

VU Research Portal

Asymmetric interlimb coupling strength in rhythmic bimanual coordination

de Poel, H.J.

2007

document version

Publisher's PDF, also known as Version of record

[Link to publication in VU Research Portal](#)

citation for published version (APA)

de Poel, H. J. (2007). *Asymmetric interlimb coupling strength in rhythmic bimanual coordination*. [PhD-Thesis - Research and graduation internal, Vrije Universiteit Amsterdam]. Print Partners Ipskamp.

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

vuresearchportal.ub@vu.nl

Asymmetric interlimb coupling strength in rhythmic bimanual coordination

Harjo de Poel

The work in this thesis is part of the research program of the Institute for Fundamental and Clinical Human Movement Sciences (IFKB), and was carried out at the Faculty of Human Movement Sciences, VU University, Amsterdam, The Netherlands. This research was made possible by Aspasia grant 015.001.040 of the Netherlands Organization for Scientific Research (NWO).

ISBN: 978-90-8659-103-9

Cover design: Harjo de Poel & Marja Wijnand

Printed by: Print Partners Ipskamp, Enschede

© H.J. de Poel, 2007

All rights reserved. No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording or any information storage and retrieval system, without the written permission from the author.

VRIJE UNIVERSITEIT

Asymmetric interlimb coupling strength in rhythmic bimanual coordination

ACADEMISCH PROEFSCHRIFT

ter verkrijging van de graad Doctor aan
de Vrije Universiteit Amsterdam,
op gezag van de rector magnificus
prof.dr. L.M. Bouter,
in het openbaar te verdedigen
ten overstaan van de promotiecommissie
van de faculteit der Bewegingswetenschappen
op donderdag 7 juni 2007 om 10.45 uur
in het auditorium van de universiteit,
De Boelelaan 1105

door

Harke Johan de Poel

geboren te Emmen

promotor: prof.dr. P.J. Beek
copromotor: dr. C.E. Peper

Contents

1	General introduction	7
2	Handedness-related asymmetry in coupling strength in bimanual coordination: Furthering theory and evidence	19
3	Intentional switches between bimanual coordination patterns are primarily effectuated by the nondominant hand	57
4	Laterally focused attention modulates asymmetric coupling in rhythmic interlimb coordination	79
5	Attentional asymmetry affects relative phase through amplitude disparity rather than asymmetric coupling	105
6	Epilogue	143
	References	153
	Summary	163
	Samenvatting (Dutch summary)	167
	Dankwoord (Acknowledgements)	173
	List of publications	177

Chapter 1

General introduction

Introduction

Many movements that we perform in everyday life involve some degree of coordination between two or more limbs. In such instances, the limbs produce movements that are to some extent related to each other in achieving a common task goal. For instance, when walking, the two legs move in an alternating pattern in order to produce forward displacement of the body in a stable manner. Also when the participating limbs perform less similar movements, like in screwing the lid off a jar, peeling a potato, or tying one's shoelaces, the movement patterns of the individual limbs are tuned to each other and seem to be organized such that stable coordination between the limbs arises.

Nonetheless, simultaneous performance of different tasks with the limbs is often very difficult. Even when the subtasks are very easy to perform separately, their concurrent performance can give rise to substantial interference due to (unwanted) interactions (or: coupling) between the limbs' movements. A classic demonstration in this regard (with nearly guaranteed success at [children's] birthday parties) involves simultaneously patting the head with one hand and rubbing your tummy making a circular trajectory with the other hand. You may find that one of the hands (or both) is patting in circles, clearly indicating that the individual limbs do not move independently, but interact.

For myself, these interlimb interactions become (frustratingly) apparent when I play the drums, a task which involves mutual coordination of (the timing of) the movements of all four limbs. Just keeping a stationary rhythm is not so difficult. However, when I want my right leg (operating the bass drum pedal) to produce an occasional syncopating (i.e., intermediate) beat during the rhythmic pattern, the right arm (beating the hi-hat with a drum stick) involuntarily 'follows' the rhythm of my leg and performs a syncopating stroke as well. Thus, the variation in the movement of the leg invokes a reaction in the movement of the arm, which suggests a tight coupling between the movements of my right arm and leg. Most interestingly in the context of the present thesis, however, in the converse situation, when the arm is 'commanded' to make an intermediate stroke, the movement of my leg is *not* affected. Thus, it seems that the movements of my right arm are more strongly coupled to those of my right leg than vice versa. In other words, this introspective example illustrates that the movements of the separate limbs may influence each other to different degrees.

Such asymmetries in the strength of interlimb coupling are the main theme of the present thesis.

Although the preceding examples highlight the interlimb interactions in terms of their limitations on performance, these interactions also have important beneficial effects. For example, in spastic children the movements of the affected hand may be improved by influences stemming from the unaffected hand (Steenbergen, Hulstijn, De Vries, & Berger, 1996). Typically, in the performance of rhythmic movements (like drumming), beneficial effects of coupling can be readily appreciated. For these kinds of movements, the mutual influences between the limbs result in attraction to particular coordination patterns (Haken, Kelso, & Bunz, 1985; Peper, Beek, & Van Wieringen, 1995c) that are resistant to internal and external perturbations (Post, Peper, & Beek, 2000; Post, Peper, Daffertshofer, & Beek, 2000). Thus, due to the interlimb interactions some coordination patterns can be performed in a stable manner, while other patterns are obstructed and often require a great deal of practice (Peper et al., 1995c; Tuller & Kelso, 1989; Yamanishi, Kawato, & Suzuki, 1980; Zanone & Kelso, 1992). The coordination dynamics approach (e.g., Beek, Peper, & Stegeman, 1995; Haken et al., 1985; Kelso, 1995; Kugler, Kelso, & Turvey, 1980) offers an expedient framework for studying such rhythmic coordination, in which the (in)stability of these coordination patterns is explained with reference to the coupling between the limbs (e.g., Haken et al., 1985; Haken, Peper, Daffertshofer, & Beek, 1996). Most studies in this regard, however, pertain to the analysis of the (stability of) overall patterns of rhythmic coordination (i.e., the phase or frequency relation between the limbs), with few studies investigating the interlimb interactions themselves in head-on fashion. Hence, although the coupling between the limbs as the alleged source of coordinative stability plays a central role in this approach, it has been insufficiently addressed to date.

To help fill this lacuna, the present thesis focuses primarily on the interactions between the limbs in a simple rhythmic coordination task, with special emphasis on the way in which the overall coordination (in terms of relative phasing between the limbs) is mediated by asymmetries in these interactions. On the basis of demonstrations that handedness (e.g., Treffner & Turvey, 1995) and deliberate division of attention (i.e., focusing on either hand; Amazeen, Amazeen, Treffner, & Turvey, 1997) induce asymmetries in the relative phase dynamics, these two factors are examined as potential sources of

asymmetry in the interlimb interactions. Furthermore, empirical findings (Byblow, Bysouth-Young, Summers, & Carson, 1998; Peper, Beek, & Van Wieringen, 1995a, 1995c; Summers, Davis, & Byblow, 2002) as well as theoretical interpretations (Amazeen et al., 1997; Treffner & Turvey, 1995) have suggested that asymmetries in the strength of interlimb coupling are in fact beneficial for the quality of coordinative performance, which may be useful when seeking to improve (impaired) bimanual performance. The primary aim of the present research was therefore to identify *if* these proposed sources of asymmetry indeed affect the coordination at the level of the interlimb interactions and, second, *how* such coupling asymmetries may influence (the stability of) the overall coordinative performance. However, the question *why* handedness and attentional focus may lead to coordinative asymmetries was deemed beyond the scope of this thesis.

Handedness: An intrinsic source of asymmetry

In human (bi)manual behavior, perfect symmetry is the exception rather than the rule (cf., Summers et al., 2002). Indeed, in everyday bimanual behavior, the role of the two hands is seldom equivalent, as performance is often characterized by a distinct ‘division of labor’ between the hands (Guiard, 1987; Peters, 1994). For instance, while pouring a cup of tea, one hand manipulates the teapot while the other one holds the cup being filled. Moreover, this role division is correlated with the typical functional laterality of the upper limbs, referred to as handedness or hand dominance. That is, for most people there is a bias towards using either the right hand (i.e., approximately 89% of the population) or the left hand (i.e., approximately 11% of the population) for manual tasks that require some degree of skill, while only very few people are ambidextrous (McManus, 2002). Hence, the fact that the majority of everyday bimanual tasks comprise two coordinated subtasks that differ in their degree of required skill can account for the expression of the functional laterality of the upper limbs. As a consequence, although the hands demonstrably work together as a synergy (Guiard, 1987), performance differences between the dominant and the nondominant hand can be readily observed in both unimanual and bimanual tasks. For instance, the dominant hand performs a simple repetitive finger tapping task more consistently and can reach a higher rate than the nondominant hand (Peters, 1980). In bimanual tasks, the dominant limb typically performs the

most complex subtask or the one that is most directly related to the main goal (for instance, lighting a match), while the nondominant hand performs a more subserving, stabilizing role (e.g., holding the matchbox; Guiard, 1987).

The effects of handedness on coordinative performance become readily apparent when role reversals are introduced (Peters, 1994). For instance, try to light a match with your nondominant hand, and you will find that this is exceedingly more difficult. In all likelihood, you may even see that you attempt to skim the box over the match, rather than the match over the box. Another example can be found in multifrequency performance, where the faster cadence is preferably produced by the dominant hand (Peters, 1980; Peters & Schwartz, 1989). When the nondominant hand is assigned to move at the faster rate, this has a detrimental effect on the quality of coordination (Byblow & Goodman, 1994; Byblow et al., 1998; Summers et al., 2002; see also Peters, 1981, 1985). Hence, also in rhythmic tasks, handedness represents a ubiquitous intrinsic asymmetry that influences (the quality of) performance in bimanual coordination: As will be argued below, its effects may (partly) result from an asymmetry in interlimb coupling strength.

Handedness appears to be related to differences in the neurophysiological processes underlying the movement control of the limbs and is therefore typically considered with reference to the functional specialization of the two hemispheres (e.g., Haaland & Harrington, 1996; Sainburg, 2002; Serrien, Ivry, & Swinnen, 2006). Furthermore, neural structures and processes that have been proposed as candidates in mediating the interlimb coupling (e.g., interhemispheric cross-talk via the corpus callosum; for a review, see Carson, 2005) have been demonstrated to exhibit asymmetries associated with handedness (e.g., Serrien, Cassidy, & Brown, 2003). Although the possible neurophysiological underpinnings of (the effects of) handedness will be briefly discussed in Chapter 2, the present thesis focuses primarily on handedness-related asymmetries at the behavioral level.

Attention as a source of asymmetry

A more psychological account of handedness was proposed by Peters (1989, 1994). He submitted that effects of handedness in bimanual coordination can be interpreted as a reflection of the amount of attention that is directed to each hand, with the dominant hand receiving most attention, because in

bimanual tasks the goal of the joint activity is typically related primarily to the contributions of this hand. In this view, handedness and asymmetric attentional focus are closely related and may thus have similar influences on the bimanual behavior. In line with this assertion, bimanual performance has been shown to improve when attention is directed deliberately to the dominant hand (e.g., Amazeen et al., 1997; Peters, 1981, 1985; Peters & Schwartz, 1989). Moreover, examination of the phase relation between the limbs during a rhythmic bimanual task indicated that the effects of manipulation of lateral attentional focus were similar to those of handedness (Amazeen et al., 1997).

Whereas the effects of handedness on interlimb coupling strength can only be examined by comparing selected handedness groups, the proposed relation between handedness and attentional focus provides a potential means to induce systematic manipulations of the coupling asymmetry. Therefore, the present thesis also includes extensive analyses of the effects of attentional focus on (asymmetries in) interlimb coupling strength and the relative phasing between the limbs. Moreover, comparison of the ways in which handedness and attentional focus affect the mutual interactions between the limbs allowed for an empirical test of Peters' assertion that the two are intrinsically related.

How to examine asymmetry in coupling strength?

One strategy to examine the influences of interlimb coupling is to study the simultaneous performance of two qualitatively different acts. This approach has been implemented in many studies that investigated the coordination between movements with disparate spatial characteristics. When moving the two limbs in a different direction and/or with different orientations (cf. patting versus rubbing), spatial interference becomes readily apparent in the performance of one or both of the limbs (Franz, 1997; Swinnen, Dounskaia, Levin, & Duysens, 2001; Swinnen et al., 1998; Lee, Almeida, & Chua, 2002), unless the corpus callosum has been dissected (Franz, Eliassen, Ivry, & Gazzaniga, 1996). In a similar vein, movements of unequal amplitudes tend to assimilate (e.g., Marteniuk, MacKenzie, & Baba, 1984; Sherwood, 1994; Heuer, Spijkers, Kleinsorge, Van Der Loo, & Steglich, 1998; Spijkers & Heuer, 1995). Patently, differential task constraints produce subtask-related asymmetries in the bimanual interference (e.g., Swinnen, Walter, Young, & Serrien, 1991).

In addition, such patterns of bimanual spatial interference are influenced by handedness (e.g., Sherwood, 1994; Spijkers & Heuer, 1995). When drawing circles with both hands in the same allocentric (i.e., nonmirror-symmetric) direction at increasing speeds, trajectory distortions and direction reversals occur primarily in the nondominant hand (Byblow, Chua, Bysouth-Young, & Summers, 1999; Semjen, Summers, & Cattaert, 1995; Wuyts, Summer, Carson, Byblow, & Semjen, 1996). Such results of spatial accommodation may indicate that the two upper limbs influence each other to different degrees as a function of handedness. This notion was already put forward by Van Riper (1935) who studied bimanual graphic performance and observed that when the drawing orientation of both limbs was gradually changed from drawing in the frontal plane to drawing in the transverse plane, it was the nondominant limb that altered its initial drawing direction.

A second class of bimanual tasks consisting of two different subtasks that has been examined extensively involves moving the hands simultaneously at different frequencies. Performance of simple rhythms (e.g., 1:1, 2:1, 3:1), in which the movement frequency of one limb is an integer multiple of that of the other, is less difficult and shows less variability than the production of polyrhythms (e.g., 3:2, 5:3; Deutsch, 1983; Peper et al., 1995c; Summers, Rosenbaum, Burns, & Ford, 1993). When stressing performance by increasing the movement tempo, loss of the rhythmic pattern and subsequent transitions to simple ratios can be observed (Peper, Beek, & Van Wieringen, 1995b). These phenomena are related to the coupling between the two limbs. The performance of such multifrequency tasks appears to be associated with asymmetries in coupling strength, in which the fast hand (receiving the focal attention; Peters 1994) has a larger influence on the slow hand than vice versa (Byblow & Goodman, 1994; Peper et al., 1995a, 1995c; Summers et al., 1993). Also in this case, marked effects of handedness become visible when the roles are reversed (Byblow et al., 1998; Summers et al., 2002; however, see also Peper et al., 1995a, 1995c).

In sum, when performing bimanual tasks, the movements of the two limbs are coupled (both spatially and temporally), leading to stable performance of specific interlimb coordination patterns. However, although in most bimanual tasks coordinative asymmetries can be readily appreciated in terms of the different roles adopted by the two hands, the analysis of the 'intrinsic' dynamics associated with handedness may be confounded by qualitative differences

between those roles (cf. Verheul & Geuze, 2003). Therefore, an alternative paradigm is adopted in the present thesis, namely rhythmic bimanual coordination in a 1:1 (or iso) frequency relation. For this kind of bimanual task, the (in)stability of coordination is formally explained in terms of the coupling between the limbs (Haken et al., 1985), thereby offering an expedient entry point for examining asymmetries therein. This will be further elucidated in the following sections.

Isofrequency coordination

The studies reported in this thesis all pertain to coordination tasks involving cyclical movements of the upper limbs moving at a common frequency (i.e., isofrequency coordination). The advantage of this task is that the two subtasks are identical, thus providing an excellent context for examining asymmetries in the interlimb interactions that are not related to inherent, qualitative differences between those subtasks (cf. Carson, 1993). In addition, the very goal of this type of task is comprised by the movement itself. That is, isofrequency coordination has no other goal than achieving a specific spatiotemporal relation between the movements of the limbs, which allows for examination of (the effects of) interlimb interactions independently of (other) task-specific constraints. Although, admittedly, the selected experimental task is far removed from daily-life activities, and thus may be less relevant for the specific understanding of such activities, it is highly significant in view of the fundamental insights into interlimb coordination it may provide.

A well-known formal account of the dynamics of isofrequency coordination is the so-called HKB model (Haken et al., 1985), which captures the dynamics of the relative phasing (ϕ) between the movements of the limbs by means of a potential. This potential reflects stable coordination patterns as well as changes therein due to variations in movement frequency. In agreement with empirical results (e.g., Yamanishi et al., 1979; Zanone & Kelso, 1992), at a sufficiently low movement frequency, the model exhibits two stable states to which the bimanual behavior is attracted: in-phase (i.e., 0° phase difference between the limbs) and antiphase (i.e., 180° phase difference), with in-phase coordination being more stable than antiphase coordination. Increase in movement frequency causes a decrease in the coordinative stability, which may eventually (i.e., at a critical frequency) lead to loss of stability of the antiphase

pattern and an abrupt transition to the more stable in-phase pattern (e.g., Kelso, 1984).

