1989, 1994) this asymmetric effect is predicted to be reduced when attention is directed to the ND limb compared to the condition in which attention is focused on the D limb.

Besides the relative adjustments of the individual limb movements, the stability of bimanual coordination was analyzed by examining the swiftness of relaxation back to the original coordination pattern after the perturbed arm had been released (i.e., the relaxation time). Since the attractive strength of the movements of the D limb was predicted to be stronger than that of the ND limb, the relaxation to the original bimanual pattern was expected to be quicker after perturbation of the D limb than after perturbation of the ND limb (cf. De Poel et al., in press). In line with the just formulated hypotheses, this asymmetry in relaxation time was expected to be smaller when attention was focused on the ND limb compared to when attention was focused on the D limb.

Finally, to relate the present empirical findings to previous studies, the phase relation between the limbs during stationary rhythmic performance was investigated as well. Given the relation between asymmetric coupling strength and relative phasing (cf. De Poel et al., in press; Peper et al., 2004a) and empirically established effects of laterally focused attention on the phase relation between the limbs (Amazeen et al., 1997; Franz, 2004; Pellegrini et al., 2004; Riley et al., 1997; Swinnen et al., 1996), it was expected that the phase lead of the D limb would be larger (smaller) when attention was focused on the D (ND) limb. Based on the results of Amazeen et al. (1997) and the asymmetric potential proposed by Treffner and Turvey (1995, 1996), variability of ϕ (as a second index of pattern stability) was expected to be higher when attention was focused on the ND limb. Because the (asymmetry in) coordination dynamics is also dependent on the performed coordination mode and movement frequency (e.g., De Poel et al., in press; Treffner & Turvey, 1995, 1996), performance was examined for both in-phase and antiphase coordination at two different movement frequencies.

Methods

Participants

Twenty-two healthy volunteers (10 women and 12 men, aged 19–39 years) participated in the study. Based on a Dutch version of the Edinburgh handedness inventory (Oldfield, 1971), the handedness quotient (or laterality quotient: LQ) was determined for each participant, with LQ = –100 indicating extreme left-handedness and LQ = +100 indicating extreme right-handedness. Ten participants were labeled as right-handed (mean LQ = 94, range 71–100), the other 12 as left-handed (mean LQ = –95, range –54 to –100).[2] The participants gave their informed consent prior to the experiment and were paid a small fee for their services.

Apparatus

Participants were seated on a modified chair. Both lower arms rested comfortably in premolded carbon fiber splints that were mounted on vertical axes, allowing rotation of the lower arms in the horizontal plane only. The armrests were adjusted with respect to these axes, such that each elbow's epicondylus medialis was located above the center of rotation. The angular position of each axis was measured with a hybrid potentiometer (Sakae, type 22HHPS-10; accuracy 0.2°; sampling rate: 300 Hz). Two torque motors in combination with Digital Actuator Controllers (developed by Fokker Aerospace) were used to induce systematic online controlled frictional loads to either rotation axis, in order to perturb the arm movements. The applied maximal friction (i.e., 60 Nm) resulted in an instant arrest of the corresponding manipulandum. Computer-generated auditory pacing stimuli (pitch: 200 Hz, duration: 50 ms) were presented through headphones (Sennheiser HD 520 II). To manipulate the direction of attention, two light emitting diodes (LEDs) were

---

[2] The exclusion of one LH participant following a more stringent selection criterion (i.e., $|LQ| > 70$, cf. De Poel et al., in press) yielded qualitatively similar results.

placed approximately 1 m in front of the participant. One LED was placed 50 cm to the left of the body's midline, while the other was placed 50 cm to its right.

Procedure

The participants performed bimanual oscillatory movements with the lower arms in the in-phase and antiphase coordination modes at two movement frequencies (i.e., 1 and 1.5 Hz) that were specified by means of the auditory metronome. One metronome pulse was presented for each half cycle of the movement. In the in-phase condition, participants were instructed to extend both arms at a given beep and to flex the arms at the next beep. During the antiphase trials, flexion of one arm and extension of the other arm had to coincide with the stimuli. Trial length was 30 cycles in all conditions.

At the start of each trial, either the left or the right LED was illuminated, thereby indicating the required direction of attention. The participants were instructed to concentrate on the indicated arm's movements during the entire trial, and to visually monitor these movements (cf. Franz, 2004; Swinnen et al., 1996; Wuyts et al., 1996). They were told to turn the head slightly towards the arm indicated by the LED. By doing so, a cardboard cylinder (attached to the headphones) that encircled the face prevented vision of the contralateral arm, so that the participants could only see the attended arm. The experimenter ascertained that no head rotations towards the other arm (e.g., in response to perturbation of that arm) were made during the trial. The participants were instructed to start the trial by first coordinating the arm movements with the pacing signal and subsequently directing their attention to the indicated arm. Once the head was turned in the required direction, the experimenter waited for three more movement cycles and then started the recording of 30 experimental cycles.

In 80% of the trials, a mechanical perturbation was delivered to either the left or the right arm, thereby altering the actually performed (i.e., initial) phase relation. The perturbation consisted of a complete arrest of the arm in question, and had a duration of 0.25 of the cycle time (corresponding to approximately 90° phase change). Participants were instructed to try to keep on moving the arms 'as if no perturbation had been applied' and to re-establish the initial coordination pattern after the perturbed arm had been released. The perturbation was delivered at or very close to the moment of zero velocity at peak elbow extension of the perturbed arm. Perturbation at this movement phase does not invoke large sudden changes in kinetic energy, while allowing an equally adequate estimation of relaxation time as at other movement phases (cf. Kay, Saltzman, & Kelso, 1991). The perturbation was applied randomly between the 12th and the 17th cycle of the trial, with the moment of its onset being extrapolated online from the eight preceding movement cycles. To avoid anticipation of the perturbation, the design also involved 'dummy trials' (i.e., without perturbation). The data of these dummy trials were included in the analysis of stationary performance.

The trials were grouped in two 'coordination mode blocks' (in-phase and antiphase), which were counterbalanced over participants. Within each block, the frequency, attention, and perturbation conditions were pooled and presented in a completely random order. Each experimental condition was performed four times, while the dummies were carried out two times per attention × coordination mode × frequency condition. For each participant, this resulted in a total of 76 trials, yielding an experimental session of approximately 1.5 h (including breaks). All procedures adhered to the ethical guidelines of the American Psychological Association and were approved by the Ethics Committee of the Faculty of Human Movement Sciences of the Vrije Universiteit, Amsterdam.

Data reduction

Angular position data of both arms were low-pass filtered (bi-directional second-order Butterworth filter, cut-off frequency: 10 Hz) and subsequently high-pass filtered (bi-directional second-order Butterworth filter, cut-off frequency: 0.1 Hz) to remove slow variations in the center of oscillation. Angular velocity was calculated, using a five-point approximation differentiation method, and was normalized through division by the angular frequency as prescribed by the pacing signal (cf. Beek & Beek, 1988). [This normalization procedure was appropriate because in all trials the differences between the required and actually performed frequencies were negligible (see Results).] The continuous phase angle (θ, in degrees) was derived for each arm, according to $\theta_i = \tan^{-1}(\dot{x}_i^*/x_i)$, with x_i denoting angular position, $\dot{x}_i^*$ denoting normalized angular velocity, and i indicating the sample index. Continuous relative phase between the arms (ϕ) for each sample index was defined as $\phi = \theta_D – \theta_{ND}$ (cf. Swinnen et al., 1996). Thus, $\phi > 0$ indicated a phase lead of the D limb (i.e., right limb lead for RH and left limb lead for LH participants), and $\phi < 0$ indicated a phase lead of the ND limb.