Asymmetries in the performance of isofrequency coordination emerge when the inertial characteristics of the limbs differ, either intrinsically (e.g., arm-leg; Jeka & Kelso, 1995) or due to external manipulations (e.g., by adding weight to one of the limbs; Peper, Nooij, & Van Soest, 2004; or by oscillating two pendulums that differ in eigenfrequency; e.g. Sternad, Amazeen, & Turvey, 1996). These coordinative asymmetries have been accounted for by adding a ‘detuning’ parameter to the HKB-model (Kelso, Delcolle, & Schöner, 1990), representing a difference between the two oscillating components of the underlying system of coupled oscillators with respect to their preferred frequency of oscillation (or: eigenfrequency; Fuchs, Jirsa, Haken, & Kelso, 1996).

Another asymmetry in isofrequency performance was reported by Treffner and Turvey (1995, 1996), who demonstrated a handedness effect for in-phase and antiphase coordination. For both left-handers and right-handers the dominant hand was slightly leading in time, entailing a small, but significant phase shift compared to the intended symmetric coordination pattern (e.g., $\phi = 8^\circ$ instead of 0°). Furthermore, on the basis of the proposition that effects of handedness are a reflection of an asymmetry in the amount of attention that is directed to each hand (Peters, 1994), Amazeen et al. (1997) observed that deliberately focusing attention on either hand indeed influenced the coordination in a manner similar to handedness. That is, focusing attention on the dominant (nondominant) hand increased (decreased) the relative phase shift, while the coordination was most stable when attention was directed to the dominant hand (in line with Peters’ proposal). By adding a symmetry-breaking term to the (symmetric) HKB potential, these effects of handedness and attention were formally accounted for (Treffner & Turvey, 1995) and, based on this model extension, interpreted to result from an asymmetry in the coupling strength. The recent formalization of this interpretation by Peper, Daffertshofer, and Beek (2004; see Chapter 2) underscored the theoretical possibility that these effects of handedness and directed attention result from an asymmetry in the strength of interlimb interactions.

As discussed in the previous section, when the coordinated subtasks differ from each other, changes observed in the spatiotemporal characteristics of the movements of (one of) the limbs are readily interpreted as the result of interlimb

interactions. However, this is not so straightforward when the two subtasks do not differ, as is the case in isofrequency coordination. Here, the interlimb interactions *themselves* are difficult to analyze in a direct manner. Instead, coordination measures like relative phase and its variability are usually studied as indices of the underlying interlimb interactions, and interpretations regarding the interlimb coupling are typically inferred from pertinent models (e.g., Treffner & Turvey, 1995). In order to address the coordinative influences of asymmetries in interlimb coupling in a more direct manner, it was therefore necessary to disrupt the stable phase relation between the limbs by means of mechanical perturbations or inducing coordinative instabilities (i.e., phase transitions) and to analyze the subsequent phase adjustments that were made by the limbs during the transient stage, that is, until a stable coordination pattern was (re)established. This method was applied extensively in the present thesis. By examining the phase adjustments for a variety of transient situations (see below), the (effects of) asymmetric interlimb coupling strength in isofrequency coordination could be tested head on in relation to handedness (as proposed by Treffner & Turvey, 1995) and laterally focused attention (Amazeen et al., 1997).

Outline of the thesis

In the following chapters the specific effects of handedness and asymmetric attentional focus on the interlimb coordination are assessed in detail. Chapter 2 provides, for both right- and left-handed participants, an extensive analysis of the effects of handedness on the interlimb interactions by examining the phase adjustments observed in both limbs in response to mechanical perturbations of the bimanual coordination pattern as well as during spontaneous (i.e., frequency-induced) phase transitions. To this end, new graded measures of coupling strength asymmetry were developed, capturing the relative contributions that the individual limbs made to the observed changes in relative phasing. In this way, the hypothesis was tested that the movements of the nondominant limb were more strongly influenced by those of the dominant limb than vice versa. In Chapter 3, the same hypothesis was addressed using a slightly different paradigm. Here, voluntary switches from in-phase to antiphase coordination or vice versa were analyzed to determine the degree to which these switches were mediated by phase changes in the movements of the dominant and nondominant limb.

Motivated by indications that attentional asymmetries affect bimanual coordination in a manner similar to handedness (Amazeen et al., 1997; Swinnen, Jardin, & Meulenbroek, 1996), Chapters 4 and 5 address the question whether the influence of focusing attention on either limb on the interlimb phase relation may indeed be accounted for by a modulation of the underlying asymmetry in coupling strength. In the study reported in Chapter 4, the same perturbation paradigm was adopted as in Chapter 2, in order to examine whether handedness and attentional focus are indeed related with respect to their effect on the asymmetry in coupling strength. As will become evident, the influence of laterally focused attention on the coordination between the limbs was not as straightforward as expected: Distinct effects of asymmetric attentional focus at the different sublevels of the analysis potentially confounded the analysis of the overall coordinative performance. Therefore, ensuing from Chapter 4, the study reported in Chapter 5 aimed at disentangling these distinct (but not mutually exclusive) effects of attentional focus on the overall relative phasing between the limbs. Finally, Chapter 6 summarizes the main findings of this thesis in relation to extant models of interlimb coordination and underscores that analysis of the collective behavior (i.e., the relative phase dynamics) alone is insufficient to fully capture the intricate relation between interlimb coupling and coordinative stability.

Chapter 2

Handedness-related asymmetry in coupling strength in bimanual coordination: Furthering theory and evidence

Published as:

De Poel, H. J., Peper, C. E., & Beek, P. J. (2007). Handedness-related asymmetry in coupling strength in bimanual coordination: Furthering theory and evidence. *Acta Psychologica*, *124*, 209-237.

The original article is retrievable at www.sciencedirect.com.

DOI: 10.1016/j.actpsy.2006.03.003

Abstract

The effects of handedness on bimanual isofrequency coordination (e.g., phase advance of the dominant limb) have been suggested to result from an asymmetry in interlimb coupling strength, with the nondominant limb being more strongly influenced by the dominant limb than vice versa. A formalized version of this hypothesis was tested by examining the phase adjustments in both limbs in response to mechanical perturbation of the bimanual coordination pattern and during frequency-induced phase transitions, for both right- and left-handed participants. In both situations, the phase adaptations were made predominantly by the nondominant limb in right-handers, whereas this effect failed to reach significance in left-handers. Thus, the asymmetry in coupling strength was less pronounced in the latter group. In addition, the degree of asymmetry depended on movement frequency. The observed asymmetry was discussed in relation to pertinent neurophysiological findings.

Introduction

A hallmark property of human manual performance is the functional asymmetry between the upper limbs, which is referred to as handedness or hand dominance and is manifested in the quality of performance of single-handed tasks. For example, when performing repetitive finger tapping movements with one hand, the dominant hand taps faster and more consistently than the nondominant hand (Peters, 1980), while in unimanual aiming tasks the dominant limb is more efficiently controlled than the nondominant limb (Bagesteiro & Sainburg, 2002; Sainburg, 2002). Most everyday manual tasks, however, require some degree of collaboration between the two hands. In accordance with the expressions of handedness in single-handed movements, the dominant hand typically performs the more complex or continuous movements with a manipulative role, while the nondominant hand has a more subservient, stabilizing role (Guiard, 1987; Peters, 1994). This asymmetry in hand use is observed in various bimanual activities, such as unscrewing a lid from a jar, striking a match, and handwriting (in which the nondominant hand positions the writing substrate while the dominant hand manipulates the pen). In the context of bimanual multifrequency performance (i.e., simultaneous performance of two fixed, but different movement frequencies) right-handers demonstrated a preference for using the right hand for the faster rhythm (Peters & Schwartz, 1989) and, accordingly, performance turned out to be better when the faster rhythm was assigned to the dominant hand (Byblow, Bysouth-Young, Summers, & Carson, 1998; Summers, Davis, & Byblow, 2002; see also Peters, 1985). Thus, execution of the more demanding subtask by the dominant hand is not only preferred, it is also beneficial for the overall bimanual performance.

Handedness and bimanual isofrequency coordination

Although in most bimanual tasks the influences of handedness can be readily appreciated in terms of the different roles adopted by the two hands, its precise influence on each hand's performance is more difficult to examine, given the qualitative distinctions between the subroutines performed (cf. Verheul & Geuze, 2003). Because the subtasks of the hands are identical in coordination tasks between two homologous limbs moving at identical frequencies (i.e., isofrequency coordination), this type of task constitutes an

interesting model for examining the effects of hand dominance on bimanual performance (Carson, 1993).

Key characteristics of isofrequency coordination stem from the interactions between the moving limbs. Due to these interactions only two coordination patterns can be stably performed (e.g., Yamanishi, Kawato, & Suzuki, 1979; Zanone & Kelso, 1992): the in-phase pattern (i.e., the limbs oscillate symmetrically) and the antiphase pattern (i.e., the limbs oscillate in an alternating fashion). More specifically, the phase difference (or relative phase) $\phi = \theta_L - \theta_R$ (with θ_L, θ_R representing the phase angles of the individual limb movements) between the left (L) and the right (R) limb is attracted towards $\phi = 0^\circ$ (in-phase) and $\phi = 180^\circ$ (antiphase). The well-known HKB model (Haken, Kelso, & Bunz, 1985) captures the stability characteristics of these two phase relations and provides an account for the spontaneous transition to in-phase coordination that occurs when the frequency of antiphase performance is gradually increased and reaches a critical value (e.g., Kelso, 1984).

Interestingly, the stationary performance of bimanual isofrequency patterns was found to be influenced by hand dominance: For left-handed (LH) participants the left hand was, on average, slightly leading in time, whereas the opposite was true for right-handed (RH) individuals (Semjen, Summers, & Cattaert, 1995; Stucchi & Viviani, 1993; Swinnen, Jardin, & Meulenbroek, 1996; Treffner & Turvey, 1995, 1996). For one-dimensional oscillatory movements this implied small but significant deviations from the intended relative phases of 0° and 180° (i.e., for in-phase, $\phi > 0^\circ$ for LH individuals, and $\phi < 0^\circ$ for RH individuals). These phase shifts appeared to be larger for antiphase than for in-phase coordination (Treffner & Turvey, 1995) and increased with movement frequency (Treffner & Turvey, 1996; see also Stucchi & Viviani, 1993).

To account for their results, Treffner and Turvey (1995) extended the HKB potential with two additional terms:

$$V(\phi) = -a \cos(\phi) - b \cos(2\phi) + c \sin(\phi) + d \sin(2\phi) \quad [2.1]$$

with

$$\dot{\phi} = -\frac{dV(\phi)}{d\phi} = -a \sin(\phi) - 2b \sin(2\phi) - c \cos(\phi) - 2d \cos(2\phi) \quad [2.2]$$

The two cosine terms in Equation 2.1 were adopted from the original, symmetric HKB model, while the sine terms introduced an asymmetry in the potential. The

minima of this potential reflect the stable states of the system towards which bimanual performance is attracted. The signs and magnitudes of parameters c and d determine the direction and degree of the invoked asymmetry (see Figure 2.1). Equation 2.2 represents the corresponding order parameter equation, which describes the time-evolution (i.e., dynamics) of relative phase. The empirically obtained phase shifts were quite small, which corresponded to a slightly asymmetric potential and implied that c and d were small relative to a and b . Because assigning nonzero values to d was sufficient to induce the observed phase shifts with respect to both 0° and 180° ($d > 0$ for right-handers and $d < 0$ for left-handers; see Figure 2.1), c was set to zero (Treffner & Turvey, 1995). Indeed, the Treffner and Turvey model provided an adequate account of the empirically observed effects of handedness onto bimanual isofrequency coordination in terms of both mean relative phasing and coordinative stability (Amazeen, Amazeen, Treffner, & Turvey, 1997; Treffner & Turvey, 1996).

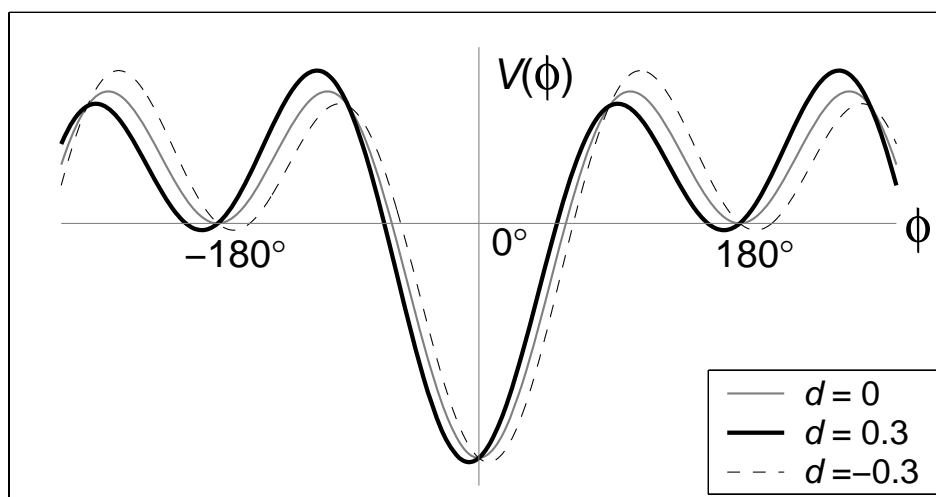


Figure 2.1. The influence of handedness on the coordination dynamics according to Equation 2.1, for $d = 0$, $d > 0$ and $d < 0$ ($a = b = 1$; $c = 0$); $d > 0$ corresponds to right-handers (right limb leads) and $d < 0$ corresponds to left-handers (left limb leads). For presentational purposes, rather large values of d were used.

Because two homologous limbs have rather similar peripheral (e.g., biomechanical) properties (cf. Stucchi & Viviani, 1993; Treffner & Turvey, 1996), it was suggested that the observed phase shifts may have resulted from a handedness-related asymmetry in the strength of the interaction between the limbs (Treffner & Turvey, 1995). This suggestion was in agreement with the

common interpretation of empirically observed influences of hand dominance on the way in which frequency-induced transitions between coordination modes were effectuated (Carson, 1993). For RH participants, such phase transitions have been shown to be predominantly associated with the nondominant, left hand changing its phasing (Byblow, Carson, & Goodman, 1994; Byblow, Chua, & Goodman, 1995). In a similar vein, increasing the frequency of directionally asymmetric bimanual circling movements resulted in more changes in the circling direction of the left hand than of the right hand for RH participants (Byblow, Chua, Bysouth-Young, & Summers, 1999; Carson, Thomas, Summers, Walters, & Semjen, 1997; Semjen et al., 1995), while the opposite was observed for LH individuals (Wuyts, Summers, Carson, Byblow, & Semjen, 1996). These findings suggested that the coupling between the limbs is asymmetrical, with the nondominant limb being more strongly influenced by the dominant limb than vice versa.

Despite the agreement between these empirical findings and the extended HKB potential proposed by Treffner and Turvey (1995), the two were never formally related. Because the potential was formulated in terms of the relative phase itself (i.e., the phase relation between the limbs) it does not, by definition, permit conclusive interpretations regarding the way in which the relative phase dynamics result from the interactions between the limbs (cf., Peper, Daffertshofer, & Beek, 2004; Peper, Ridderikhoff, Daffertshofer, & Beek, 2004). Byblow et al. (1998) argued that the observed transition characteristics complied with the predominance of a specific transition route (viz., increasing or decreasing values of ϕ) predicted by the asymmetric potential of Treffner and Turvey. However, this suggested formal relation between these empirical findings and the proposed potential cannot be corroborated, because transition routes expressed in terms of ϕ are not unequivocally associated with phase adaptations in either hand (viz., a decrease [increase] in ϕ may involve deceleration of the left [right] hand as well as acceleration of the right [left] hand). Thus, although intuitively the suggested asymmetry in coupling strength may have provided a compelling explanation of the relative phase dynamics as captured by Equations 2.1 and 2.2, this suggestion was not backed-up by formal analyses. Recently, however, Peper, Daffertshofer, and Beek (2004) demonstrated that the asymmetric potential of Treffner and Turvey (1995) is indeed consistent with the proposed asymmetry in coupling strength, in which the nondominant limb is more strongly influenced by the dominant limb than

vice versa. Their theoretical argument provided the motivation for the present experiment and is explained in the next section.

Asymmetric relative phase dynamics may result from asymmetric coupling strength

The logic of Peper, Daffertshofer, and Beek's (2004) argument is most readily explained with reference to the order parameter equation (i.e., Equation 2.2), using $\phi = \theta_L - \theta_R$. The order parameter equation captures the relative phase dynamics of the bimanual system and can be decomposed into the phase dynamics of the two components, because $\dot{\phi} = \dot{\theta}_L - \dot{\theta}_R$ (cf. Haken et al., 1985; Kopell, 1988; Sternad, Turvey, & Schmidt, 1992). Assuming that the functional form of the coupling is identical in both directions (Haken et al., 1985; Kopell, 1988; Sternad et al., 1992), $\dot{\theta}_L$ and $\dot{\theta}_R$ (which reflect the changes in oscillation phase θ of the individual components due to the interactions with each other) can be defined as

$$\dot{\theta}_L = a_L \sin(\theta_R - \theta_L) + 2b_L \sin 2(\theta_R - \theta_L) - 2d_L \cos 2(\theta_R - \theta_L) \quad [2.3a]$$

or, equivalently, in anticipation of the required subtraction $\dot{\phi} = \dot{\theta}_L - \dot{\theta}_R$

$$\dot{\theta}_L = -a_L \sin(\theta_L - \theta_R) - 2b_L \sin 2(\theta_L - \theta_R) - 2d_L \cos 2(\theta_L - \theta_R) \quad [2.3b]$$

and

$$\dot{\theta}_R = a_R \sin(\theta_L - \theta_R) + 2b_R \sin 2(\theta_L - \theta_R) - 2d_R \cos 2(\theta_L - \theta_R) \quad [2.4]$$

Subtracting Equation 2.4 from Equation 2.3b results in the order parameter equation:

$$\dot{\phi} = -(a_L + a_R) \sin \phi - 2(b_L + b_R) \sin 2\phi - 2(d_L - d_R) \cos 2\phi \quad [2.5]$$

which is consistent with Equation 2.2 (with $c = 0$). Note that the derivation of Equation 2.5 on the basis of Equations 2.3 and 2.4 is fully consistent with the original formulation by Haken et al. (1985). As can be appreciated from Equations 2.3 and 2.4, the changes in the oscillation phases of the individual limbs depend on the phase relation between them ($\theta_L - \theta_R$) and on the strength of the interaction influences as indexed by parameters a_j , b_j , and d_j ($a_j, b_j > 0$; $d_j \geq 0$; $j = L, R$). In this context it is useful to note that, given the assumption of (nearly) harmonic behavior (cf. Haken et al., 1985; Peper, Daffertshofer, & Beek, 2004; Kopell, 1988) and the definition of the oscillatory limb movements

as $x_j = \cos(\omega_j t + \theta_j)$ (with x_j denoting the displacement of oscillator j ; cf. Haken et al., 1985), $\dot{\theta}_j$ reflects the changes in phase (i.e., θ_j) due to *external* influences (here, the coupling influences stemming from the other oscillator). That is, $\dot{\theta}_j = 0$ when the oscillations are determined solely by $\omega_j t$ (with ω_j denoting the frequency of oscillation), as is the case when the oscillators are uncoupled. Thus, parameters a_j , b_j , and d_j in Equations 2.3-2.5 reflect the degree to which oscillator j is influenced by the other oscillator. Because Equations 2.3 and 2.4 capture the phase dynamics of the individual oscillators, the equations reflect the compound result of both the interaction signals stemming from (the control of) the contralateral limb and the susceptibility to these signals of the limb in question. In other words, at this level of analysis, the associated coupling influences result from the underlying properties of both the oscillating components (the limbs) and the interactions between them.

An asymmetry in the strength of these coupling influences between the two oscillators has different implications for the sine and cosine terms in Equation 2.2. An asymmetry between a_L and a_R (i.e., $a_L \neq a_R$; $a_j > 0$) does not affect the relative phase of the stable state supported by the first sine term (i.e., $\phi = 0^\circ$). The same holds for $b_L \neq b_R$ ($b_j > 0$), implying that the second sine term always supports attraction of ϕ to exactly 0° and exactly 180° . In other words, an asymmetry in coupling strength does not affect the symmetry in the relative phase dynamics of the original HKB model. The situation is different for the third term in Equation 2.5. This term reflects a competition between two interaction processes operating in opposite directions. For symmetric coupling strengths (i.e., $d_L = d_R$; $d_j > 0$) this term cancels out, reducing Equation 2.5 to the original (symmetric) order parameter equation developed by Haken et al. (1985). Unequal values of d_L and d_R , on the other hand, determine the sign of the associated cosine term, thereby affecting the relative phase dynamics qualitatively. For $d_L > d_R$ (corresponding to $d > 0$ in Equation 2.2) the stable attractors are slightly shifted so that the right limb is leading in time, whereas the reverse is true for $d_L < d_R$. The former situation, with a larger coupling influence of the right limb onto the left limb (indexed by d_L) than in the opposite direction (indexed by d_R), corresponds to RH performance, whereas the latter situation corresponds to the performance observed for LH participants.

Thus, Peper, Daffertshofer, and Beek (2004) provided a formal link between the empirically observed phase shifts due to handedness as modeled by

Treffner and Turvey (1995) and the indications that hand dominance induces an imbalance in interlimb coupling strength (e.g., Byblow et al., 1994; Byblow et al., 1998). Given the observed phase lead of the dominant limb (e.g., Stucchi & Viviani, 1993; Swinnen et al., 1996; Treffner & Turvey, 1995, 1996), Equations 2.3-2.5 predict that the handedness-related asymmetries in relative phase dynamics (captured by Equation 2.1) originate from an asymmetry in interlimb coupling strength, in that the nondominant limb is more strongly influenced by the dominant limb than vice versa. In the remainder of this article this hypothesis is referred to as the asymmetric coupling strength hypothesis. Although, as pointed out in the preceding, the observed characteristics of frequency-induced transitions have been interpreted in terms of a handedness-related asymmetry in coupling strength, a dedicated, head-on test of this hypothesis has not been carried out to date. In the present experiment such a test is provided, based on predictions derived from Equations 2.3-2.5.

Rationale of the experiment

To examine the effects of handedness on the mutual coupling between the two limbs in a rigorous fashion, several prerequisites have to be met. First, it is essential to examine whether the indications of asymmetric coupling strength are also present in LH participants, given the fact that LH individuals cannot simply be regarded as ‘inverted’ RH individuals (Kandel, Schwartz, & Jessel, 1991; McManus, 2002; Peters, 1994).¹ Second, whereas previous studies revealed that frequency-induced transitions were in most instances (predominantly) mediated by the nondominant (left) hand (based on the nominal/ordinal categorizations ‘left’, ‘right’, or ‘both’), examination of the (asymmetric) *mutual* coupling influences (cf. Equation 2.5) requires a more detailed, graded analysis in which

¹ Both LH and RH individuals participated in the experiments of Treffner and Turvey (1995, 1996; see also Amazeen et al., 1997; Riley et al., 1997) that revealed the effects of handedness on the relative phase dynamics of one-dimensional, bimanual isofrequency coordination. However, these studies did not address the strength of coupling between the limbs. Most studies that revealed an asymmetry in the phase adaptations of the two limbs during frequency-induced transitions (interpreted as a sign of asymmetric coupling strength; Byblow et al., 1994; Byblow et al., 1995; Byblow, Chua, et al., 1999; Carson et al., 1997) only examined RH participants. With respect to two-dimensional isofrequency coordination (circle drawing), an exception is found in Wuyts et al. (1996), who compared the performance of LH and RH participants.

the relative contributions of both limbs are delineated. Third, the previous findings have to be complemented with an alternative assessment of the imbalance in interlimb coupling strength that (a) provides an independent test of the common interpretation of the predominance of nondominant hand adaptations during frequency-induced transitions, and (b) allows for examination of the coupling asymmetry at movement frequencies below the critical frequency (i.e., at frequencies for which the handedness-related phase shifts that motivated Equation 2.1 were obtained).

These requirements were met in the current experiment. This was achieved by examining, for both LH and RH participants, two independent cases of transient behavior: (a) frequency-induced transitions between coordination patterns, and (b) relaxation behavior following mechanical perturbations. Evidently, both instances of transient behavior imply phase adaptations in the movements of one or both limbs. For a system involving bidirectional coupling (cf. Equation 2.3-2.5) asymmetric coupling strength results in an asymmetry in the relative contributions of the two limbs to the change in the relative phasing between them (i.e., the degree to which they change their phasing relative to each other). In general, it was predicted that during the transients the phase adjustments in the nondominant limb would be larger than in the dominant limb.

To test this prediction, sensitive graded measures of coupling strength asymmetry were developed, based on the relative contributions that the individual limbs made to the change in relative phasing (as opposed to the commonly applied nominal/ordinal categorization). As mentioned above, the prediction was tested in two ways. In analogy with previous studies, spontaneous transitions from antiphase to in-phase coordination were induced by gradually increasing movement frequency. The corresponding phase adaptations in the nondominant limb were predicted to be larger than those in the dominant limb. In addition, mechanical perturbations of the interlimb coordination pattern were introduced as an independent manipulation to examine the same general prediction. Following such a perturbation the original pattern is typically restored, a characteristic which has been used to study coordinative stability (i.e., the resistance to perturbation; e.g., Court, Bennett, Williams, & Davids, 2002; Post, Peper, & Beek, 2000; Post, Peper, Daffertshofer, & Beek, 2000; Scholz, Kelso, & Schöner, 1987). For our current purposes, however, it was essential to develop an alternative analysis, focused on the phase adaptations of the individual limbs during the relaxation period.

In testing the asymmetric coupling strength hypothesis, the perturbation paradigm has several advantages over the transition paradigm. First, an involuntary change in the interlimb coordination pattern can be induced by selectively perturbing the movements of either the dominant or the nondominant limb. As such, it allows systematic, well controlled examination of how either limb affects the movements of the (unperturbed) contralateral limb. Because the mutual coupling between the limbs implies that both limbs attract each other towards a stable interlimb coordination pattern, the relaxation back to the original pattern was expected to be mediated not only by the limb that was actually perturbed, but also by phase adaptations in the contralateral, unperturbed limb. Given the proposed asymmetry in coupling strength, the specific prediction to be tested in this context was that the contribution made by the (unperturbed) contralateral limb would be larger when the dominant limb was perturbed than when the nondominant limb was perturbed. In addition, within this paradigm the asymmetric coupling strength hypothesis can be examined for various movement frequencies, whereas the transition paradigm is necessarily limited to the critical frequency at which the transition takes place. Given the previously reported effect of movement tempo on the phase advance of the dominant hand (Treffner & Turvey, 1996) and the suggestion that an asymmetry in coupling strength may scale with frequency (Carson, 1993), the asymmetry in coupling strength was expected to increase with movement frequency, which was examined using three different tempos of performance.

Methods

The experiment consisted of two parts (a Perturbation and a Transition part) that were conducted in a single session lasting approximately 2.5 hours (including breaks). The order of the two parts was counterbalanced over participants. 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 VU University, Amsterdam.

Participants

Twenty healthy volunteers (10 women and 10 men, aged 19-35 years) were selected for the experiment. 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 = 89, range 73 to 100; selection criterion: > 70), the other 10 as left-handed (mean LQ = -94, range -85 to -100; selection criterion: < -70). None of the participants indicated a preference for the nondominant hand over the dominant hand with respect to any of the tasks in the questionnaire. The participants gave their informed consent prior to the experiment and were paid a small fee for their services.

Apparatus

Perturbation part

Participants were seated on a modified chair. Both lower arms rested comfortably (with the upper arms abducted by approximately 60°) in premolded carbon fiber splints that were filled up with cloth, rendering arm movements within the splints virtually impossible. The armrests were mounted on vertical axes, allowing rotation of the lower arms in the horizontal plane only, and 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: 200 Hz). For each arm, a Digital Actuator Controller in combination with a torque motor (developed by Fokker Aerospace) was able to systematically induce online controlled frictional loads to the rotation axis. 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).

Transition part

Because pilot measurements had revealed that transitions from antiphase to in-phase coordination could hardly be induced in bimanual lower arm coordination performed in the apparatus described above, a different apparatus was used for this part of the experiment. Participants sat comfortably in a height-adjustable chair with their elbows slightly flexed, their forearms placed on armrests in a neutral position (thumbs up and palms facing inward). Displacement of the lower arms was restricted by a support surface on the ventral side and by adjustable foam-coated supports on the dorsal and lateral

side. Both hands were fixed against flat manipulanda by two straps, with all fingers extended. The manipulanda allowed for flexion-extension movements about the wrist in the horizontal plane only and were mounted coaxially with a potentiometer (Sakae, type FCP40A-5k). The potentiometer's output voltage was digitized by a 12-bit ADC (Labmaster DMA) and stored on a microcomputer with a sampling frequency of 200 Hz (accuracy: 0.1°). Computer-generated auditory pacing stimuli (pitch: 200 Hz, duration: 50 ms) were presented using headphones (Sennheiser HD 520 II).

Procedure

Perturbation part

The participants performed bimanual oscillatory movements with the lower arms in the in-phase and antiphase coordination modes at three different movement frequencies that were specified by the auditory metronome. One metronome pulse was presented for each half cycle. In the in-phase condition, participants were instructed to synchronize extension of both arms with a given beep and flexion with the next beep. During the antiphase trials, simultaneous flexion of one arm and extension of the other arm had to coincide with the stimuli. The required movement frequencies were 1 Hz, 1.25 Hz, and 1.5 Hz and trial length was 30 cycles in all conditions. In two-thirds 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 left or the right arm, and lasted 0.25 of the cycle time (corresponding to approximately 90° phase change). Participants were instructed to try to keep 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, while looking straight ahead during the entire trial. The perturbation was delivered at or 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 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 trials without perturbation (referred to as 'steady-state' trials). Thus, the experiment involved

three perturbation conditions: arrest of the left arm, arrest of the right arm, and no perturbation (i.e., steady-state). The trials were grouped in two ‘coordination mode blocks’ (in-phase and antiphase), which were counterbalanced over participants. Within each block, three ‘frequency blocks’ (one for each frequency condition) were presented in random order. Within these frequency blocks, each perturbation condition was presented four times in a completely randomized order.

Transition part

The participants started out in the antiphase coordination mode, while in each trial the tempo prescribed by the auditory metronome was gradually increased from 1.2 Hz to 3.4 Hz, in 11 steps of 0.2 Hz (resulting in 12 frequency plateaus, consisting of 10 movement cycles each). For three participants, who did not show the expected transitions to in-phase coordination for this frequency range in the first two trials, the frequency increase was extended with three additional steps up to 4 Hz in the subsequent six trials. Again, the pacing signal consisted of two beeps per movement cycle. Participants were instructed to look straight ahead and to keep pace with the metronome as accurately as possible (including the increases in frequency). Although they were instructed to perform the antiphase pattern, they were also told that, should the pattern tend to change, they were not to intervene (cf. Kelso, 1995). One familiarization trial preceded the eight experimental trials that were performed by each participant.

In addition, the transition part of the experiment contained steady-state trials, involving the same two coordination modes and the same three frequencies as examined in the perturbation part. The steady-state trials were presented in two counterbalanced ‘coordination mode blocks’, within which the three frequency conditions were presented in random order. Each condition was performed four times in a row. The order of the steady-state trials and transition trials was counterbalanced over participants.

Data reduction

Perturbation part

Angular position data 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: 0.2 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 difference between the required and actually performed frequencies was negligible [see Results].) The continuous phase angle (θ ; in degrees) was derived for each arm, using $\theta_i = \tan^{-1}(\dot{x}_i^* / x_i)$, with x_i denoting angular position, \dot{x}_i^* denoting normalized angular velocity, and i indicating the sample index. The continuous relative phase between the arms (ϕ) for each sample index was defined as $\phi = \theta_L - \theta_R$.

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

$$\theta_{M,i} = \theta_{M,i-1} + 360^\circ \cdot (0.5 f_{M,i} / f_S) \quad [2.6]$$

where i is the sample index, $f_{M,i}$ is the metronome frequency at sample i , and f_S is the sampling rate of 200 Hz. The phase relations between the limbs and this reference signal were defined as $\phi_{L-M} = \theta_L - \theta_M$ for the left arm and as $\phi_{R-M} = \theta_R - \theta_M$ for the right arm.

Transition part

The angular position signals were low-pass filtered (bi-directional second-order Butterworth filter, cut-off frequency: 10 Hz) and subsequently differentiated (five-point approximation) to obtain angular velocity. Inspection of the position data of the transition trials revealed unsystematic variations in the center of oscillation. These variations rendered the calculation of the movement phases unreliable, even when the position data were first detrended with a high-pass filter (as was done for the Perturbation data). To resolve this problem, angular position was normalized to the associated amplitude for each half cycle. This yielded a signal in the range of -1 to 1 for each half movement cycle. Equivalently, angular velocity was normalized to peak velocity for each half cycle. (Application of this normalization procedure did not distort the phase portraits because the recorded movement trajectories were largely harmonic.) In this way, a time-varying pseudo-continuous phase angle (cf. Byblow et al., 1998) was determined for each hand. For each trial, the phase angles were ‘unwrapped’ (i.e., the phase angles were summed over successive cycles), resulting in a progressively increasing phase angle for each hand (i.e., θ_L and

θ_R). The continuous relative phase between the hands ($\phi = \theta_L - \theta_R$) was calculated, as was the phase relation of each hand with respect to the reference signal (ϕ_{L-M} , ϕ_{R-M}), with θ_M being determined using Equation 2.6.

Analysis

Perturbation part

Using circular statistics (Mardia, 1972), performance in the steady-state trials was evaluated on the basis of the mean of ϕ ($\bar{\phi}$) and its variability, as obtained for the 4th to the 26th cycle of each trial. The mean phase shift ($\Delta\phi$) was expressed relative to the required relative phase (ϕ_{req}), that is, $\Delta\phi = \bar{\phi} - \phi_{\text{req}}$, with $\phi_{\text{req}} = 0^\circ$ (in-phase) or $\phi_{\text{req}} = 180^\circ$ (antiphase). The stability of coordination in the steady-state trials was indexed by the variability of the relative phasing between the lower arms, with low variability corresponding to a high degree of stability (cf. Schöner, Haken, & Kelso, 1986). To this end, the within-trial variability of ϕ was assessed by means of the transformed circular variance (*TCV*) of ϕ (Mardia, 1972). This measure of variability is analogous to the ordinary standard deviation, with low values of the *TCV* indicating low variability.