To determine adaptations in the phasing of the individual arms in response to the perturbation, a reference phase signal (θ_M) was created (De Poel et al., in press), based on the frequency specified by the metronome (f_M), using

$$\theta_{M,i} = \theta_{M,i-1} + 360^\circ(0.5 f_M / f_S) \quad (1)$$

where i is the sample index, f_M is the metronome frequency (two beeps per movement cycle), and f_S is the sampling rate of 300 Hz. The phase relations between the limbs and this reference signal were defined as $\phi_{D-M} = \theta_D - \theta_M$ for the D arm and as $\phi_{ND-M} = \theta_{ND} - \theta_M$ for the ND arm.

Analysis

Using circular statistics (Mardia, 1972), steady-state performance was evaluated on the basis of the mean of $\phi(\bar{\phi})$ and its variability, as obtained for the 2nd to the 11th cycle of each trial. The mean phase shift ($\Delta\phi$) was expressed relative to the required relative phase (ϕ_{req}), that is, $\Delta\phi = \bar{\phi} - \phi_{req}$, with $\phi_{req} = 0^\circ$ (in-phase) or $\phi_{req} = 180^\circ$ (antiphase). The stability of steady-state coordination was indexed by the within-trial variability of ϕ, with low variability corresponding to a high degree of stability (cf. Schöner, Haken, & Kelso, 1986). Variability was assessed by means of the transformed circular variance (TCV) of ϕ (Mardia, 1972), which is reminiscent of the ordinary standard deviation, with low values of the TCV indicating low variability.

Furthermore, the relative contribution of the individual arms to the relaxation back to the bimanual coordination pattern was determined, using the procedure developed by De Poel et al. (in press). To this end, the amount to which the perturbed arm (P) and the unperturbed arm (NP) altered their phasing after the perturbation was calculated, based on the phase difference between the arm and the reference signal (i.e., ϕ_{P-M} and ϕ_{NP-M}, with P = D or ND and NP = ND or D, depending on the perturbation condition). First, the trial segment in which the relaxation took place was determined for each trial. The start of this segment was defined by the moment at which the arrested arm was released (t_0). The segment ended at the moment at which the initial coordination pattern was re-established (t_{end}), which was determined by comparing the post-perturbation values of ϕ_i (as determined for each sample index i) and TCV$_i$ (as derived over a 21-point window centered around the corresponding sample index) to their mean values obtained for the eight cycles preceding the perturbation (i.e., ϕ_{pre} and TCV$_{pre}$). The relaxation process was deemed to have ended when $|\phi - \phi_{pre}| < 30^\circ$ and $\text{TCV}_i \leq \text{TCV}_{pre}$. A trial was excluded from further analysis if: (1) the difference between mean ϕ before and after the relaxation period was larger than 90°; (2) after the perturbation, ϕ remained larger than 45°; or (3) no stable pre- or post-perturbation behavior was established (i.e., $\text{TCV}_{pre,post} > 45^\circ$). On the basis of these criteria, 67 of the 1,408 trials (i.e., <5%) were excluded. Binomial tests revealed significantly uneven distributions of these trials over the coordination modes, $p < 0.001$ (in-phase: 18, antiphase: 49), frequency, $p < 0.0001$ (1 Hz: 8, 1.5 Hz: 59), and attention conditions, $p < 0.05$ (D: 23, ND: 44), but not for the perturbation conditions (D: 29, ND: 38).

The amount of change in the phasing of the perturbed arm during the relaxation period (as illustrated by the light gray areas in Fig. 1) was derived using

$$A_P = \int_{t_0}^{t_{end}} (\phi_{P-M} - \phi_0) \quad (2)$$

with ϕ_0 being the value of ϕ_{P-M} as determined at t_0. In the same fashion, A_{NP} was calculated to determine the change in phasing of the unperturbed arm (cf. dark gray areas in Fig. 1). The relative contribution of the unperturbed arm to the relaxation process was expressed by the index of coupling (IC):

$$\text{IC} = -\frac{A_{NP}}{|A_P| + |A_{NP}|} \quad (3)$$

The unperturbed arm could either accelerate ($A_{NP} > 0$) or decelerate ($A_{NP} < 0$) with respect to the metronome, resulting in IC < 0 or IC > 0, respectively. Because the 90° arrest always resulted in $A_P < 0$ (i.e., the perturbed arm was always delayed with respect to the metronome), IC > 0 indicated that the unperturbed arm decelerated to 'wait for' the perturbed arm, thereby reducing the effect of the perturbation onto the coordination between the two arms (cf. Fig. 1a). This corresponded to the expected changes in phasing in the unperturbed arm due to coupling influences exerted by the perturbed arm, as outlined in the Introduction. IC < 0, on the other hand, implied that the unperturbed arm accelerated, so that the perturbed arm had to adapt more than 90° to 'catch up' with the unperturbed arm (cf. Fig. 1b). Although also in this situation the unperturbed arm adapted its phasing in response to the perturbation, the direction of this response was not in line with the expectations (here indicated by a negative sign of IC). Note that IC = 0 if the unperturbed arm does not participate in the relaxation process (i.e., when it does not adjust its phasing), that is, if the relaxation is solely achieved by adjustments in the phasing of the perturbed arm.

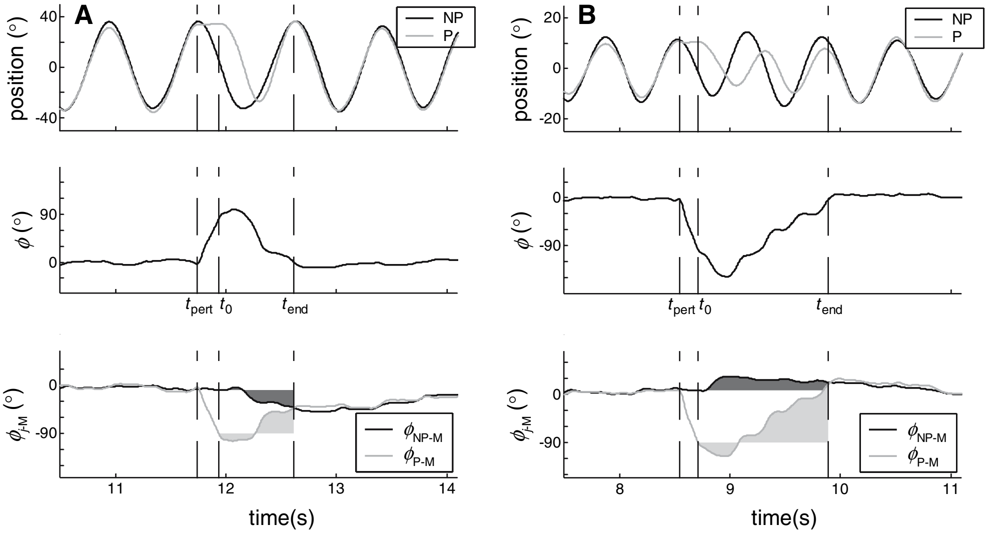

Fig. 1 Two in-phase trials illustrating the derivation of A_{P} and A_{NP}. The *dashed lines* represent perturbation onset (t_{pert}), moment of arm release (t_0), and the end of the relaxation process (t_{end}). **a** Perturbation of the right arm (movement frequency: 1.5 Hz). **b** Perturbation of the left arm (movement frequency: 1.5 Hz). *Upper panels* angular position as a function of time, for both arms (*NP* unperturbed arm, *P* perturbed arm). *Middle panels* relative phase (ϕ) as a function of time. *Lower panels* the associated $\phi_{\mathrm{P-M}}$ and $\phi_{\mathrm{NP-M}}$ as a function of time. *Gray-shaded* areas illustrate the amount of adjustment made by each arm, *light gray* perturbed arm (A_{P}), *dark gray* unperturbed arm (A_{NP})

Finally, for trials in which a perturbation was applied, stability of the bimanual pattern was indexed by the swiftness of relaxation back to the original coordination pattern after the perturbed arm had been released, which entailed analysis of the time evolution of ϕ. For the purpose of making comparisons across the three frequency conditions, the time series of ϕ were resampled with respect to cycle duration (De Poel et al., in press; for related procedures, see Bardy, Oullier, Bootsma, & Stoffregen, 2002; Court et al., 2002) prior to the analysis of the return signal, using an anti-aliasing (low-pass) finite impulse response (FIR) filter with a 10-point Kaiser window (available in the Matlab® Signal Processing Toolbox). Subsequently, the return signal (i.e., the evolution of ϕ after release of the perturbed arm) was analyzed using the procedure outlined by Post et al. (2000b). In brief, the data were fitted from the point where ϕ reached a value of 45° (i.e., $\phi_{t=0} = 45°$), using an exponential decay function that also accounted for damped oscillations in the return signal:

$$\phi(t) = p + q\mathrm{e}^{-\lambda t}\cos(\omega_{\mathrm{osc}}t + \theta_{\mathrm{osc}}) \tag{4}$$

where p is the offset in ϕ, $q = \phi_{t=0} - p$, λ is the decay parameter, ω_{osc} indicates the oscillation frequency of ϕ, and θ_{osc} denotes the phase of this oscillation (for illustrations and more details, we refer to Post et al., 2000b). Note that this procedure yields adequate estimations of λ both in the presence and absence of oscillations in the return signal of ϕ. The decay parameter λ reflects the quickness of the relaxation process and, therefore, provides an expedient measure of pattern stability. Following the criteria formulated by Post et al. (2000b), a trial was excluded from further analysis if: (1) the difference between mean ϕ before and after the transient was larger than 90°; (2) after the perturbation, ϕ remained larger than 45°; (3) no stable post-perturbation behavior was established (TCV > 45°); (4) the return signal was not a decay function within the observation interval ($\lambda < 0$); (5) the fit was unreliable (standard error of $\lambda >$ median of λ, as determined for the four different initial conditions used in the fitting procedure). Accordingly, 183 trials (i.e., 13%; evenly distributed over the groups and conditions) were excluded from further analysis. Unfortunately, for two participants (one RH and one LH) this resulted in an empty cell for one condition. As a result, the data of these two participants could not be included in the statistical analysis of λ. To minimize the effect of outliers within a set of values, median values of λ were determined for each condition.

Statistical analysis

All dependent variables were submitted to a repeated measures analysis of variance (ANOVA) with the between-subjects factor handedness (LH, RH) and the within-subjects factors attention (D, ND), coordination mode (in-phase, antiphase), frequency (1, 1.5 Hz), and (if applicable) the factor perturbed arm (D, ND). Post hoc analyses of significant interactions were based on examination of the appropriate simple effects (Keppel, 1991). The significance level was set at $p < 0.05$. In addition, the corresponding effect sizes (f) were calculated based on the partial eta squared (η^2_p, Cohen, 1988).

Results

Steady-state performance

Movement frequency

To verify that participants had achieved the required 1:1 frequency locking between the arms, the movement frequencies of the individual arms were analyzed. For six trials (which were evenly distributed over the conditions), the mean frequencies of the left and the right arm differed 5–15%. These trials were excluded from further analysis. For the remaining 1,674 trials, this frequency difference was 3% or smaller, indicating that the movements were 1:1 frequency locked. The prescribed frequencies were adequately performed, with averages and corresponding standard deviations of 1.004 Hz (SD = 0.009) and 1.508 Hz (SD = 0.017).

Effects of handedness on the mean phase shift ($\Delta\phi$)

A phase shift larger than 0° implied a phase lead of the D limb, relative to the required coordination pattern. A one-sample t test, $t(21) = 4.47$, $p < 0.001$, with an effect size (d) of 0.97 (see Cohen, 1988), revealed that the grand mean of the phase shifts (2.9°) was significantly larger than 0°, indicating that, indeed, the D arm tended to lead the ND arm in time (see also Fig. 2). The ANOVA revealed a main effect of coordination mode, $F(1, 20) = 7.38$, $p < 0.05$, $f = 0.61$, which implied that the D arm lead was larger for antiphase (mean $\Delta\phi = 4.1°$) than for in-phase coordination (mean $\Delta\phi = 1.7°$). The significant coordination mode × frequency interaction, $F(1, 20) = 5.11$, $p < 0.05$, $f = 0.51$, and subsequent post hoc simple effects analyses showed that the effect of coordination mode was only significant for performance at 1 Hz, $F(1, 20) = 3.58$, $p = 0.07$, $f = 0.40$, [mean $\Delta\phi = 1.1°$ (in-phase) and 2.5° (antiphase)]. The main effect of frequency was also significant, $F(1, 20) = 22.29$, $p < 0.001$, $f = 1.06$. The phase lead of the D arm increased with movement frequency [mean $\Delta\phi = 1.8°$ (1 Hz) and 4.0° (1.5 Hz)], although the significant frequency × handedness interaction, $F(1, 20) = 6.21$, $p < 0.05$, $f = 0.56$, and subsequent simple effects analyses indicated that this frequency effect was only significant for RH participants, $F(1, 9) = 27.82$, $p < 0.001$, $f = 1.76$, [mean $\Delta\phi = 2.2°$ (1 Hz) and 5.8° (1.5 Hz)].

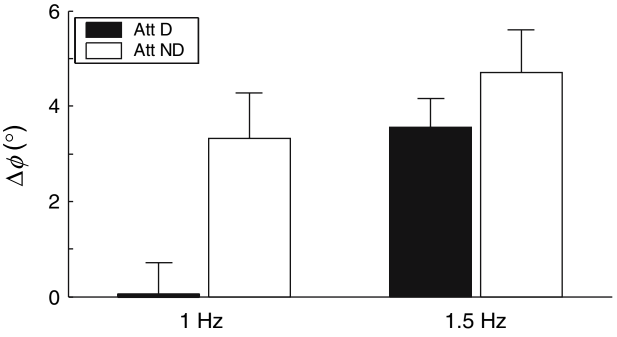

Fig. 2 Mean phase shift ($\Delta\phi$) as a function of direction of attention and movement frequency; $\Delta\phi > 0$ denotes dominant arm lead. *Att D* attention on dominant arm, *Att ND* attention on non-dominant arm. *Error bars* represent the between-subjects standard errors

Effects of attention on the mean phase shift ($\Delta\phi$)

The analysis of the mean phase shift also revealed a significant main effect of attention, $F(1, 20) = 12.03$, $p < 0.005$, $f = 0.78$. Contrary to our expectations, however, this effect implied that when attention was focused on the D limb (mean $\Delta\phi = 1.7°$) the D limb lead was smaller than when attention was focused on the ND limb (mean $\Delta\phi = 4.1°$), as can be seen in Fig. 2. Furthermore, the significant attention × frequency interaction, $F(1, 20) = 13.81$, $p < 0.005$, $f = 0.83$, and subsequent post hoc simple effects analyses revealed that the effect of attention was only significant for performance at 1 Hz, $F(1, 20) = 23.28$, $p < 0.0001$, $f = 1.08$, (see Fig. 2).