For trials in which a perturbation was applied, pattern stability was indexed by the swiftness of relaxation back to the original coordination pattern after the perturbed arm had been released. In view of comparison over the three frequency conditions, the time series of ϕ were resampled with respect to cycle duration (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 as obtained after release of the perturbed arm) was analyzed using the procedure outlined by Post, Peper, Daffertshofer, and Beek, (2000). In brief, the data were fitted from the point where ϕ reached a value of 45° (i.e., $\phi_{t=0} = 45^\circ$), using an exponential decay function that also accounted for damped oscillations in the return signal:

$$\phi(t) = p + qe^{-\lambda t} \cos(\omega_{\text{osc}} t + \theta_{\text{osc}}) \quad [2.7]$$

where p is the offset in ϕ , $q = \phi_{t=0} - p$, λ is the decay parameter, ω_{osc} is the oscillation frequency of ϕ , and θ_{osc} denotes the phase of this oscillation (for illustrations and further details we refer to Post, Peper, Daffertshofer, & Beek,

2000). 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, Peper, Daffertshofer, and Beek (2000), a trial was excluded from further analysis if: 1) the difference between mean ϕ before and after the transition was larger than 90° ; 2) after the perturbation, ϕ remained larger than 45° ; 3) no stable post-perturbation behavior was established ($TCV > 45^\circ$); 4) the return signal was not a decay function within the observation interval ($\lambda < 0$); 5) the fit was unreliable (standard error of $\lambda > \text{median of } \lambda$, as determined for the four different initial conditions used in the fitting procedure). Accordingly, 96 trials (i.e., 10%; evenly distributed over the groups and conditions) were excluded from further analysis. To minimize the effect of outliers within a set of values, median values of λ were determined for each condition.

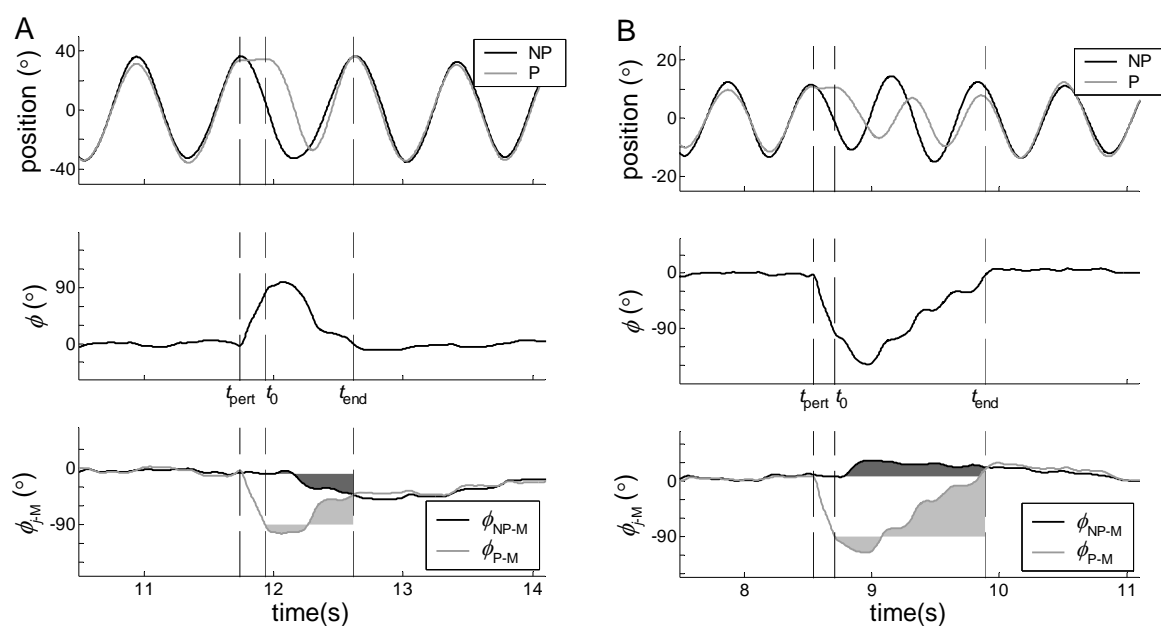


Figure 2.2. Two in-phase trials illustrating the derivation of A_P and A_{NP} . The dashed lines represent perturbation onset (t_{pert}), moment of arm release (t_0), and the end of the relaxation process (t_{end}). A: Perturbation of the right arm (movement frequency: 1.25 Hz). B: Perturbation of the 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: ϕ as a function of time. Lower panels: the associated ϕ_{P-M} and ϕ_{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}).

Furthermore, the relative contribution of the individual arms to the relaxation back to the bimanual coordination pattern was determined. 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 $P = L$ or R and $NP = R$ or L , 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 $|\phi_i - \phi_{\text{pre}}| < 30^\circ$ and $TCV_i \leq TCV_{\text{pre}}$. The amount of change in the phasing of the perturbed arm during the relaxation period (illustrated by the light gray areas in Figure 2.2) was derived using

$$A_p = \int_{t_0}^{t_{\text{end}}} (\phi_{P-M} - \phi_0) \quad [2.8]$$

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 Figure 2.2). The relative contribution of the unperturbed arm to the relaxation process was expressed by the index of coupling (IC_{pert}):

$$IC_{\text{pert}} = -\frac{A_{NP}}{|A_p| + |A_{NP}|} \quad [2.9]$$

The unperturbed arm can either accelerate ($A_{NP} > 0$) or decelerate ($A_{NP} < 0$) with respect to the metronome, resulting in $IC_{\text{pert}} < 0$ or $IC_{\text{pert}} > 0$, respectively. Because the 90° arrest always resulted in $A_p < 0$ (i.e., the perturbed arm was always delayed with respect to the metronome), $IC_{\text{pert}} > 0$ 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. Figure 2.2A). 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. $IC_{\text{pert}} < 0$, 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. Figure 2.2B). 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_{pert}). Note that $IC_{\text{pert}} = 0$ 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 attained by adjustments in the phasing of the perturbed arm.

Transition part

For the steady-state trials, the performance was evaluated on the basis of $\Delta\phi$ and TCV of ϕ , which were determined in the same fashion as described in the preceding. The asymmetry in coupling strength was predicted to result in an imbalance in the contributions of the two hands to the frequency-induced changes in interlimb phasing. To test this prediction, an index of coupling was defined based on the phase adaptations made by both hands. The calculation of this index of coupling was complicated by the observation that, although the transition trials clearly involved phase locking in ϕ (i.e., the phase relation between the hands), ϕ_{L-M} and ϕ_{R-M} often showed phase wrapping in the higher frequency ranges (see Figure 2.3A). This means that the two hands oscillated at identical frequencies that, however, did not correspond to the required movement frequency as specified by the metronome. As a result, the changes in phasing could not be determined by simply comparing the movement phase of each individual hand to the phase prescribed by the pacing signal. Therefore, an analysis was developed based on the evolutions of the individual phase angles (θ_L and θ_R) of the wrist movements.

This analysis consisted of six steps. First, the occurrence of a phase transition was determined on the basis of an interactive procedure, using a graphical representation of the obtained ϕ profile. In case ϕ exhibited an abrupt change of at least 120° (mod 360°) with respect to the initial antiphase pattern and if, in addition, the phase relations in the 3 s before and after this change were relatively constant (allowing occasional outliers around the associated mean of ϕ , with a maximum of $\pm 90^\circ$), the change in ϕ was labeled as a transition and the trial was selected for further analysis. Second, after enlargement of the graphical representation of ϕ around the transition region, the onset (t_0) and end (t_{end}) of the transition in ϕ were selected by positioning cursors at the edges of

the transition region (see Figure 2.3A). Third, for both hands the rate of change of θ (i.e., the phase velocity $\dot{\theta}$) was determined for the pre-transition region (i.e., the 3 s prior to t_0), the post-transition region (i.e., the 3 s after t_{end}), and the transition region (i.e., from t_0 to t_{end}). These $\dot{\theta}$ values were scaled to the mean $\dot{\theta}$ that was required during the transition period, as prescribed by the metronome (i.e., they were divided by the associated mean value of $\dot{\theta}_M$). Subsequently, for each region the mean scaled value of $\dot{\theta}$ was determined yielding $\bar{\dot{\theta}}_{\text{pre}}$, $\bar{\dot{\theta}}_{\text{post}}$, and $\bar{\dot{\theta}}_{\text{trans}}$, respectively, for each hand (cf. Figs. 2.3B and 2.3C). Within the transition region, deviations in the phase evolution of one or both hands (cf. Figure 2.3B) were expected to occur (effectuating the transition). To determine the size of these deviations in phase velocity, the fourth step entailed that for each hand, $\bar{\dot{\theta}}_{\text{trans}}$ was compared to an expected value of the within-transition average phase velocity ($\bar{\dot{\theta}}_{\text{exp}}$; defined as $[\bar{\dot{\theta}}_{\text{pre}} + \bar{\dot{\theta}}_{\text{post}}]/2$). The difference between $\bar{\dot{\theta}}_{\text{trans}}$ and $\bar{\dot{\theta}}_{\text{exp}}$ (i.e., $\Delta\dot{\theta} = \bar{\dot{\theta}}_{\text{trans}} - \bar{\dot{\theta}}_{\text{exp}}$) expressed (for each hand separately) the phase adaptations that occurred within the transition period, in relation to the hand's phasing before as well as after the transition. Finally, the relative contribution of each hand to the transition in relative phasing was determined using the index of coupling (IC_{trans}):

$$IC_{\text{trans}} = \frac{|\Delta\bar{\dot{\theta}}_L|}{|\Delta\bar{\dot{\theta}}_L| + |\Delta\bar{\dot{\theta}}_R|} \quad [2.10]$$

with the subscripts L and R referring to the left and right hand, respectively. For each trial, IC_{trans} (ranging from 0 to 1) revealed the degree to which a transition was mediated by adaptations in the phasing of either hand. For $IC_{\text{trans}} = .5$ both hands contributed equally, whereas $IC_{\text{trans}} > .5$ reflected larger adaptation in the phasing of the left hand ($|\Delta\bar{\dot{\theta}}_L| > |\Delta\bar{\dot{\theta}}_R|$) and $IC_{\text{trans}} < .5$ reflected larger adaptation by the right hand ($|\Delta\bar{\dot{\theta}}_L| < |\Delta\bar{\dot{\theta}}_R|$). For each participant the thus obtained values of IC_{trans} were averaged over trials.

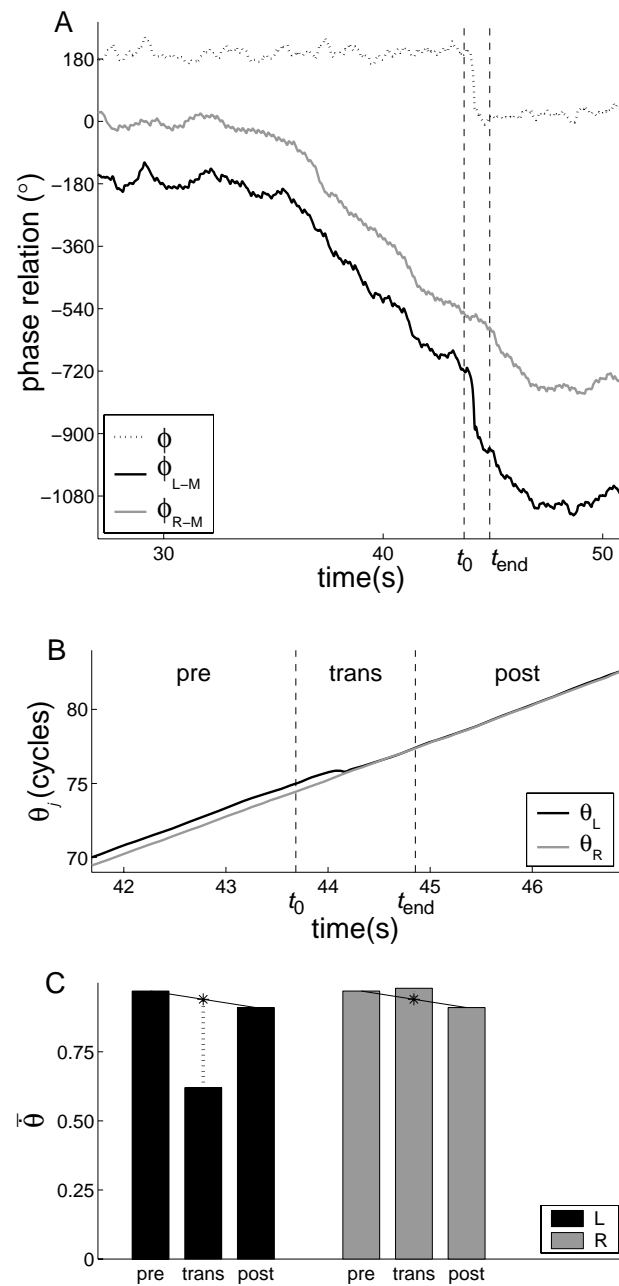


Figure 2.3. Illustration of successive steps in the derivation of IC_{trans} , based on a single representative trial. Dashed vertical lines represent the moments of onset (t_0) and end (t_{end}) of the transition. A: Abrupt transition from antiphase to in-phase coordination (ϕ), while both hands are phase wrapping with respect to the metronome (ϕ_{R-M} and ϕ_{L-M}). B: Unwrapped phase angles (θ) for each hand just before (pre), during (trans), and just after the transition (post). C: $\bar{\theta}_{pre}$, $\bar{\theta}_{trans}$ and $\bar{\theta}_{post}$ for each hand (L = left; R = right). Straight lines reflect the calculation of $\bar{\theta}_{exp}$ (indicated by *); dotted lines illustrate $\Delta\bar{\theta}_L$ and $\Delta\bar{\theta}_R$.

In addition, for every trial in which a transition was identified the transition pathway was determined as being either ‘up’ or ‘down’, corresponding to increasing or decreasing values of ϕ in the transition region, respectively (cf. Kelso & Jeka, 1992). An ‘up’ transition resulted from acceleration of the left hand and/or deceleration of the right hand (i.e., $\dot{\theta}_L > \dot{\theta}_R$ within the transition region), whereas the reverse was true for a ‘down’ transition (i.e., $\dot{\theta}_L < \dot{\theta}_R$ within the transition region). For each participant the percentage of ‘up’ transitions was used for further analysis.

Statistical Analysis

Most dependent variables were submitted to a repeated measures analysis of variance (ANOVA) with between-subjects factor handedness (LH, RH) and within-subjects factors coordination mode (in-phase, antiphase), frequency (1, 1.25, 1.5 Hz), and (if applicable) perturbed arm (left, right). In case the assumption of sphericity was violated, the degrees of freedom were adjusted using the Huynh–Feldt procedure. The significance level (α) was set at .05. In addition, the corresponding effect sizes (f) were calculated based on the partial eta squared (η_p^2 , Cohen, 1988). Significant interactions were further scrutinized by analyzing appropriate simple effects (Keppel, 1991) which were completed, if necessary, by post-hoc paired-samples t -tests (using a modified Bonferroni α -level correction procedure that takes the correlation between conditions into account; see Uitenbroek, 1997). The mean IC_{trans} values obtained for the two handedness groups were compared using independent-samples and one-sample t -tests ($\alpha = .05$). In this case, the effects sizes were calculated in terms of Cohen’s d (Cohen, 1988).

Results

Perturbation part

Steady-state performance

The absolute difference in mean movement frequency between the left and the right arm never exceeded 0.01 Hz. Hence, in all trials the participants maintained the required 1:1 frequency locking between the arms. The prescribed frequencies were adequately performed: The interindividual averages and

corresponding standard deviations were 1.001 Hz ($SD = 0.002$), 1.251 Hz ($SD = 0.004$), and 1.503 Hz ($SD = 0.009$).

Statistical analysis of $\Delta\phi$ revealed a significant effect of handedness, $F(1, 18) = 6.72$, $p < .05$, $f = 0.61$. In RH participants the right arm was, on average, leading the left arm in time (mean $\Delta\phi = -2.0^\circ$), while in LH participants the left arm was leading (mean $\Delta\phi = 1.9^\circ$). In addition, there was a significant Coordination Mode \times Frequency \times Handedness interaction, $F(2, 27) = 3.65$, $p < .05$, $f = 0.45$. Post-hoc simple effects analyses in combination with the corresponding post-hoc paired-samples t -tests indicated that for antiphase coordination movement frequency influenced the phase lead of the dominant limb, given that the mean $\Delta\phi$ differed between LH (mean $\Delta\phi = 1.3^\circ$ [1 Hz]; 2.5° [1.25 Hz]; and 5.9° [1.5 Hz]) and RH participants (mean $\Delta\phi = -1.2^\circ$ [1 Hz]; -3.7° [1.25 Hz]; and -2.4° [1.5 Hz]) for the two highest frequencies. For in-phase coordination, however, frequency did not significantly affect $\Delta\phi$ (mean $\Delta\phi$ for LH: 0.2° [1 Hz], 1.3° [1.25 Hz], and 0.3° [1.5 Hz]; for RH: -2.0° [1 Hz], -1.5° [1.25 Hz], and -1.5° [1.5 Hz]).