Relative phase variability (TCV)

Analysis of the variability of relative phase revealed significant effects of coordination mode, $F(1, 20) = 90.65$, $p < 0.001$, $f = 2.13$, frequency, $F(1, 20) = 27.11$, $p < 0.001$, $f = 1.16$, and the coordination mode × frequency interaction, $F(1, 20) = 16.04$, $p < 0.005$, $f = 0.90$. All post hoc simple effects analyses regarding this interaction revealed significant differences, $F(1,20) > 23.48$, $p < 0.0001$; $f > 1.06$. Variability increased with movement frequency and was significantly larger for antiphase coordination than for in-phase coordination, while the latter effect was more pronounced at the higher frequency [mean TCV = 8.0° (in-phase) and

12.3° (antiphase)] than at the lower frequency [mean TCV = 6.9° (in-phase) and 9.4° (antiphase)].

Perturbation analysis

Index of coupling

Statistical analysis of IC revealed a main effect of perturbed arm, $F(1, 20) = 5.08$, $p < 0.05$, $f = 0.50$. As expected, IC was larger when the perturbation was applied to the D arm (mean IC = 0.31), indicating that the adaptations of the (unperturbed) ND arm were larger when the D arm was perturbed than those of the (unperturbed) D arm in response to ND arm perturbation (mean IC = 0.24). The significant perturbed arm × attention interaction, $F(1, 20) = 11.21$, $p < 0.005$, $f = 0.75$, and subsequent simple effects analyses revealed that the effect of perturbed arm was only significant when attention was focused on the D limb, $F(1, 20) = 10.51$, $p < 0.005$, $f = 0.72$. In agreement with our predictions, this result implied that the handedness-related asymmetry in coupling strength (indexed by IC) was reduced when attention was focused on the ND limb (see Fig. 3). In addition, the coordination mode × frequency interaction was significant, $F(1, 20) = 9.40$, $p < 0.01$, $f = 0.69$. Post hoc simple effects analyses revealed that for in-phase coordination the 1 Hz frequency condition yielded significantly larger values of IC (mean IC = 0.34) than the 1.5 Hz frequency condition (mean IC = 0.23), $F(1, 20) = 8.09$, $p < 0.01$, $f = 0.64$.

Stability: decay parameter (λ)

The ANOVA revealed that solely the effect of perturbed arm was significant, $F(1, 18) = 9.19$, $p < 0.01$, $f = 0.71$. Values of λ were larger for D arm perturbation (mean $\lambda = 0.84$) than for ND arm perturbation (mean $\lambda = 0.65$). This result implied that in the latter condition more movement cycles were required for the relaxation to the original bimanual pattern.

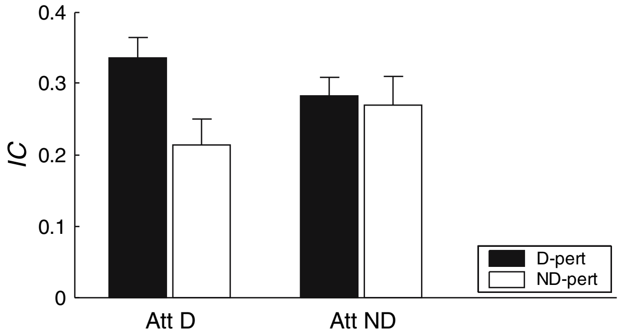

Fig. 3 Mean values of IC (i.e., relative contribution of unperturbed arm to the relaxation process) as a function of perturbed arm and attention. *Att D* attention on dominant arm, *Att ND* attention on non-dominant arm, *D-pert* perturbation of dominant arm, *ND-pert* perturbation of non-dominant arm. *Error bars* represent the between-subjects standard errors

Discussion

In line with the suggestion that influences of handedness on bimanual coordination are a reflection of an attentional bias (Peters, 1989, 1994), previous studies have demonstrated that the effects of attentional asymmetries on the relative phasing between the limbs are comparable to those of handedness (e.g., Amazeen et al., 1997; Swinnen et al., 1996). The present study extended and deepened the empirical investigation of this conjecture by examining the influence of laterally focused attention at the level of the (asymmetry in) coupling processes that govern the relative phase dynamics. Based on recent theoretical and empirical results regarding the effects of hand dominance on interlimb coupling strength, it was hypothesized that the influence of the D limb on the ND limb was larger than vice versa and that this effect would be reduced when attention was focused on the ND limb. Falsification of the latter hypothesis would refute Peters' (1989, 1994) suggestion that effects of handedness in bimanual coordination are expressions of an attentional bias. Relatedly, the typically observed D limb phase lead was predicted to increase (decrease) when attention was focused on the D (ND) limb. Before we turn to the discussion of the effects of laterally focused attention, the effects of handedness will be addressed first.

Handedness

All predictions with regard to handedness were confirmed. In line with the findings of De Poel et al. (in press), the contribution of the ND limb to relaxation of the bimanual pattern (as indexed by the IC) in response to a perturbation of the D limb was larger than the contribution of the D limb after the ND limb was perturbed. This revealed an asymmetry in the strength of the coupling between the limbs, with the ND limb being more strongly influenced by the D limb than vice versa (De Poel et al., in press; Peper et al., 2004a; see also Byblow et al., 1994; Carson, 1993). Whereas, in general, expressions of handedness are less consistent for left-handers than for right-handers (cf. Peters, 1994; Shen & Franz, 2005), no such indications were found in the present study (in contrast to De Poel et al., 2006, in press). Furthermore, analysis of the quickness of relaxation after the perturbation (as indexed by λ) indicated a faster return to the original bimanual coordination pattern after perturbation of the D arm, corroborating previous findings (De Poel et al., in press; Post et al., 2000b). This result supported the prediction that the ND limb is more strongly influenced (attracted) by the D limb than vice versa.

The results regarding the mean phase shift ($\Delta\phi$) revealed that for both RH and LH participants the D limb was leading the ND limb in time (for similar results see, e.g., Amazeen et al., 1997; De Poel et al., in press; Swinnen et al., 1996; Treffner & Turvey, 1995, 1996). This phase lead of the D limb was larger for antiphase than for in-phase coordination (cf. De Poel et al., in press; Treffner & Turvey, 1995) and increased with movement frequency (cf. De Poel et al., in press; Stucchi & Viviani, 1993; Treffner & Turvey, 1996), although the latter effect was only significant for RH participants.

In combination, these results corroborated the results of De Poel et al. (in press) and the theoretical argumentation of Peper et al. (2004a) that the handedness-related asymmetry in the relative phasing (as captured by the potential proposed by Treffner & Turvey, 1995) results from an asymmetry in interlimb coupling strength.

Attentional asymmetries: interlimb coupling strength

Effects of the direction of attention on the asymmetry in coupling strength were also observed, indicating that the intrinsic coupling asymmetry was indeed modulated by attentional focus. In accordance with the hypothesis, a clear asymmetry in coupling strength was observed when attention was directed to the D limb, whereas this asymmetry was reduced when attention was focused on the ND limb (see Fig. 3). The fact that both handedness and asymmetric attentional focus affected the asymmetry in interlimb coupling strength [with the ND (unattended) limb being more strongly influenced by the D (attended) limb than vice versa] is in line with the assertion that effects of handedness in bimanual coordination are a reflection of an (inherent) attentional asymmetry (Peters, 1989, 1994; see Introduction). This interpretation was further substantiated by comparing the results obtained for the present conditions (involving asymmetrical attentional focus) to an attentionally neutral condition. This was possible because 12 participants (6 LH and 6 RH) had been recruited from the participants in the experiment of De Poel et al. (in press), which involved the same perturbation design (i.e., D and ND limb perturbation) without manipulation of attentional focus. For these 12 participants, the IC values in this attentionally neutral condition were compared to those obtained in the two attention conditions (D, ND) of the present experiment. A repeated measures ANOVA with the factors attention (D, ND, neutral) and perturbed arm (D, ND) revealed a significant perturbed arm × attention interaction, $F(1, 20) = 4.68$, $p < 0.05$, $f = 0.67$. Subsequent post hoc simple effects analyses indicated that IC differed over the two perturbation conditions when attention was focused on the D limb, $F(1, 10) = 6.14$, $p < 0.05$, $f = 0.78$ (D limb perturbed: 0.34; ND limb perturbed: 0.21), and for the neutral condition, $F(1, 10) = 5.32$, $p < 0.05$, $f = 0.70$ (D limb perturbed: 0.34; ND limb perturbed: 0.23), whereas this was not the case when the ND limb was attended (D limb perturbed: 0.28; ND limb perturbed: 0.29). This comparison provides additional evidence that the handedness-related asymmetry in coupling strength was modulated by attentional focus, in a manner that was consistent with Peters' proposition.

Attentional asymmetries: relative phase and amplitude

The results showed that attentional asymmetry affected the phase relation (ϕ) between the limbs, but the direction of this effect was opposite to the expected effect. Focusing attention on the D limb decreased the D limb lead, whereas an increase was observed when attention was focused on the ND limb.[3] This finding does not accord with the common observation that attentional focus on the D limb enhanced the D limb phase lead (Amazeen et al., 1997; Franz, 2004; Pellegrini et al., 2004; Riley et al., 1997; Swinnen et al., 1996), and contradicts the predictions derived from the asymmetric HKB-potential (Amazeen et al., 1997; Treffner & Turvey, 1995) built on the assumption that attention has a similar effect on the coordination dynamics as handedness (following Peters, 1989, 1994).

To explain this unexpected result, the amplitudes of the limb movements were taken into consideration, because recent studies indicated that an imposed difference between the amplitudes of the limbs'

---

[3] Inclusion of the attentionally neutral condition in the ANOVA for the 12 participants that also participated in the experiment by De Poel et al. (in press; see previous section) also revealed a main effect of attention, $F(1, 20) = 12.13, p < 0.001, f = 1.10$. Post hoc simple effects analyses revealed that directing attention towards the D limb (mean $\Delta\phi = 0.8°$) decreased the D limb phase lead when compared to the neutral condition (mean $\Delta\phi = 2.7°$), $F(1, 10) = 8.43$, $p < 0.05$, $f = 0.95$, whereas the increase that was observed when attention was directed to the ND limb (mean $\Delta\phi = 4.5°$) did not reach significance.

periodic movements resulted in a phase lead of the limb performing the smallest amplitude (Amazeen et al., 2005; Heuer & Klein, 2005; for similar results obtained for bimanual circle drawing, see Buchanan & Ryu, 2006). Because in general unpaced (uncoupled) oscillations at larger amplitudes involve slower movement frequencies, the observed phase leads were argued to be related a difference in the uncoupled frequencies (eigenfrequencies) of the two limbs. It is well documented that when the limbs differ in this regard, the 'faster' limb tends to lead the 'slower' limb in time (see, e.g., Jeka & Kelso, 1995; Peper, Nooij, & Van Soest, 2004b; Sternad, Amazeen, & Turvey, 1996), a phenomenon that has been accounted for by another extension of the HKB-model (Fuchs et al., 1996; Kelso, Delcolle & Schöner, 1990) capturing the coordination between two components with unequal eigenfrequencies ($\Delta\omega$). Indeed, various studies investigating unimanual oscillatory movements have shown that movement frequency is inversely related to movement amplitude (for hand movements: e.g., Kay, Kelso, Saltzman, & Schöner, 1987; Rosenbaum, Slotta, Vaughan, & Plamondon, 1991; for lower arm movements: e.g., Beek, Rikkert, & Van Wieringen, 1996; Hatsopoulos & Warren, 1996; Rosenbaum et al., 1991). Moreover, Rosenbaum et al. (1991) demonstrated that performance at a larger prescribed amplitude resulted in a lower (unprescribed) movement frequency. In view of these considerations, a difference in amplitude between the limbs may be expected to result in a lead–lag relationship given the associated difference in the uncoupled movement frequencies (Amazeen et al., 2005; Buchanan & Ryu, 2006).

This interpretation motivated us to analyze the amplitudes of the individual limb movements, in particular because it has been demonstrated (for rhythmic circle drawing) that focusing attention on the movements of a limb affects the spatial extent of the limb's movement. For instance, visually monitoring unimanual circling movements of a particular limb increased the size of these movements (Zelaznik & Lantero, 1996) and focusing (either visual or non-visual) attention on one of the limbs during bimanual circling resulted in a larger excursion of the movements of the attended limb (Franz, 2004). Given the preceding argumentation, this larger amplitude of the attended limb is associated with a lower uncoupled frequency, resulting in a modulation of the lead–lag relationship between the limbs that is consistent with that obtained in the present study. Therefore, we examined whether the observed effect of attentional focus on the relative phase shift was indeed associated with an attention-related difference in amplitude.