Variability of steady-state ϕ was indexed by TCV . The effect of coordination mode was significant, $F(1, 18) = 94.78$, $p < .0001$, $f = 2.29$, with antiphase (mean $TCV = 8.0^\circ$) being more variable than in-phase (mean $TCV = 5.9^\circ$), as was the main effect of frequency, $F(2, 48) = 11.45$, $p < .0001$, $f = 0.80$, which showed that variability increased with movement frequency (mean $TCV = 6.5^\circ$ [1 Hz]; 7.0° [1.25 Hz]; and 7.5° [1.5 Hz]).

	LH group	RH group
In-phase		
1 Hz	2.02 (0.85)	2.85 (0.90)
1.25 Hz	1.41 (0.73)	2.11 (0.99)
1.5 Hz	1.98 (1.86)	1.37 (0.78)
Antiphase		
1 Hz	1.51 (0.88)	2.68 (1.32)
1.25 Hz	1.95 (1.80)	1.45 (0.73)
1.5 Hz	0.82 (0.41)	1.55 (1.05)

Table 2.1. Means and standard deviations (between parentheses) of λ per handedness group for each Coordination Mode \times Frequency combination. Values (arbitrary units) are collapsed across perturbed arm conditions.

Perturbation: Coordinative stability

Frequency had a significant effect on the decay parameter λ , $F(2, 36) = 7.67$, $p < .005$, $f = 0.65$. The mean values of λ were smaller for performance at higher frequencies, indicating slower relaxation (i.e., more movement cycles were required) and, thus, lower stability (mean $\lambda = 2.26$ [1 Hz]; 1.72 [1.25 Hz]; 1.42 [1.5 Hz]). A significant Coordination Mode \times Frequency \times Handedness interaction, $F(2, 36) = 3.98$, $p < .05$, $f = 0.47$, and subsequent post-hoc simple effects analyses and corresponding paired-samples t -tests revealed that for RH individuals the effect of frequency was present for both antiphase and in-phase coordination, whereas for LH participants this effect was only observed for antiphase (see Table 2.1). In addition, a significant Perturbed Arm \times Handedness interaction was obtained, $F(1, 18) = 7.36$, $p < .05$, $f = 0.64$. Analysis of the simple effects revealed that for LH participants λ was larger when the left, dominant arm was perturbed (indicating faster relaxation) than when the right, nondominant arm was perturbed (see Figure 2.4). For RH participants the difference in λ as obtained for perturbation of the dominant arm and nondominant arm was not significant.

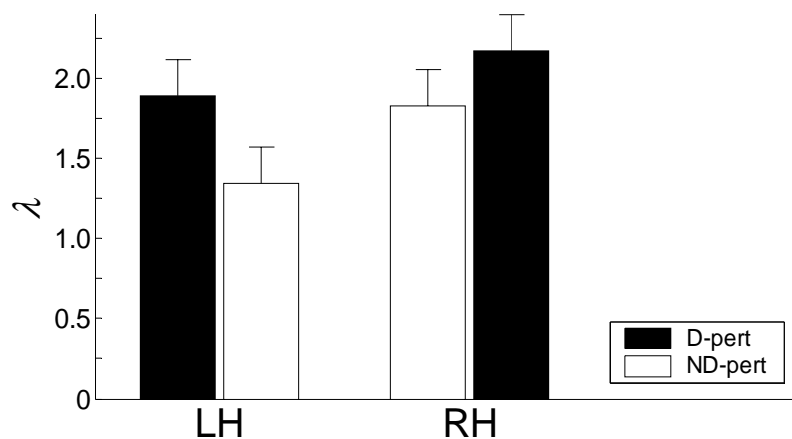


Figure 2.4. Mean values of the decay parameter (λ) as a function of handedness and perturbed arm. LH = left-handed group; RH = right-handed group; D-pert = perturbation of dominant arm; ND-pert = perturbation of nondominant arm. Error bars represent the between-subjects standard errors.

Perturbation: Index of coupling

Figure 2.5 shows that the mean values of IC_{pert} were larger than zero, which indicated that the unperturbed arm also contributed to the relaxation process. The significant main effect of coordination mode, $F(1, 18) = 4.47$, $p < .05$, $f = 0.50$, revealed larger values of IC_{pert} for antiphase (mean $IC_{\text{pert}} = 0.34$)

than for in-phase coordination (mean $IC_{\text{pert}} = 0.26$), implying that during antiphase coordination the unperturbed arm contributed more to the relaxation process than during in-phase coordination. A significant Coordination Mode \times Frequency interaction, $F(1.5, 27) = 4.40$, $p < .05$, $f = 0.50$, and subsequent post-hoc simple effects analyses and paired-samples t -tests revealed an effect of frequency for in-phase coordination, but not for antiphase coordination: In the in-phase conditions IC_{pert} increased with frequency (mean $IC_{\text{pert}} = 0.20$ [1 Hz]; 0.25 [1.25 Hz]; 0.33 [1.5 Hz]), implying an increasing contribution of the unperturbed arm. For antiphase coordination no significant effect of frequency was observed, and the obtained values (mean $IC_{\text{pert}} = 0.36$ [1 Hz]; 0.34 [1.25 Hz]; 0.31 [1.5 Hz]) were statistically similar to those obtained for in-phase performance at the highest movement frequency.

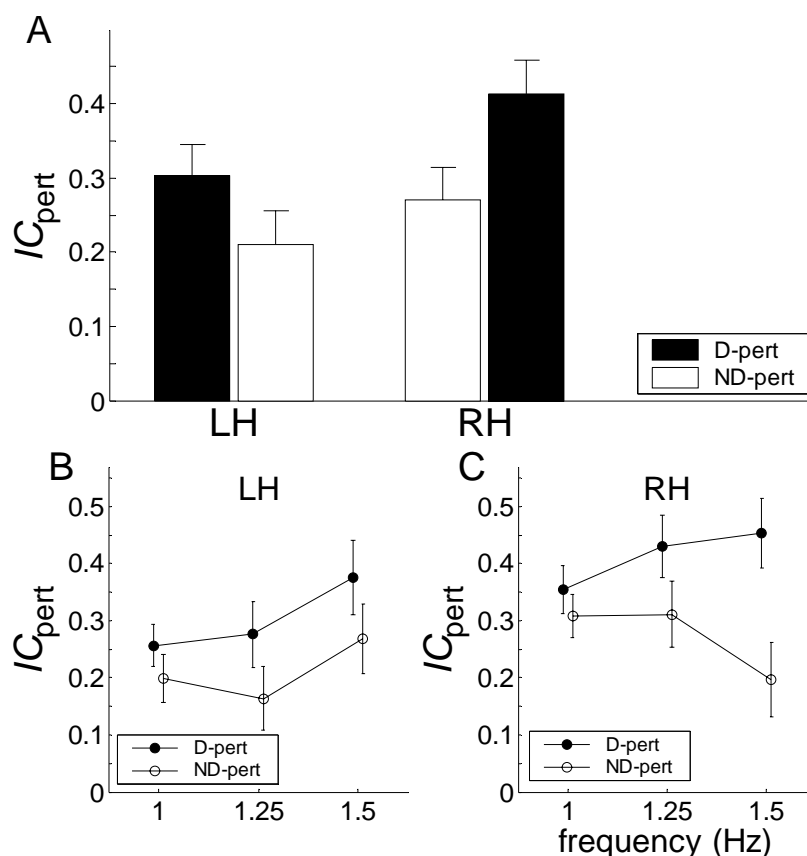


Figure 2.5. Mean values of IC_{pert} (i.e., relative contribution of unperturbed arm to relaxation process) as a function of handedness and perturbed arm (A), and as a function of perturbed arm and frequency for left-handers (B) and right-handers (C). LH = left-handed group; RH = right-handed group; D-pert = perturbation of dominant arm; ND-pert = perturbation of nondominant arm. Error bars represent the between-subjects standard errors.

The significant Perturbed Arm \times Handedness interaction (cf. Figure 2.5A), $F(1, 18) = 13.02$, $p < .005$, $f = 0.85$, and subsequent simple effects analysis demonstrated that for right-handers IC_{pert} was larger when the right arm was perturbed. For LH participants IC_{pert} tended to be larger when the left arm was perturbed (see Figure 2.5A), but this difference failed to reach significance ($p = .08$). Hence, for RH participants the adjustments made by the (unperturbed) nondominant arm in response to perturbation of the dominant arm were larger than the adjustments made by the (unperturbed) dominant arm in response to perturbation of the nondominant arm, while for the LH group this tendency was less manifest. The Frequency \times Handedness interaction, $F(2, 36) = 3.77$, $p < .05$, $f = 0.45$, and the Perturbed Arm \times Frequency \times Handedness interaction, $F(2, 36) = 3.68$, $p < .05$, $f = 0.45$, were also significant. The post-hoc simple effects analyses and paired-samples t -tests revealed that for LH individuals, IC_{pert} at 1.5 Hz was significantly larger than at 1.25 Hz, regardless of which arm was perturbed (see Figure 2.5B). For RH participants, IC_{pert} increased with frequency when the dominant, right arm was perturbed (see Figure 2.5C), whereas no difference was obtained between the frequency conditions when the nondominant, left arm was perturbed (see Figure 2.5C), resulting in a significant difference in IC_{pert} between left- and right-arm perturbation at the two highest frequencies.

Transition part

Steady-state performance

The absolute difference in mean movement frequency between the left and the right hand never exceeded 0.01 Hz, which confirmed that all trials were 1:1 frequency locked. The required frequencies were adequately performed: The interindividual averages and corresponding standard deviations were 1.001 Hz ($SD = 0.003$), 1.254 Hz ($SD = 0.013$), and 1.516 Hz ($SD = 0.047$).

The analysis of $\Delta\phi$ of the steady-state wrist oscillations yielded significant Coordination Mode \times Handedness interaction, $F(1, 18) = 5.61$, $p < .05$, $f = 0.56$. Post-hoc simple effects analyses revealed that for in-phase coordination $\Delta\phi$ did not differ significantly between LH (mean $\Delta\phi = -1.7^\circ$) and RH participants (mean $\Delta\phi = -3.0^\circ$). For antiphase coordination, however, RH individuals showed negative values of $\Delta\phi$ (mean $\Delta\phi = -3.6^\circ$; indicating right hand lead) that were

significantly different from the $\Delta\phi$ values obtained for LH participants (mean $\Delta\phi = 2.0^\circ$; indicating left hand lead).

The analysis of relative phase variability (TCV) yielded a significant effect of coordination mode, $F(1, 18) = 51.70$, $p < .0001$, $f = 1.70$. Antiphase coordination (mean $TCV = 13.1^\circ$) was more variable than in-phase coordination (mean $TCV = 9.8^\circ$).

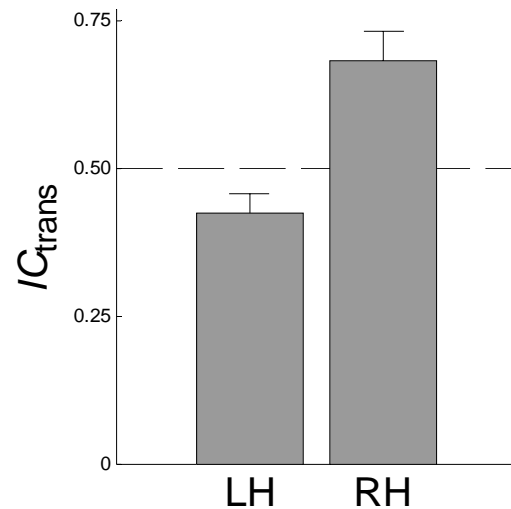


Figure 2.6. Mean values of IC_{trans} (i.e., relative contribution of left hand to the transition) as a function of handedness. LH = left-handed group; RH = right-handed group. Dashed line indicates value of IC_{trans} corresponding to equal contribution of left and right hand. Error bars represent the between-subjects standard errors.

Transitions

One LH participant did not show any transitions from antiphase to in-phase coordination (even though the participant was exposed to movement frequencies up to 4 Hz) and was therefore excluded from the analyses of the transition regions. In the remaining dataset, 55% of the trials resulted in a transition between coordination patterns.² For these trials IC_{trans} was determined and the mean IC_{trans} values as obtained for the LH and RH groups were subjected to an independent-samples t -test. Right-handers showed significantly higher values of IC_{trans} than did left-handers (see Figure 2.6), $t(17) = -3.77$, $p < .005$, $d = 1.53$. Because $IC_{trans} = .5$ implied equal adjustments by the right hand

² Ten participants showed a transition in four or more of the eight trials while nine participants showed transitions in less than four trials. The rather low incidence of spontaneous transitions for some participants may be partly due to stabilizing effects of the applied double pacing (cf. Fink, Foo, Jirsa, & Kelso, 2000).

and the left hand, the average values per group were subsequently tested against this value with one-sample t -tests. These t -tests revealed that the values of IC_{trans} as obtained for the RH group were significantly higher than .5, $t(8) = 3.25$, $p < .05$, $d = 1.07$. Although for the LH group the values of IC_{trans} tended to be lower than .5, this difference did not reach significance ($p = .09$). Hence, the transitions from antiphase to in-phase coordination were predominantly mediated by phase adjustments in the movements of the nondominant hand, although this effect was not significant for LH participants.

Furthermore, the incidence of the ‘up’ and ‘down’ transition routes was examined for each participant that exhibited spontaneous transitions in coordination. Although for some participants individual preferences for a particular (‘up’ or ‘down’) transition route were observed, an independent-samples t -test on the percentage of ‘up’ transitions revealed no significant difference between the LH (35%) and RH (54%) groups. Neither differed the averages of the two groups significantly from 50% (corresponding to an equal amount of ‘up’ and ‘down’ transitions) on one-sample t -tests.

Discussion

This study examined whether handedness-related asymmetries in the dynamics of bimanual isofrequency coordination are associated with an asymmetry in the strength of coupling between the two limbs. Although this hypothesis has been advanced in speculative form in the literature, it was neither formalized nor directly tested in previous research. The present study casted the hypothesis into a formal model and tested the prediction that (due to an asymmetry in interlimb coupling strength) the nondominant limb would show larger adaptations in its phasing than the dominant limb during transient behavior. To this end, transient forms of bimanual coordination were induced experimentally by means of external perturbations and phase transitions, followed by a detailed analysis of the contributions of the individual limbs to those transient behaviors. This required analysis methods that aimed specifically at establishing the relative contributions of the individual limbs to changes in the interlimb phase relation. Before addressing the results that speak to the predicted asymmetry in interlimb coupling strength, it is useful to briefly compare the obtained characteristics of steady-state performance to related findings in the

literature, in order to determine whether the coordination dynamics as obtained in the current study indeed adhered to those captured by Equations 2.1 and 2.2.

In agreement with previous findings (Amazeen et al., 1997; Riley, Amazeen, Amazeen, & Turvey, 1997; Semjen et al., 1995; Stucchi & Viviani, 1993; Swinnen et al., 1996; Treffner & Turvey, 1995, 1996), the results obtained for steady-state performance revealed a small, but significant phase lead of the dominant limb (for RH individuals $\Delta\phi < 0$; for LH participants $\Delta\phi > 0$, with the exception of in-phase wrist oscillations). Furthermore, the observed phase lead by the dominant limb was amplified at higher movement frequencies during antiphase coordination (cf. Rogers et al., 1998), which was consistent with the previously observed dependence of $\Delta\phi$ on coordination pattern and movement frequency (cf. Semjen et al., 1995; Stucchi & Viviani, 1993; Treffner & Turvey, 1995, 1996). In addition, analysis of the variability of relative phase (*TCV*) demonstrated that antiphase coordination was less stable than in-phase coordination, and that coordinative stability decreased with increasing frequency (e.g., Post, Peper, Daffertshofer, & Beek, 2000; Treffner & Turvey, 1995).³ The latter effect was also corroborated by the relaxation characteristic after perturbation (λ). Because these results were consistent with the previously identified asymmetry in the relative phase dynamics as captured by the extended HKB potential developed by Treffner and Turvey (1995; i.e., Equation 2.1), the predictions based on the demonstration that this potential may result from an asymmetry in coupling strength (see Introduction; Peper, Daffertshofer, & Beek, 2004) could be meaningfully addressed.

Relaxation process was mediated primarily by the nondominant arm

Given the predicted asymmetry in coupling strength (cf. Introduction), the externally imposed 90° phase perturbation of the dominant arm during bimanual coordination was expected to invoke larger adaptations in the phasing of the

³ Although for lower arm oscillations movement frequency affected both $\Delta\phi$ and *TCV*, no significant effects of frequency were obtained for the wrist oscillations. This may be due to a higher preferred movement frequency in the latter situation (viz. 1.10 Hz and 1.49 Hz for unimanual lower arm oscillations and flexion-extension movements about the wrist, respectively, as reported by Beek, Rikkert, & Van Wieringen, 1996; Peper & Beek, 1998b). As a result, for the lower arm movements the higher frequency conditions entailed frequencies that exceeded the preferred movement frequency, whereas this was not the case for the wrist oscillations.

(unperturbed) nondominant arm than perturbation of the nondominant arm would invoke in the phasing of the (unperturbed) dominant arm. As expected, the phase of both arms (rather than the phase of the perturbed arm alone) was adjusted in order to regain the required phase relation after the perturbation, thereby underscoring the effects of interlimb coupling (cf. Post, Peper, & Beek, 2000; Post, Peper, Daffertshofer, & Beek, 2000). When the dominant arm was perturbed, the return process back to the initial phase relation involved considerable phase adaptations in the movements of the contralateral (nondominant) arm. The contribution of the dominant arm after perturbation of the nondominant arm was significantly smaller in right-handers (see Figure 2.5A), reflecting the predicted larger coupling influence stemming from the dominant arm onto the nondominant arm than vice versa. For LH participants, however, this tendency failed to reach significance.