A repeated measures ANOVA conducted on mean angular amplitude of stationary performance, with the factors arm (D, ND) and attention (D, ND), revealed a significant arm × attention interaction, $F(1, 20) = 38.00$, $p < 0.0001$, $f = 1.38$.[4] Post hoc simple effects analyses indicated that, in line with the results of Zelaznik and Lantero (1996), the movement amplitude of an arm was larger when it was monitored (D: 15.8°; ND: 15.6°) than when it was not monitored (D: 14.5°; ND: 14.7°) for both the D arm, $F(1, 20) = 30.10$, $p < 0.0001$, $f = 1.23$, and the ND arm, $F(1, 20) = 17.48$, $p < 0.001$, $f = 0.93$, and that the amplitude of the attended arm was significantly larger than the amplitude of the unattended arm, both when attention was directed to the D limb, $F(1, 20) = 6.92$, $p < 0.05$, $f = 0.59$, and to the ND limb, $F(1, 20) = 8.40$, $p < 0.01$, $f = 0.65$. In accordance with the preceding, this result revealed an attention-related difference in amplitude between the arms, with the attended arm performing larger movements than the unattended arm (cf. Franz, 2004). Averaged over participants, the difference in amplitude was 1.5° (corresponding to 10% of the amplitude of the attended limb). Judging from the results obtained for unimanual lower arm movements by Beek et al. (1996; see their Fig. 3) and Rosenbaum et al. (1991; see their Fig. 1), this amplitude difference is associated with an uncoupled frequency difference ($\Delta\omega$) ranging from 0.1 to 1.0 Hz. This range of eigenfrequency differences has been demonstrated to have considerable effects on the mean phase shift (e.g., Schmidt, Shaw & Turvey, 1993; Sternad et al., 1996; Treffner & Turvey, 1995). On the basis of the preceding argumentation it is, thus, likely that the presently established lead–lag relationships indeed resulted from the observed attention-related difference in amplitude between the limbs (associated with a difference in uncoupled frequencies).[5]

To summarize, the present results revealed two distinct effects of laterally focused attention: (1) The handedness-related asymmetry in coupling strength

---

[4] Cycle amplitude (in degrees) was defined as the average of the half-cycle peak-to-peak excursions, divided by 2. Since we were specifically interested in the effect of attention on the difference in amplitude of both arm movements, the values were averaged over coordination mode and frequency conditions.

[5] Given this relation, it is useful to emphasize that the observed D limb phase lead was not related to an amplitude difference, because the ANOVA on mean angular amplitude did not reveal a main effect of arm (D, ND). Moreover, re-analysis of the attentionally neutral condition (as obtained by De Poel et al., in press) also revealed no significant difference between the amplitudes of the D and ND arm.

was decreased (increased) when attention was directed to the ND (D) limb; (2) The attended limb oscillated with a larger amplitude than the unattended limb. According to the dynamical model associated with asymmetric coupling strength (Peper et al., 2004a; Treffner & Turvey, 1995), the former result was expected to be associated with a decrease (increase) in the phase lead of the D limb when attention was focused on the ND (D) limb. On the other hand, the latter result implied that the D limb lead would increase (decrease) when attention was directed to the ND (D) limb (as revealed by the coordination dynamics identified for systems with different uncoupled frequencies; e.g., Fuchs et al., 1996; Kelso et al., 1990). Thus, these two tendencies affect the relative phasing between the limbs in opposite directions. Given the present finding that the D limb lead was larger when attention was directed to the ND limb, this may suggest that, with regard to the mean relative phasing between the limbs, the effects of the attentional modulations of the asymmetry in coupling strength were masked by the influence of an attention-related difference in amplitude.

Performance stability

The finding that (intentionally) focusing the attention on one of the limbs induced modulations in the asymmetry in coupling strength suggests that coupling parameters may be intentionally adjusted. This is in line with previous indications that the coupling asymmetry is affected by intentional processes (Byblow, Summers, Semjen, Wuyts, & Carson, 1999; Byblow, Lewis, Stinear, Austin, & Lynch, 2000; Carson et al., 1996; De Poel et al., 2006). The question remains, however, whether the ability to adjust the coupling has beneficial consequences for bimanual performance, particularly in view of previous indications that an asymmetry in coupling strength may be advantageous for bimanual coordination (Byblow et al., 1998; Peper et al., 1995a; Peper, Beek, & Van Wieringen, 1995b; Summers et al., 2002). Indeed, previous studies indicated that focusing attention on the movements of the D hand enhanced stability of relative phase during bimanual performance (Amazeen et al., 1997; Swinnen et al., 1996). In contrast to these studies, however, the present results revealed that the stability of coordination (as indexed by both TCV and λ) was equivalent for the two attention conditions (for similar results see Franz, 2004; Pellegrini et al., 2004; Wuyts et al., 1996), whereas only the well-established stability difference between in-phase and antiphase coordination and the lower stability at higher movement frequency (e.g., Post et al., 2000b; Treffner & Turvey; 1995; for a review see Kelso, 1995) were confirmed [as indicated by the variability of relative phase (TCV)]. As such, these findings are not in agreement with the asymmetric HKB potential (Treffner & Turvey, 1995), which predicts that coordinative stability increases with larger asymmetry (Amazeen et al., 1997). However, also in this context, it is possible that the effects of asymmetric coupling strength on the stability of coordination have been obscured by the effect of differential uncoupled frequencies (corresponding to the attention-related imbalance in amplitude between the limbs). To gain more insight in this regard, it is necessary to disentangle the influences of asymmetries in the coupling and/or the components, for instance by determining IC for various combinations of prescribed movement amplitudes.

Conclusion

The present study indicated that manipulation of attentional focus affected bimanual coordination at both the level of the coupling and the components, which had opposite effects on the relative phasing between the limbs. These results emphasized the importance of combining multiple levels of analysis in studying rhythmic bimanual coordination, also in view of the fact that similar relative phase dynamics may result from distinct underlying system properties and processes (cf. Peper et al., 2004c).

The findings regarding IC unequivocally corroborated our prediction that the asymmetry in interlimb coupling strength diminishes when attention is directed to the ND limb. Although this result was in line with Peters' (1989, 1994) proposal that handedness effects are a reflection of asymmetrically divided attention during bimanual movements, some caution is in order when interpreting the present results as evidence for this suggestion. After all, on the basis of behavioral results alone, a causal relation between attentional focus and handedness cannot be established unambiguously. In this context it is interesting to note that, although the present results indicated that focusing attention on the ND limb attenuated the handedness-related asymmetry in coupling, the asymmetry was not reversed in this situation. As a consequence, it can be concluded that the coupling asymmetry caused by an inherent (handedness-related) asymmetry was stronger than the voluntary attentional modulation as induced in the present experiment. At this point it remains to be established whether the inherent asymmetry indeed has an attentional basis (as proposed by Peters, 1989, 1994), or whether this asymmetry and the effects of voluntary attentional focus are associated with distinct, unrelated mechanisms.

In further unraveling this relation, essential additional insights may be obtained by extending the analysis to the neural or neurophysiological level. For upper limb movements, handedness-related asymmetries in cortical (e.g., Dassonville, Zhu, Ugurbil, Kim, & Ashe, 1997; Jancke et al., 1998; Kim et al., 1993; Viviani, Perani, Grassi, Bettinardi, & Fazio, 1998) and corticospinal activity (e.g., De Genarro et al., 2004; Triggs, Calvanio, & Levine, 1997; Triggs, Calvanio, Macdonell, Cros, & Chiappa, 1994) have been established as well as changes in brain activity in response to attentional manipulations (Johansen-Berg & Matthews, 2002). However, the relation between the neurophysiological correlates of these two factors has (to our knowledge) not been examined to date. In particular, also in view of the recent suggestion that the lateralized functional involvement of both hemispheres is flexible and may be modulated by various factors at different time scales (including attention and learning; Serrien et al., 2006), the current behavioral results indicate that it would be worthwhile to examine whether and how attentional focus on one of the limbs affects the neurophysiological handedness-related asymmetries.