The asymmetry in coupling strength may also underlie the observation (obtained for LH participants; see Figure 2.4) that the relaxation of the bimanual pattern elapsed more quickly (viz. larger values of λ) when the dominant arm was perturbed (for comparable results regarding RH participants, see Post, Peper, Daffertshofer, & Beek, 2000). That is, because the unperturbed nondominant limb was more strongly attracted by the perturbed dominant limb than in the reverse situation, the interlimb phasing returned more swiftly to its original pattern in this condition.

Examination of the effects of movement frequency revealed that, for in-phase coordination, the relative contributions of the unperturbed arm (as indexed by IC_{pert}) increased with movement frequency. This effect was not observed for antiphase coordination, possibly due to a ceiling effect, given the high values of IC_{pert} obtained for this coordination mode for all movement frequencies. Note that the increase in IC_{pert} as obtained for in-phase coordination indicates that movement frequency affected the asymmetry in the contributions of the perturbed and unperturbed arms, irrespective of which arm (dominant or nondominant) was actually perturbed. Accordingly, for the LH individuals the relative contribution of the unperturbed arm increased with movement frequency, regardless of whether the dominant or the nondominant arm was perturbed. For RH participants, however, this frequency effect was only observed for the unperturbed nondominant arm, whereas the relative contribution of the unperturbed dominant arm was not affected by movement frequency (see Figure 2.5C). This resulted in a significant increase in the

difference between the relative contributions of the unperturbed nondominant (left) and dominant (right) arm, indicating that the handedness-related asymmetry in coupling strength increased with movement frequency for RH individuals. Although this finding is at variance with Treffner and Turvey's (1995) proposal that the handedness-related parameter d (in Equations 2.1 and 2.2) is insensitive to changes in movement frequency⁴, it is consistent with the proposition that the dominant and nondominant limb differ with regard to the degree to which coupling strength scales (inversely) with increases in oscillation frequency (Carson, 1993; see also Carson et al., 1994).

Frequency-induced transitions were mediated mainly by the nondominant hand

In frequency-induced transitions from antiphase to in-phase coordination, the phasing of one or both limbs is altered in such a way that the combined behavior (i.e., the relative phase between the hands) changes by approximately 180°. Based on the asymmetric coupling strength hypothesis, it was predicted that such transitions would be predominantly mediated by phase changes in the movements of the nondominant limb. Indeed, the results revealed that, for both RH and LH participants, transitions from antiphase to in-phase involved larger phase adaptations in the nondominant hand than in the dominant hand (see Figure 2.6), although this effect failed to reach significance for the LH group. This result supports the hypothesis that the coupling influences exerted by the dominant hand onto the nondominant hand were stronger than vice versa.

The asymmetric potential (Equation 2.1) demonstrates a small asymmetry in the stability properties of the two attractors, in that the two sides of the corresponding potential wells are slightly different with respect to their height and steepness (see Figure 2.1). This implies that for left-handers a small bias may be expected towards transitions involving increasing values of ϕ ('up'), while right-handers may exhibit more transitions involving a decrease in ϕ ('down') (see also Byblow et al., 1998). However, the current observation that

⁴ In later studies (Amazeen et al., 1997; Riley et al., 1997) d was shown to capture not only the effects of handedness, but also those of asymmetrically focused attention. Riley et al. (1997) found that the latter situation resulted in d varying (inversely) with movement frequency, whereas with respect to the effects of handedness this parameter was considered to be frequency independent.

handedness did not result in a significant predominance of a particular transition route ('up' or 'down') indicated that the associated asymmetry in the potential was either not present, or simply too small to induce noticeable differences in this regard.⁵ Hence, the effects of handedness on the manner in which the transition is effectuated are best captured in terms of the relative contributions of the individual hands (consistent with the decomposition of Equation 2.2 into Equations 2.3 and 2.4), rather than in terms of the relative phasing between the hands (as captured by Equations 2.1 and 2.2).

Together with the results of the Perturbation part, these findings provided substantial support for the notion that handedness affects bimanual coordination through an asymmetry in coupling strength, with a stronger influence of the dominant limb on the nondominant limb than vice versa. As such, the results indicated that the asymmetry in the relative phase dynamics (accounted for by the potential developed by Treffner & Turvey, 1995) is likely to result from this asymmetry in coupling strength, in accordance with the derivation presented by Peper, Daffertshofer, and Beek (2004; see also Introduction).

In interpreting this result it is useful to recall that, because the latter derivation captures the phase dynamics of the individual limbs, the associated coupling influences result from the underlying properties of both the oscillating components (the limbs) and the interactions between them. As a consequence, at this level of analysis, it is immaterial what precisely caused the asymmetry in the coupling influences. After all, from a mathematical point of view one can either introduce an asymmetry in the components or in the interactions between them (cf. Daffertshofer, Van den Berg, and Beek 1999, Appendix A). Thus, additional knowledge about its source(s) is required to attribute the observed asymmetry in coupling strength to either the components or the interaction processes between them (or both). As outlined in the next section, several studies have shown that specific neurophysiological sources of interlimb interaction are characterized by handedness-related asymmetries, indicating that the demonstrated asymmetry in coupling strength may stem (partly) from these

⁵ In addition, the lack of asymmetry in the observed transition routes lends further support for the assertion that the effects of handedness cannot be captured adequately by the extended HKB-potential involving asymmetry in the components' eigenfrequencies (cf. Carson, Goodman, Kelso, & Elliott, 1996; Carson et al., 1997; Treffner & Turvey, 1996), because in this model small phase shifts are associated with more pronounced tendencies towards one of the two transition routes ('up' or 'down', cf. Kelso & Jeka, 1992).

interaction processes. However, the possibility that the asymmetry in the strength of the mutual influences is (also) associated with unilateral differences between the components themselves (for instance, due to differences in the way in which the dominant and the nondominant limb are controlled; Bagesteiro & Sainburg, 2002; Sainburg, 2002) cannot be ruled out a priori and awaits further examination.

Asymmetries in neural control and coupling processes

Hand dominance is usually considered to be a cortical phenomenon resulting from hemispheric lateralization. Differential specialization is evident for the left hemisphere for language-associated functions but also for motor control (for a review, see Serrien, Ivry, & Swinnen, 2006). The importance of the left hemisphere for movement control of both limbs (Haaland & Harrington, 1996) is underscored by the observation that left hemisphere lesions were likely to show deficits in the control of either hand, whereas right hemisphere lesions were mainly associated with the contralateral hand (Wyke, 1971) and that, for RH individuals, unimanual movements of the left limb resulted in more activation of the ipsilateral motor cortex than the right limb did (Kim et al., 1993; Kobayashi, Hutchinson, Schlaug, & Pascual-Leone, 2003; Singh et al., 1998). Furthermore, on the basis of observed differences in left- and right arm control for right-handers, it has been proposed that the left hemisphere controls the task dynamics (e.g., the movement trajectory), whereas the right hemisphere regulates limb position and posture through feedback mediated mechanisms (Bagesteiro & Sainburg, 2002). However, the laterality of such distinctive processes may be altered, for instance through learning (Debaere, Wenderoth, Sunaert, Van Hecke, & Swinnen, 2004) or by means of directed attention (Johansen-Berg & Matthews, 2002), yielding flexibility in human brain lateralization via interhemispheric communication (Serrien et al., 2006). Nevertheless, studies of unimanual movement signify a disparity of hemispheric functioning, which may be of importance for the organization of bimanual movements (Serrien et al., 2006).

In addition, studies examining both RH and LH individuals demonstrated handedness-related asymmetries in anatomical structures (Amunts, Schlaug, Schleicher, Steinmetz, Dabringhaus, & Roland, 1996; Volkman, Schnitzler, Witte, & Freund, 1998), in the excitability of corticospinal pathways (De Genarro et al., 2004; Triggs, Calvanio, & Levine, 1997; Triggs, Calvanio,

Macdonell, Cros, & Chiappa, 1994), and in the hemispheric activation during unimanual tasks (Dassonville, Zhu, Ugurbil, Kim, & Ashe, 1997, Kim et al., 1993). Handedness-related hemispheric asymmetries were also identified during bimanual coordination, with the hemisphere contralateral to the dominant limb being more important for the performance of bimanual tasks for both RH (e.g., Gerloff & Andres, 2002; Jancke et al., 1998; Serrien, Cassidy, & Brown, 2003) and LH individuals (Viviani, Perani, Grassi, Bettinardi, & Fazio, 1998), which emphasizes the relation between handedness and the hemispheric organization during bimanual coordination.

The present study indicated an asymmetry in coupling during bimanual coordination. Bimanual coupling implies that each hand is somehow influenced by the movement (to be) executed by the other hand. An asymmetry in this coupling may be expressed through several neural structures and processes (for a review, see Carson, 2005). It has been proposed that the phase shift (or time lag) between the dominant and nondominant limb in rhythmic bimanual tasks results from a temporal delay in the transfer of timing information via the corpus callosum from the dominant to the nondominant hemisphere (Stucchi & Viviani, 1993), which has been suggested to be related to the observed differences in hemispheric activation (Viviani et al., 1998). However, although this unilaterally acting temporal delay indeed provides an account for the observed phase shifts, our data regarding the relative contributions of the two limbs during transient stages of performance suggest instead that the coordinative asymmetry results from bilaterally acting coupling influences.

An alternative source of interlimb interactions may be found in the presence of uncrossed corticospinal pathways, given the undecussated portion (approximately 10-25%) of the descending fibers in the corticospinal tract (Nathan, Smith, & Deacon, 1990). Simulations by Cattaert, Semjen, and Summers (1999) suggested that the (asymmetric) coordination characteristics of bimanual circle drawing may indeed result from ‘neural cross-talk’ due to these uncrossed fibers. A recent TMS study revealing handedness-related asymmetries in the ipsilateral (i.e., uncrossed) neural pathways innervating the musculature in the upper limbs (Kagerer, Summers, & Semjen, 2003) revealed that, during bimanual coordination, the movements of the nondominant (left) limb were more strongly influenced by brain activity associated with activation of the dominant (right) limb than vice versa.

In addition, it has been demonstrated (using short-interval bilateral TMS) that the inhibitory influences that the dominant hemisphere exerts on (signals stemming from) the nondominant hemisphere are stronger than in the reverse direction (Kobayashi et al., 2003; Netz, Ziemann, & Homberg, 1995; Stinear & Byblow, 2004). Thus, the effects of hand dominance may be associated with the dominant hemisphere being more efficient in inhibiting the hemispheric drive stemming from the nondominant side than vice versa (Serrien et al., 2003), rendering the dominant limb less susceptible to influences stemming from the nondominant limb than vice versa.

Apart from asymmetries associated with efferent processes, the role of afferent signals in this regard cannot be ruled out a priori, especially in view of the effects of the mechanical perturbations as applied in the present experiment. After all, phase adaptations in the unperturbed, contralateral arm require sensory information about the altered phasing of the perturbed arm. Although tendon vibration studies have indicated that distortion of the kinesthetic feedback of either the left or the right limb had different effects on the relative phasing between the limbs (Steyvers, Verschueren, Levin, Ouamer, & Swinnen, 2001; Verschueren, Swinnen, Cordo, & Dounskaia, 1999), it is presently unclear how and to what extent feedback-related influences during bimanual coordination are modulated by hand dominance.

In sum, bimanual control is likely to be achieved by an assembly of widely distributed processes over the whole CNS (including the supplementary motor area, cerebellum, and basal ganglia, for reviews see Cardoso de Oliveira, 2002; Carson, 2005; Donchin, Cardoso de Oliveira, & Vaadia, 1999; Swinnen, 2002), which implies that the asymmetrical signatures of bimanual coordination may result from various neural structures and processes. As noted above, candidate sources of interlimb interaction (cf. Carson, 2005) indeed exhibit asymmetries, with a primary role for signals stemming from the dominant side. As such, these neurophysiological findings are consistent with the current behavioral results that indicated an asymmetry in bilateral interactions between the limbs, with the movements of the nondominant limb being more strongly influenced by those of the dominant limb than vice versa.

Handedness effects were less pronounced in left-handers

Although the present results demonstrated that, in general, the nondominant limb adjusted its phasing to a larger extent than the dominant limb,

the associated effects failed to reach significance in the LH group. This indicated that the asymmetry in interactions between the limbs was less evident for LH than for RH participants (see Figs. 2.5 and 2.6). It has been suggested that performance differences between the two groups result from the fact that, on average, left-handers are less consistent in terms of lateralization (i.e., to be more ambidextrous) than right-handers (cf. Peters, 1994; Shen & Franz, 2005). Indeed many (self-proclaimed) left-handers are inconsistent left-handers, in that for some skills (e.g., writing) the left hand is dominant, while for other skills (e.g., throwing) the right hand is dominant, leading to heterogeneity with respect to handedness for this group (cf. McManus, Porac, Bryden, & Boucher, 1999; Peters & Servos, 1989). However, given the stringent inclusion criteria applied in the present study it seems unlikely that the LH group (mean LQ = -94) tended to more ambidextrous performance than the RH group (mean LQ = 89), rendering this explanation unsatisfactory. Nevertheless, the present results clearly indicated that the asymmetry in coupling strength was less pronounced in LH individuals than in RH individuals. This difference between the groups may be associated with the fact that LH and RH individuals are not neural ‘mirror images’ of one another (cf. Amunts et al., 1996; Kandel et al., 1991). For instance, empirical results suggest that the prominent role of the left hemisphere in the control of both limbs may also surpass the level of hand preference (see Serrien et al., 2006), which would imply that these motor functions are associated with the nondominant hemisphere in LH individuals (as opposed to the dominant hemisphere in RH persons). Alternatively, the reduced asymmetry in coupling strength in left-handers may also be interpreted in terms of functional adaptations to the ‘right-handed world’ (McManus, 2002; Provins, 1997).

Conclusion

The present study revealed a handedness-related asymmetry in interlimb coupling strength during rhythmic bimanual coordination, and demonstrated that this asymmetry may underlie previously identified characteristics of the relative phase dynamics. The identified asymmetry in coupling strength entails that the nondominant limb is affected more strongly by influences stemming from the dominant limb than vice versa. This result was less evident in LH participants than in RH participants, indicating that also in the context of isofrequency bimanual performance left-handedness can not be simply regarded as a ‘mirror

image' of right-handedness. The observed asymmetry in coupling strength is consistent with the notion that the nondominant hand is primarily subservient to the dominant hand in other, more complex bimanual tasks in everyday life (cf. Guiard, 1987; Peters, 1994). Hence, the current results indicate that, although the two hands unambiguously influence each other bi-directionally when performing purposeful bimanual coordination, it is indeed the dominant hand that dominates these mutual influences.

Chapter 3

Intentional switches between bimanual coordination patterns are primarily effectuated by the nondominant hand

Published as:

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.

Abstract

Based on indications that hand dominance is characterized by asymmetrical interlimb coupling strength (with the dominant hand exerting stronger influences on the nondominant hand than vice versa), intentional switches between rhythmic bimanual coordination patterns were predicted to be mediated primarily by phase adaptations in the movements of the nondominant hand. This hypothesis was supported for both right-handed and left-handed participants who performed voluntary switches from in-phase to antiphase coordination and vice versa, at four different frequencies. In accordance with previous indications that handedness is expressed less consistently in left-handers, the asymmetry between the hands was less pronounced in left-handed than in right-handed participants. The asymmetry was smaller for switches from in-phase to antiphase coordination (i.e., in the direction opposite to spontaneous transitions) than for switches in the reverse direction, suggesting that (the expression of) the handedness-related asymmetry in coupling strength was weakened by intentional processes associated with these switches.

Introduction

Rhythmic interlimb coordination is characterized by attraction to a limited number of frequency and phase relations (Peper, Beek, & Van Wieringen, 1995c; Tuller & Kelso, 1989, Yamanishi, Kawato, & Suzuki, 1980; Zanone & Kelso, 1992), which owe their stability to (mutual) interactions between the participating limbs. For isofrequency coordination, the empirically observed stability properties have been accounted for in terms of a dynamical model of coupled oscillators, commonly referred to as the HKB model (Haken, Kelso, & Bunz, 1985). Although the interactions between the limbs were originally modeled by means of a symmetric coupling between the associated oscillators, converging evidence indicates that the strength of coupling between the upper limbs is asymmetric as a function of hand dominance. This implies that the effects of handedness are not limited to the quality of unimanual task performance (e.g., Bagesteiro & Sainburg, 2002; Peters, 1980; Sainburg, 2002) and a preference for assigning manipulative roles to the dominant hand and stabilizing roles to the nondominant hand (cf. Guiard, 1987; Peters, 1994), but extend to the degree to which the limbs influence each other in bimanual tasks consisting of two identical subtasks (i.e., oscillation at a common frequency).

The assertion that hand dominance is associated with an asymmetry in the degree to which the upper limbs influence each other is based on both theoretical and empirical – neurophysiological and behavioral – evidence. On the theoretical side, the subtle, yet systematic effects of handedness on the relative phase dynamics (e.g., shifts in mean relative phasing), were captured by adding additional symmetry-breaking sine terms to the original (symmetric) HKB potential (Treffner & Turvey 1995, 1996). Peper, Daffertshofer, and Beek (2004) recently demonstrated that this asymmetric potential and, thus, the associated handedness-related coordination phenomena, can be formally understood in terms of an asymmetry in the strength of the coupling between the oscillating limbs, with the dominant limb exerting a stronger influence on the nondominant limb than vice versa (see also Chapter 2; for related suggestions, see Carson, 1993).

This interpretation is consistent with neurophysiological findings regarding candidate sources of interlimb interactions. For instance, interlimb coupling effects may ensue from uncrossed corticospinal pathways (cf. Carson, 2005; Cattaert, Semjen, & Summers, 1999). Recent TMS studies examining the

influence of these uncrossed pathways on muscle activation in the ipsilateral limb indicated that the nondominant (left) limb was more strongly influenced by brain activity associated with the dominant (right) limb than vice versa (Kagerer, Summers, & Semjen, 2003). In addition, short-interval bilateral TMS studies revealed stronger inhibitory influences from the dominant onto the nondominant hemisphere than in the reverse direction (Kobayashi, Hutchinson, Schlaug, & Pascual-Leone, 2003; Netz, Zieman, & Homberg, 1995; Stinear & Byblow, 2004). This finding is consistent with the suggestion that the dominant hemisphere is more efficient in inhibiting the hemispheric drive stemming from the nondominant side than vice versa (Serrien, Cassidy, & Brown, 2003), which is in accordance with the suggested asymmetry in interlimb coupling strength.

Finally, there is considerable behavioral evidence for a handedness-related asymmetry in coupling strength. A frequently addressed phenomenon in isofrequency coordination is the spontaneous transition from antiphase (originally defined as alternating activation of homologous muscles; relative phase $\phi = 180^\circ$) to in-phase coordination (simultaneous activation of homologous muscles; $\phi = 0^\circ$) that occurs when movement tempo is gradually increased (Kelso, 1984). During such a transition at least one of the limbs has to change its phasing so that the new phase relation is attained. In Chapter 2 it was demonstrated that in both left-handed (LH) and right-handed (RH) participants the associated phase adaptations were larger in the nondominant hand than in the dominant hand, although the difference between the hands in this regard was larger for RH than for LH participants (for whom the difference did not reach significance). This result was consistent with previous observations obtained for RH individuals (Byblow, Carson, & Goodman, 1994; Byblow, Chua, & Goodman, 1995). Similarly, transitions from asymmetric to symmetric bimanual circle drawing have been shown to be mainly mediated by a change in movement direction of the nondominant hand (Byblow, Chua, Bysouth-Young, & Summers, 1999; Carson, Thomas, Summers, Walters, & Semjen, 1997; Wuyts, Summers, Carson, Byblow, & Semjen, 1996). Because the transient stage during such spontaneous transitions is governed by the stability properties that result from the interactions between the limbs, the observed predominance of adaptations in the phasing of the nondominant limb is consistent with the postulated asymmetry in interlimb coupling strength. This interpretation was further underscored by the characteristics of the relaxation process in response to an external perturbation of the interlimb coordination pattern. The

restabilization of the original coordination pattern appeared to be mediated primarily by phase adaptations in the nondominant limb, reflecting the proposed asymmetry in interlimb coupling strength (Chapter 2). Although this effect was observed for both LH and RH participants, it was more pronounced for the RH group.

In sum, theoretical considerations in combination with recent neurophysiological findings regarding the effects of hand dominance onto interlimb coupling strength are consistent with the behavioral characteristics observed during transient stages that are governed by the stability features of rhythmic interlimb coordination. Another form of transient behavior is observed when voluntary switches between coordination patterns are performed. Although in this situation the changes in relative phasing do not follow from the ('intrinsic') coordinative stability properties, several studies have demonstrated that the quickness of such switches (i.e., the switching time) depends on the stability of the coordination patterns involved. In particular, switches from patterns with lower stability (e.g., antiphase) to patterns with higher stability (e.g., in-phase) are typically performed faster than switches in the reverse direction (Byblow, Lewis, Stinear, Austin, & Lynch, 2000; Carson, Byblow, Abernethy, & Summers, 1996; Serrien & Swinnen, 1999; Kelso, Scholz, & Schöner, 1988; Scholz & Kelso, 1990), which is consistent with the theoretical predictions formulated by Kelso et al. (1988; see also Scholz & Kelso, 1990). The observed influence of coordinative stability in this regard indicates that the performance of intentional switches is (partly) shaped by the interactions between the limbs, suggesting that the handedness-related asymmetry in coupling strength may affect the way in which the switches are effectuated.

Indeed, several results obtained for RH participants point in this direction. Whereas, for bimanual circle drawing, switching time was demonstrated to be independent of the hand that mediated the switch (Byblow, Summers, Semjen, Wuyts, & Carson, 1999; Wuyts, Byblow, Summers, Carson, & Semjen, 1998; but see also Byblow et al., 2000), switches that were (by instruction) mediated by the dominant hand resulted in larger disruptions in the movement pattern of the contralateral hand (reflecting interlimb interactions) than did switches mediated by the nondominant hand (Byblow et al., 2000; Byblow, Summers, et al., 1999). For bimanual coordination of rhythmic supination-pronation movements, Carson, Byblow, et al. (1996) found that in most cases switches from in-phase to antiphase coordination were mediated by the nondominant

(left) hand. Verheul and Geuze (2004), on the other hand, argued that in their experiment (involving intentional switches between bimanual finger tapping patterns) the switching strategy primarily depended on the resulting change in relative phasing (viz., increasing or decreasing) rather than on the hand that mediated the phase change. However, they also reported that switches mediated by slowing down the nondominant (left) hand occurred most often.

Together, these results obtained for RH participants suggest that the way in which intentional changes in rhythmic interlimb coordination are carried through is influenced by hand dominance. Whereas, at first sight, one may expect that the dominant limb is used to mediate the voluntary change in interlimb phasing (given its more efficient control; cf. Bagesteiro & Sainburg, 2002; Sainburg, 2002), these studies indicated that the phase adaptations were predominantly made by the nondominant limb instead. Although these findings are consistent with the proposed asymmetry in interlimb coupling strength, with the nondominant limb being more strongly influenced ('attracted') by the dominant limb than vice versa (e.g., Byblow et al., 2000; Carson, 1993; Peper, Daffertshofer, & Beek, 2004; Treffner & Turvey, 1995, 1996), a thorough evaluation of the effects of hand dominance in this regard requires a systematic comparison of the performance of LH and RH individuals. Explicit examination of the differences between these two groups is important, because LH persons cannot be simply regarded as 'inverted' RH persons. In the majority of LH individuals, hemispheric specialization corresponds to that observed in right-handers (e.g., language areas are located in the left hemisphere; Kandel, Schwartz, & Jessell, 1991), and handedness-related motor-cortical asymmetries have been reported to be more pronounced in RH than in LH individuals (Amunts et al., 1996; Kandel et al., 1991). In addition, there are many indications that left-handers are less consistent in their expression of hand dominance than right-handers (e.g., Chapter 2; McManus, Porac, Bryden, & Boucher, 1999; Peters & Servos, 1989; Shen & Franz, 2004), which may be associated with neurophysiological differences in lateralization or with the fact that left-handers have typically been raised in a 'right-handed world' (McManus, 2002; Provins, 1997).

To test the hypothesis that intentional switches between coordination patterns were influenced by hand dominance, an experiment was conducted involving both RH and LH participants. In particular, it was predicted that, due to the handedness-related asymmetry in coupling strength, the transition would

be primarily mediated by phase adaptations in the nondominant hand. In addition, these effects were predicted to be more pronounced for RH participants than for LH participants, in line with the results of Chapter 2.

Before turning to the experiment, it is useful to highlight some important differences between intentional switches and frequency-induced spontaneous transitions. The first difference concerns the direction of the switch. For spontaneous transitions the changes in relative phasing are directly dictated by the difference in coordinative stability between the two patterns, resulting in transitions from the less stable to the more stable pattern, whereas this difference does not constrain the direction of intentional switches. For isofrequency coordination, this implies that intentional switches from antiphase to in-phase as well as switches in the opposite direction can be examined. Previous results have indicated that voluntary switches in these two directions are performed in different ways (Byblow, Summers, et al., 1999; Carson, Byblow, et al., 1996). In addition, it has been suggested that voluntary switches and spontaneous transitions may involve different neurophysiological processes (Byblow et al., 2000; Byblow, Summers, et al., 1999). Accordingly, the way in which hand dominance affects intentional switching behavior cannot be simply inferred from the characteristics of frequency-induced, spontaneous transitions in LH and RH participants (as obtained in Chapter 2).

Another striking difference is that, unlike frequency-induced spontaneous transitions, voluntary switches can be examined at various tempos of performance. Higher movement frequencies have been shown to result in faster switches between coordination patterns (Carson, Byblow, et al., 1996; Scholz & Kelso, 1990). However, it is currently unclear whether this frequency dependence of switching time is associated with variations in the degree to which the switch is mediated by either hand. Given recent indications that the asymmetry in coupling strength increases with movement frequency (Chapter 2), it may be expected that the handedness-related asymmetry between the hands (regarding their respective contributions to the switch) is larger when the patterns are performed at a higher tempo. This third prediction was also tested in the experiment.

The three predictions motivated in the preceding were examined by comparing how LH and RH participants performed intentional switches from the in-phase to the antiphase coordination pattern and vice versa. In particular, the

analyses focused on the relative contributions of the individual hands in effectuating the intended change in interlimb phasing.

Methods

Participants

Fourteen volunteers (8 females and 6 males, aged 18-24 years) were invited to participate in the experiment. They were selected on the basis of the experimenters' impression of their hand preference. 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. To preserve the naivety of the participants with respect to the purpose of the study, this handedness questionnaire was filled out after the experiment was completed. Participants with an LQ > 33% were labeled as RH, while participants with an LQ < -33% were labeled as LH. Seven participants were right-handed (mean LQ = 82%, range 47% to 100%), while six were left-handed (mean LQ = -88%, range -71% to -100%). One anticipated LH participant was excluded from the analyses because he turned out to be ambidextrous (LQ = -7%). The participants gave their informed consent prior to the experiment.

Apparatus

Participants were seated in a height-adjustable chair. The lower arms were placed on arm rests in a neutral position (thumbs up and hand palms facing inward) and their position was secured by the support surface on the medial and ventral side, by two adjustable vertical foam-coated rods on the dorsal side, and one adjustable horizontal foam-coated rod on the lateral side. Both hands were fixed against flat manipulanda by two straps, with all fingers extended. The manipulanda allowed for flexion-extension movements about the wrist in the horizontal plane only and were mounted on a vertical axis with a potentiometer at its lower end (Sakae, type FCP40A-5k, linearity 0.1%). The potentiometer's output voltage was digitized by a 12-bit ADC (Labmaster DMA) and stored on a microcomputer with a sampling frequency of 200 Hz. Computer-generated auditory pacing stimuli (pitch: 200 Hz, duration: 50 ms) were presented using headphones (Sennheiser HD 520 II). A green light emitting diode (LED;

diameter: ca. 1.0 cm) positioned 1.5 m in front of the participant served as visual stimulus to trigger the intended switch in coordination.

Procedure

The participants performed bimanual oscillatory movements in either in-phase or antiphase coordination at four different frequencies that were specified by means of the auditory pacing signal. One pulse was presented for each half cycle of the movement. During in-phase coordination, participants were instructed to synchronize extension of both hands with a given beep and flexion with the next beep. In the antiphase mode, simultaneous flexion of one hand and extension of the other hand had to coincide with the pacing signal. Participants were instructed to start off in either the in-phase or antiphase mode and to switch to the other mode when indicated to do so by the visual stimulus. To this end, the LED was turned on at a random moment between the 5th and the 15th cycle and remained illuminated for 3 s. The switch had to be performed in a fluent fashion within the illumination period, and it was emphasized that there was no need to react as fast as possible, since the task was not a reaction time task. The required movement frequencies were 1 Hz, 1.25 Hz, 1.5 Hz, and 1.75 Hz and trial length was 25 cycles in all conditions. The trials were grouped in two ‘switch condition blocks’ (in-phase to antiphase and antiphase to in-phase), the order of which was counterbalanced over participants. Within each block, four ‘frequency blocks’ were presented in random order. Each condition was repeated four times in a row. One familiarization trial for each condition preceded the 32 experimental trials.

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 VU University, Amsterdam.

Data reduction

The angular position signals were low-pass filtered (bi-directional second-order Butterworth filter, cut-off frequency 10 Hz) and subsequently differentiated (five-point approximation) to obtain angular velocity. Inspection of the position data revealed unsystematic variations in the center of oscillation, especially during the switching period. Therefore, angular position was normalized to the associated amplitude for each half cycle, yielding a signal

ranging from -1 to 1 . Equivalently, angular velocity was normalized to peak velocity for each half cycle. For both normalizations the onset and end of each half cycle were established by means of a custom-made peak-picking algorithm applied to the position data. The continuous phase angle (θ , in degrees) was determined for each hand, using $\theta_i = \tan^{-1}(\dot{x}_i^*/x_i^*)$, with x_i^* denoting normalized angular position, \dot{x}_i^* denoting normalized angular velocity, and i indicating the sample index. For each trial, the phase angles were ‘unwrapped’ (i.e., summed over successive cycles), resulting in a progressively increasing phase angle per hand (i.e., θ_L and θ_R). The continuous relative phase between the hands (ϕ) was defined as $\phi = \theta_L - \theta_R$.

Analysis

Pre- and post-switch performance

In order to relate the empirical results regarding the asymmetry in coupling strength to the previously identified coordination dynamics, steady-state behavior was analyzed. That is, the mean movement frequency of the right and left hand as well as the mean of ϕ ($\bar{\phi}$) and its standard deviation ($SD\phi$) were determined: for pre-switch performance (as obtained for the five cycles preceding the onset of the visual stimulus) and for post-switch performance (as obtained for the five cycles after the stimulus went off). This yielded two values (‘pre’ and ‘post’) per trial for each of these performance measures. The mean phase shift ($\Delta\phi_j$, with j denoting ‘pre’ or ‘post’) was expressed relative to the required relative phase ($\phi_{req,j}$), that is, $\Delta\phi_j = \bar{\phi}_j - \phi_{req,j}$, with $\phi_{req,j} = 0^\circ$ (in-phase) or $\phi_{req,j} = 180^\circ$ (antiphase). $SD\phi_j$ was used as an index of performance stability with low $SD\phi_j$ corresponding to a high degree of stability (cf. Schöner, Haken, & Kelso, 1986). A trial was excluded from further analysis if $|\bar{\phi}_{post} - \bar{\phi}_{pre}| > 360^\circ$ or if no stable pre- or post-switch behavior was established ($SD\phi_j > 30^\circ$; this criterion was based on the obtained frequency distribution of the $SD\phi_j$ values). In seven trials $SD\phi_{pre}$ or $SD\phi_{post}$ exceeded this criterion due to a brief change in ϕ_j of more than 270° . In these cases the performance measures were determined for five consecutive pre- or post-switch cycles that did not involve such a change. Finally, eight trials were excluded from further analysis. These trials were equally distributed over participants and conditions.

Switching time

The main focus of this study concerned the transient stage of the bimanual behavior, that is, the coordination switch. To determine the behavioral measures during the switch, the switch region had to be defined first. To this end, the onset and end of the pattern change were determined following a procedure inspired by analyses performed by Byblow et al. (1994) and Wuyts et al. (1998). First, for the period of stimulus illumination, the point at which ϕ first deviated from $\bar{\phi}_{\text{pre}} \pm 2SD\phi_{\text{pre}}$ and the point at which ϕ first attained a value within the range of $\bar{\phi}_{\text{post}} \pm 2SD\phi_{\text{post}}$ were identified. These two points in time defined, respectively, the start and end of the period over which a linear regression line for ϕ was fitted. The intersections of this line with the values of $\bar{\phi}_{\text{pre}}$ and $\bar{\phi}_{\text{post}}$ were adopted as the exact onset (t_0) and end (t_{end}) of the switch, respectively. Switching time (τ_{sw}) was defined by $\tau_{\text{sw}} = t_{\text{end}} - t_0$. In addition, the values of τ_{sw} were normalized with respect to the pre-switch mean cycle duration (yielding τ_{sw}^*), in order to analyze switching time also in terms of the number of cycles (rather than time) needed for the switch.

Index of coupling

To determine the relative contributions of the hands to the intended phase adjustment, an analysis similar to that developed in Chapter 2 for unintended transitions was applied. Detailed inspection of the trials revealed that although the two hands oscillated at identical frequencies, they did not always fully adhere to the required movement frequency as specified by the auditory pacing signal (see also Results). As a consequence, the changes in phasing could not be determined reliably by simply comparing the movement phase of each individual hand to the phase prescribed by the pacing signal. Therefore, the evolutions of the individual phase angles (θ_L and θ_R , see Figure 3.1B) of the wrist movements were analyzed using the rate of change of θ (i.e., the phase velocity $\dot{\theta}$) as determined for the two hands, yielding $\dot{\theta}_L$ and $\dot{\theta}_R$ (see Figure 3.1C). Subsequently, for each hand, the mean value of $\dot{\theta}$ as obtained for the pre-switch period ($\bar{\dot{\theta}}_{\text{pre}}$) was subtracted from $\dot{\theta}$, thereby normalizing for the actual movement frequency. The amount of change in the phasing of the left hand (A_L) during the switching period (as illustrated by the dark gray areas in Figure 3.1C) was derived using

$$A_L = \int_{t_0}^{t_{\text{end}}} (\dot{\theta}_L - \bar{\dot{\theta}}_{L,\text{pre}}) dt \quad [3.1]$$

In the same fashion, A_R was calculated to determine the change in phasing of the right hand (cf. light gray areas in Figure 3.1C). The relative contribution of the left hand to the pattern change was expressed by the index of coupling (IC)⁶:

$$IC = \frac{|A_L|}{|A_L| + |A_R|} \quad [3.2]$$

Thus, for each trial, IC (ranging from 0 to 1) revealed the degree to which the switch was mediated by adaptations in the phasing of either hand. For $IC = .5$ both hands contributed equally, whereas $IC > .5$ reflected larger adaptation in the phasing of the left hand ($|A_L| > |A_R|$) and $IC < .5$ reflected larger adaptation by the right hand ($|A_R| > |A_L|$). For each participant the thus obtained values of IC were averaged for each experimental condition.