References

Amazeen, E. L., Amazeen, P. G., Treffner, P. J., & Turvey, M. T. (1997). Attention and handedness in bimanual coordination dynamics. *Journal of Experimental Psychology: Human Perception and Performance, 23*, 1552–1560.

Amazeen, E. L., Ringenbach, S. D., & Amazeen, P. G. (2005). The effects of attention and handedness on coordination dynamics in a bimanual Fitts' law task. *Experimental Brain Research, 164*, 484–499.

Bardy, B. G., Oullier, O., Bootsma, R. J., & Stoffregen, T. A. (2002). Dynamics of human postural transitions. *Journal of Experimental Psychology: Human Perception and Performance, 28*, 499–514.

Beek, P. J., & Beek, W. J. (1988). Tools for constructing dynamical models of rhythmic movement. *Human Movement Science, 7*, 301–342.

Beek, P. J., Rikkert, W. E. I., & Van Wieringen, P. C. W. (1996). Limit cycle properties of rhythmic forearm movements. *Journal of Experimental Psychology: Human Perception and Performance, 22*, 1077–1093.

Buchanan, J. J., & Ryu, Y. U. (2006). One-to-one and polyrhythmic temporal coordination in bimanual circle tracing. *Journal of Motor behavior, 38,* 163–184.

Byblow, W. D., Bysouth-Young, D., Summers, J. J., & Carson, R. G. (1998). Performance asymmetries and coupling dynamics in the acquisition of multifrequency bimanual coordination. *Psychological Research/ Psychologische Forschung, 61*, 56–70.

Byblow, W. D., Carson, R. G., & Goodman, D. (1994). Expressions of asymmetries and anchoring in bimanual coordination. *Human Movement Science, 13*, 3–28.

Byblow, W. D., Chua, R., & Goodman, D. (1995). Asymmetries in coupling dynamics of perception and action. *Journal of Motor Behavior, 27*, 123–137.

Byblow, W. D., Lewis, G. N., Stinear, J. W., Austin, N. J., & Lynch, M. (2000). The subdominant hand increases the efficacy of voluntary alterations in bimanual coordination. *Experimental Brain Research, 131*, 366–374.

Byblow, W. D., Summers, J. J., Semjen, A., Wuyts, I. J., & Carson, R. G. (1999). Spontaneous and intentional pattern switching in a multisegmental bimanual coordination task. *Motor Control, 3*, 372–393.

Carson, R. G. (1993). Manual asymmetries: Old problems and new directions. *Human Movement Science, 12*, 479–506.

Carson, R. G., Byblow, W. D., Abernethy, B., & Summers, J. J. (1996). The contribution of inherent and incidental constraints to intentional switching between patterns of bimanual coordination. *Human Movement Science, 15*, 565–589.

Cohen J. (1988). *Statistical power analysis for the behavioral sciences*. Hillsdale: Lawrence Erlbaum Associates.

Court, M. L. J., Bennett, S. J., Williams, A. M., & Davids, K. (2002). Local stability in coordinated rhythmic movements: Fluctuations and relaxation times. *Human Movement Science, 21*, 39–60.

Daffertshofer, A., Van Den Berg, C., & Beek, P. J. (1999). A dynamical model for mirror movements. *Physica D, 132*, 243–266.

Dassonville, P., Zhu, X. H., Ugurbil, K., Kim, S. G., & Ashe, J. (1997). Functional activation in motor cortex reflects the direction and the degree of handedness. *Proceedings of the National Academy of Sciences of the United States of America, 94*, 14015–14018.

De Gennaro, L., Cristiani, R., Bertini, M., Curcio, G., Ferrara, M., Fratello, F., et al. (2004). Handedness is mainly associated with an asymmetry of corticospinal excitability and not of transcallosal inhibition. *Clinical Neurophysiology, 115*, 1305–1312.

De Poel, H. J., Peper, C. E., & Beek, P. J. (2006). Intentional switches between bimanual coordination patterns are primarily effectuated by the nondominant hand. *Motor Control, 10*, 7–23.

De Poel, H. J., Peper, C. E., & Beek, P. J. (in press). Handedness-related asymmetry in coupling strength in bimanual coordination: Furthering theory and evidence. *Acta Psychologica*.

Franz, E. A. (2004). Attentional distribution of task parameters to the two hands during bimanual performance of right- and left-handers. *Journal of Motor Behavior, 36*, 71–81.

Franz, E. A., Rowse, A., & Ballantine, B. (2002). Does handedness determine which hand leads in a bimanual task? *Journal of Motor Behavior, 34*, 402–412.

Fuchs, A., Jirsa, V. K., Haken, H., & Kelso, J. A. S. (1996). Extending the HKB model of coordinated movement to oscillators with different eigenfrequencies. *Biological Cybernetics, 74*, 21–30.

Guiard, Y. (1987). Asymmetric division of labor in human skilled bimanual action: The kinematic chain as a model. *Journal of Motor Behavior, 19*, 486–517.

Haaland, K. Y., & Harrington, D. L. (1996). Hemispheric asymmetry of movement. *Current Opinion in Neurobiology, 6*, 796–800.

Haken, H., Kelso, J. A. S., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biological Cybernetics, 51*, 347–356.

Hatsopoulos, N. G., & Warren, W. H. (1996). Resonance tuning in rhythmic arm movements. *Journal of Motor Behavior, 28*, 3–14.

Heuer, H., & Klein, W. (2005). Intermanual interactions in discrete and periodic bimanual movements with same and different amplitudes. *Experimental Brain Research, 167,* 220–237.

Jancke, J., Peters, M., Schlaug, G., Posse, S., Steinmetz, H., & Müller-Gartner, H. W. (1998). Differential magnetic resonance signal change in human sensorimotor cortex to finger movements of different rate of the dominant and subdominant hand. *Cognitive Brain Research, 6*, 279–284.

Jeka, J. J., & Kelso, J. A. S. (1995). Manipulating symmetry in the coordination dynamics of human movement. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 360–374.

Johansen-Berg, H., & Matthews, P. M. (2002). Attention to movement modulates activity in sensori-motor areas, including primary motor cortex. *Experimental Brain Research, 142*, 13–24.

Kay, B. A., Kelso, J. A. S., Saltzman, E. L., & Schöner, G. (1987). Space-time behavior of single and bimanual rhythmical movements: Data and limit cycle model. *Journal of Experimental Psychology: Human Perception and Performance, 13*, 178–192.

Kay, B. A., Saltzman, E. L., & Kelso, J. A. S. (1991). Steady-state and perturbed rhythmical movements: A dynamical analysis. *Journal of Experimental Psychology: Human Perception and Performance, 17*, 183–197.

Kelso, J. A. S., DelColle, J. D., & Schöner, G. (1990). Action-perception as a pattern formation process. In M. Jeannerod (Ed.), *Attention and performance XIII: Motor representation and control* (pp. 139–169). Hillsdale: Erlbaum.

Kelso, J. A. S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge: MIT press.

Keppel, G. (1991). *Design and analysis: A researcher's handbook* (3rd edn.). Upper Saddle River: Prentice-Hall.

Kim, S. G., Ashe, J., Hendrich, K., Ellermann, J. M., Merkle, H., Ugurbil, K., et al. (1993). Functional magnetic-resonance-imaging of motor cortex: hemispheric asymmetry and handedness. *Science, 261*, 615–617.

Mardia, K. V. (1972). *Statistics of directional data*. London: Academic.

Mottet, D., & Bootsma, R. J. (1999). The dynamics of goal-directed rhythmical aiming. *Biological Cybernetics, 80*, 235–245.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113.

Pellegrini, A. M., Andrade, E. C., & Teixeira, L. A. (2004). Attending to the non-preferred hand improves bimanual coordination in children. *Human Movement Science, 23*, 447–460.

Peper, C. E., Beek, P. J., & Van Wieringen, P. C. W. (1995a). Coupling strength in tapping a 2:3 polyrhythm. *Human Movement Science, 14*, 217–245.

Peper, C. E., Beek, P. J., & Van Wieringen, P. C. W. (1995b). Multifrequency coordination in bimanual tapping: Asymmetrical coupling and signs of supercriticality. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 1117–1138.

Peper, C. E., Daffertshofer, A., & Beek, P. J. (2004a). Dynamical models of rhythmic interlimb coordination: Relating pattern (in)stability to neural processes and effector properties. In S. Swinnen, & J. Duysens (Eds.), *Neuro-behavioral determinants of interlimb coordination*. Amsterdam: Kluwer.

Peper, C. E., Nooij, S. A. E., & van Soest, A. J. (2004b). Mass perturbation of a body segment: 2. Effects on interlimb coordination. *Journal of Motor Behavior, 36*, 425–441.

Peper, C. E., Ridderikhoff, A., Daffertshofer, A., & Beek, P. J. (2004c). Explanatory limitations of the HKB model: Incentives for a two-tiered model of rhythmic interlimb coordination. *Human Movement Science, 23*, 673–697.

Peters, M. (1989). Do feedback processing, output variability, and spatial complexity account for manual asymmetries? *Journal of Motor Behavior, 21*, 151–155.

Peters, M. (1994). Does handedness play a role in the coordination of bimanual movements? In S. P. Swinnen, J. Massion, H. Heuer & P. Casaer (Eds.), *Interlimb coordination: Neural, dynamical and cognitive constraints* (pp. 595–615). Orlando: Academic.

Peters, M., & Schwartz, S. (1989). Coordination of the two hands and effects of attentional manipulation in the production of a bimanual 2:3 polyrhythm. *Australian Journal of Psychology, 41*, 215–224.

Post, A. A., Peper, C. E., & Beek, P. J. (2000a). Relative phase dynamics in perturbed interlimb coordination: The effects of frequency and amplitude. *Biological Cybernetics, 83*, 529–542.

Post, A. A., Peper, C. E., Daffertshofer, A., & Beek, P. J. (2000b). Relative phase dynamics in perturbed interlimb coordination: Stability and stochasticity. *Biological Cybernetics, 83*, 443–459.

Riley, M. A., Amazeen, E. L., Amazeen, P. G., Treffner, P. J., & Turvey, M. T. (1997). Effects of temporal scaling and attention on the asymmetrical dynamics of bimanual coordination. *Motor Control, 1*, 263–283.

Rosenbaum, D. A., Slotta, J. D., Vaughan, J., & Plamondon, R. (1991). Optimal movement selection. *Psychological Science, 2*, 86–91.

Sainburg, R. L. (2002). Evidence for a dynamic-dominance hypothesis of handedness. *Experimental Brain Research, 142*, 241–258.

Schmidt, R. C., Shaw, B. K., & Turvey, M. T. (1993). Coupling dynamics in interlimb coordination. *Journal of Experimental Psychology: Human Perception and Performance, 19*, 397–415.

Scholz, J. P., Kelso, J. A. S., & Schöner, G. (1987). Nonequilibrium phase transitions in coordinated biological motion: Critical slowing down and switching time. *Physics Letters A, 123*, 390–394.

Schöner, G., Haken, H., & Kelso, J. A. S. (1986). A stochastic theory of phase-transitions in human hand movement. *Biological Cybernetics, 53*, 247–257.

Semjen, A., Summers, J. J., & Cattaert, D. (1995). Hand coordination in bimanual circle drawing. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 1139–1157.

Serrien, D. J., Ivry, R. B., & Swinnen, S. P. (2006). Dynamics of hemispheric specialization and integration in the context of motor control. *Nature Reviews Neuroscience, 7*, 160–167.

Shen, Y. C., & Franz, E. A. (2005). Hemispheric competition in left-handers on bimanual reaction time tasks. *Journal of Motor Behavior, 37*, 3–9.

Sherwood, D. E., & Rios, V. (2001). Divided attention in bimanual aiming movements: Effects on movement accuracy. *Research Quarterly for Exercise and Sport, 72*, 210–218.

Sternad, D., Amazeen, E. L., & Turvey, M. T. (1996). Diffusive, synaptic, and synergetic coupling: An evaluation through in-phase and antiphase rhythmic movements. *Journal of Motor Behavior, 28*, 255–269.

Stucchi, N., & Viviani, P. (1993). Cerebral dominance and asynchrony between bimanual two-dimensional movements. *Journal of Experimental Psychology: Human Perception and Performance, 19*, 1200–1220.

Summers, J. J., Davis, A. S., & Byblow, W. D. (2002). The acquisition of bimanual coordination is mediated by anisotropic coupling between the hands. *Human Movement Science, 21*, 699–721.

Swinnen, S. P., Jardin, K., & Meulenbroek, R. (1996). Between-limb asynchronies during bimanual coordination: Effects of manual dominance and attentional cueing. *Neuropsychologia, 34*, 1203–1213.

Treffner, P. J., & Turvey, M. T. (1995). Handedness and the asymmetric dynamics of bimanual rhythmic coordination. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 318–333.

Treffner, P. J., & Turvey, M. T. (1996). Symmetry, broken symmetry, and handedness in bimanual coordination dynamics. *Experimental Brain Research, 107*, 463–478.

Triggs, W. J., Calvanio, R., & Levine, M. (1997). Transcranial magnetic stimulation reveals a hemispheric asymmetry correlate of intermanual differences in motor performance. *Neuropsychologia, 35*, 1355–1363.

Triggs, W. J., Calvanio, R., Macdonell, R. A. L., Cros, D., & Chiappa, K. H. (1994). Physiological motor asymmetry in human handedness: Evidence from transcranial magnetic stimulation. *Brain Research, 636*, 270–276.

Viviani, P., Perani, D., Grassi, F., Bettinardi, V., & Fazio, F. (1998). Hemispheric asymmetries and bimanual asynchrony in left- and right-handers. *Experimental Brain Research, 120*, 531–536.

Wuyts, I. J., Summers, J. J., Carson, R. G., Byblow, W. D., & Semjen, A. (1996). Attention as a mediating variable in the dynamics of bimanual coordination. *Human Movement Science, 15*, 877–897.

Yamanishi, J. I., Kawato, M., & Suzuki, R. (1979). Studies on human finger tapping neural networks by phase-transition curves. *Biological Cybernetics, 33*, 199–208.

Zanone, P. G., & Kelso, J. A. S. (1992). Evolution of behavioral attractors with learning: Nonequilibrium phase transitions. *Journal of Experimental Psychology: Human Perception and Performance, 18*, 403–421.

Zelaznik, H. N., & Lantero, D. (1996). The role of vision in repetitive circle drawing. *Acta Psychologica, 92*, 105–118.