Switch pathway

For every trial the switch pathway was determined as being either ‘up’ or ‘down’, corresponding to increasing or decreasing values of ϕ during the switch, respectively (cf. Kelso & Jeka, 1992). An ‘up’ transition resulted from acceleration in the phasing of the left hand and/or deceleration of the right hand (i.e., $\dot{\theta}_L > \dot{\theta}_R$ within the switch period), whereas a ‘down’ transition resulted from deceleration of the left hand and/or acceleration of the right hand (i.e., $\dot{\theta}_L < \dot{\theta}_R$ within the switch period). For each participant the percentage of ‘up’ transitions was used for further analysis.

⁶ Note that $\text{mean}(\dot{\theta}_L - \bar{\dot{\theta}}_{L,\text{pre}})$ during the switch is equal to $\frac{1}{t_{\text{end}} - t_0} A_L$. Because the interval $t_{\text{end}} - t_0$ is equal for L and R, IC can also be defined as a relative measure of the average change in phase velocity of the two hands during the switch.

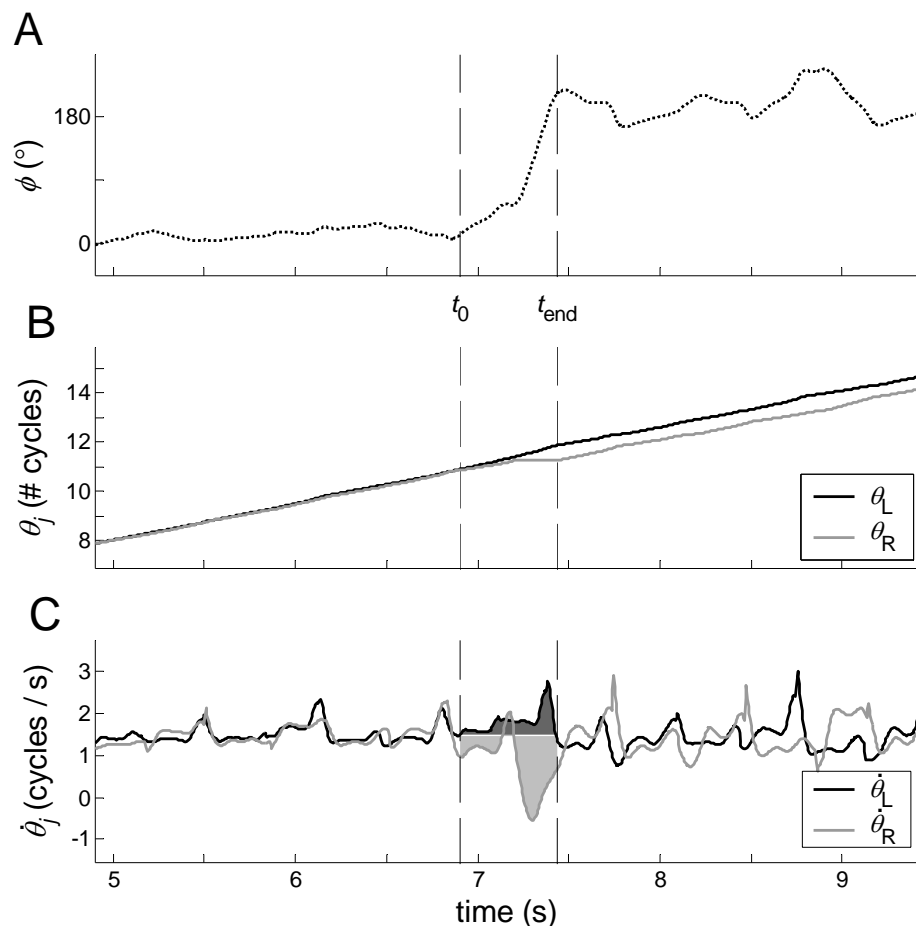


Figure 3.1. Illustration of successive steps in the derivation of *IC*, based on a single representative trial (movement frequency: 1.5 Hz) as obtained for a LH participant. Dashed vertical lines represent the moments of onset (t_0) and end (t_{end}) of the transition. A: Relative phase trajectory indicating a switch from in-phase to antiphase coordination. B: Unwrapped phase angles (θ , indexed by the number of elapsed cycles) for each hand around the switching period. C: Phase velocities $\dot{\theta}_L$ and $\dot{\theta}_R$ (L = left; R = right). Gray-shaded areas illustrate the amount of adjustment made by each arm: dark gray = left arm (A_L); light gray = right arm (A_R).

Statistical Analysis

The variables $\Delta\phi$ and $SD\phi$ were submitted to a repeated measures analysis of variance (ANOVA) with the between-subjects factor handedness (LH, RH) and the within-subjects factors coordination mode (in-phase, antiphase), frequency (1, 1.25, 1.5, 1.75 Hz), and epoch (pre-, post-switch). *IC*, τ_{sw} , and τ_{sw}^* were submitted to a repeated measures ANOVA with the between-subjects factor handedness (LH, RH) and the within-subjects factors switch condition (in-phase to antiphase, antiphase to in-phase) and frequency (1, 1.25, 1.5, 1.75 Hz). In case the assumption of sphericity was violated, the degrees of freedom

were adjusted using the Huynh–Feldt procedure. Besides significant effects ($p < .05$), tendencies towards significance ($p < .10$) were reported as well. In addition, the corresponding effect sizes (f) were calculated based on the partial eta squared (Cohen, 1988). Post-hoc comparisons were based on a combination of paired-samples and independent-samples t -tests ($p < .05$). The latter were applied for all effects involving between-group comparisons.

In addition, the mean IC values obtained for the two handedness groups were compared to $IC = .5$ using one-sample t -tests. In this case, the effects sizes were calculated in terms of Cohen's d (Cohen, 1988).

Results

Pre- and post-switch performance

Movement frequency

During pre- and post-switch performance, the absolute difference in mean movement frequency between the left and the right arm never exceeded 0.08 Hz, which confirmed that in all trials the movements were 1:1 frequency-locked. In general, the prescribed frequencies were adequately performed, although three participants experienced some difficulties in locking their movements to the highest pacing frequency of 1.75 Hz. The interindividual averages and corresponding standard deviations were 1.01 Hz ($SD = 0.03$), 1.26 Hz ($SD = 0.06$), 1.51 Hz ($SD = 0.07$), and 1.74 Hz ($SD = 0.12$).

Phase shift

Analysis of $\Delta\phi$ yielded a nonsignificant trend for handedness, $F(1, 11) = 3.65$, $p < .10$, $f = 0.26$, with mean $\Delta\phi = -4.9^\circ$ for RH participants (indicating right hand temporal lead) and mean $\Delta\phi = 0.7^\circ$ for the LH group. A significant Handedness \times Coordination Mode interaction, $F(1, 11) = 12.20$, $p < .01$, $f = 0.63$, further elucidated this tendency. Post-hoc comparisons showed that for antiphase coordination LH participants (antiphase: mean $\Delta\phi = 3.0^\circ$; in-phase: mean $\Delta\phi = -1.6^\circ$) differed significantly from RH participants (antiphase: mean $\Delta\phi = -7.0^\circ$; in-phase: mean $\Delta\phi = -2.9^\circ$), and that for LH individuals the values were significantly higher for antiphase than for in-phase coordination. Furthermore, the significant main effect of frequency, $F(3, 33) = 4.73$, $p < .01$, $f = 0.31$, and subsequent post-hoc analyses showed that, on average, the values of

$\Delta\phi$ became more negative with increasing frequency, indicating an increasing phase advance of the right hand (averaged over coordination modes and handedness groups; mean $\Delta\phi = -0.8^\circ$ [1 Hz]; -0.8° [1.25 Hz]; -3.2° [1.5 Hz]; and -4.5° [1.75 Hz]).

Relative phase variability

For $SD\phi$ the analysis revealed a significant main effect of coordination mode, $F(1, 11) = 201.01, p < .001, f = 3.04$, with antiphase (mean $SD\phi = 16.0^\circ$) being more variable than in-phase coordination (mean $SD\phi = 10.9^\circ$). The effect of frequency was also significant, $F(3, 33) = 6.10, p < .01, f = 0.39$. Post-hoc tests demonstrated that over the three lowest frequencies $SD\phi$ decreased with increasing movement frequency (mean $SD\phi = 14.8^\circ$ [1 Hz]; 13.4° [1.25 Hz]; and 12.2° [1.5 Hz]), while performance at the highest frequency (1.75 Hz; mean $SD\phi = 13.2^\circ$) only differed significantly from performance at 1 Hz.

Switch characteristics

Switching time

Analysis of switching time (τ_{sw}) revealed no significant effects (mean $\tau_{sw} = 497$ ms; $SD = 85$ ms). However, when switching time was normalized to cycle duration (τ_{sw}^*) a significant effect of frequency was obtained, $F(2.2, 23.8) = 20.14, p < .001, f = 0.86$, which indicated that the proportion of a cycle that was used to switch from one coordination pattern to the other increased with movement frequency. Subsequent post-hoc tests showed that all frequency conditions differed from one another. The mean values of τ_{sw}^* were 0.50 ($SD = 0.01$) of a cycle for 1 Hz; 0.61 ($SD = 0.17$) for 1.25 Hz; 0.73 ($SD = 0.14$) for 1.5 Hz; and 0.89 ($SD = 0.22$) for 1.75 Hz.

Index of coupling

The mean IC was significantly higher for RH participants (.67) than for LH participants (.45; see also Figure 3.2), $F(1, 11) = 71.03, p < .001, f = 1.76$, indicating that the right-handers exhibited larger adaptations of the left hand during intentional pattern switching than the left-handers. Because $IC < .5$ implied larger adjustments by the right hand and $IC > .5$ implied larger adjustments by the left hand, the average values per group were subsequently tested against $IC = .5$ (one-sample t -tests). These t -tests revealed that the values

of IC as obtained for the RH group were significantly higher than .5, $t(6) = 10.85$, $p < .001$, $d = 4.01$, whereas for the LH group a nonsignificant trend towards values lower than .5 was observed, $t(5) = -2.31$, $p < .10$, $d = 0.85$. In the LH group, 42% of the trials (between-subjects $SD = 6\%$) were predominantly mediated by the left hand (i.e., $IC > 0.5$), whereas in the RH group this was the case for 74% of the trials (between-subjects $SD = 9\%$). Hence, these results indicated that intentional switching predominantly involved phase adjustment in the movements of the nondominant hand, although this effect did not reach significance for the LH group.

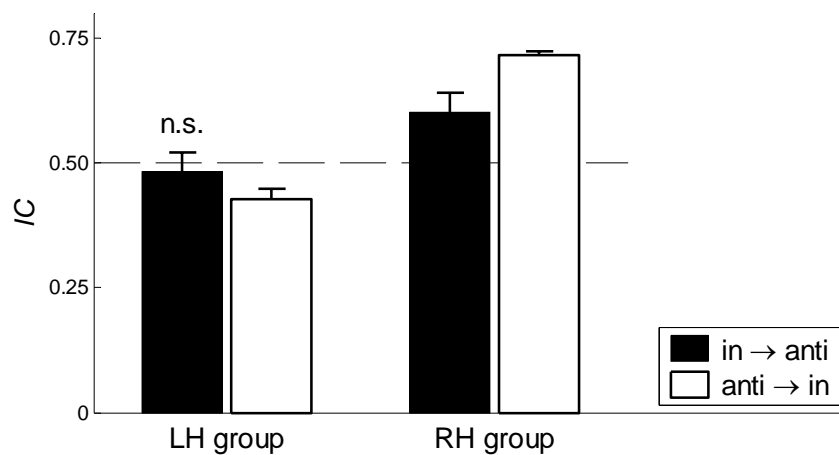


Figure 3.2. Mean values of IC as a function of handedness and switch condition. LH = left-handed group; RH = right-handed group. The dashed line indicates the value of IC corresponding to equal contributions of the left and right hand ($IC = .5$). All except one (indicated by n.s.) mean IC values differed significantly from $IC = .5$. For $IC > .5$ the switches were mainly mediated by the left hand; for $IC < .5$ they were mainly mediated by the right hand. Error bars represent the between-subjects standard errors.

The Handedness \times Switch Condition interaction was also significant, $F(1, 11) = 8.66$, $p < .05$, $f = 0.49$. Post-hoc comparisons revealed that for RH participants the values of IC were significantly higher (indicating larger left-hand adaptations) when switching from antiphase to in-phase than when switching from in-phase to antiphase. In addition, Figure 3.2 suggests that switches from antiphase to in-phase coordination resulted in a larger difference in IC between LH and RH participants than switches in the reverse direction. One-sample t -tests of the average group values for each condition against $IC = .5$ revealed that for both the in-phase to antiphase switches, $t(6) = 2.93$, $p < .05$, $d = 1.11$, and the antiphase to in-phase switches, $t(6) = 23.64$, $p < .001$, $d = 8.94$, the IC values obtained for the RH group were significantly higher than .5, revealing

that both switches were predominantly mediated by adaptations in the (nondominant) left hand. For the LH participants, however, only the antiphase to in-phase switches, $t(5) = -3.32$, $p < .05$, $d = 1.36$, resulted in a mean IC value that was significantly smaller than .5, indicating larger adaptations in the (nondominant) right hand in this condition. The percentages of trials in which the left hand primarily mediated the switch were 38% for LH and 80% for RH participants when switching from antiphase to in-phase coordination, while for switches in the opposite direction less asymmetric distributions were obtained: 46% for LH and 67% for RH participants. Together, these results demonstrated that the predominance of phase adaptations in the nondominant hand during voluntary switches was more pronounced for switches from antiphase to in-phase coordination than for switches in the opposite direction.

In line with our predictions the results indicated that, although in both groups the switches were primarily mediated by the nondominant hand, this effect was less pronounced in left-handers than in right-handers (cf. Figure 3.2). In order to test this difference between the handedness groups in a head-on fashion, we expressed IC in terms of the relative contribution of the *nondominant* (ND) hand to the switch (i.e., the numerator of Equation 3.2, A_L , was replaced by A_{ND}), yielding IC_{ND} . The repeated measures Handedness \times Switch Condition \times Frequency ANOVA performed on IC_{ND} revealed an effect of Handedness, $F(1, 11) = 21.41$, $p < .005$, $f = 0.88$, which indicated that the contribution of the nondominant hand was significantly larger in RH participants (mean $IC_{ND} = .67$) than in LH participants (mean $IC_{ND} = .55$). The effect of switch condition was also significant, $F(1, 11) = 8.66$, $p < .05$, $f = 0.49$. Note that the latter effect was identical to the Handedness \times Switch Condition interaction discussed in the previous paragraph.

Switch pathway

Although for some participants individual preferences for a particular ('up' or 'down') switch pathway were observed, a combination of paired-samples and independent samples t -tests on the percentage of 'up' switches revealed no significant effects: The switch pathways were distributed equally across groups and conditions.

Discussion

In the present experiment, it was examined how intentional switches between rhythmic coordination patterns were mediated by phase adaptations in both hands in LH and RH participants. From the (both theoretically and empirically motivated) hypothesis of a handedness-related asymmetry in interlimb coupling strength, it was predicted that the intentional switches in question were primarily mediated by adaptations in the movements of the nondominant hand. This effect was expected to be stronger in RH than in LH participants. In addition, it was examined whether the previously reported reduction in switching time at higher movement frequencies was associated with an increased asymmetry in interlimb coupling strength. To examine these predictions, the degree to which the two hands altered their phasing during voluntary switches was determined and expressed in an interlimb coupling index (*IC*).

The first two predictions were clearly supported by the experimental results. For both LH and RH individuals the switches were predominantly mediated by adaptations in the nondominant hand. Although the asymmetry in the contributions of the two hands was relatively small (cf. Figure 3.2), the *IC* values revealed significant deviations from equal contributions of both hands (except for the switches from in-phase to antiphase coordination in the LH participants). This result is consistent with the proposed asymmetry in coupling strength and extends previous indications of such an asymmetry during intentional switching in RH participants (Byblow et al., 2000; Carson, Byblow, et al., 1996). In addition, the present results underscored that coordination characteristics obtained for RH participants cannot always be smoothly generalized to LH individuals: Although in both groups the phase adjustments were mainly mediated by the nondominant hand, this effect was more pronounced in RH participants. As outlined in the Introduction, this difference between the handedness groups is in accordance with previous indications that left-handers are less consistent in their expression of handedness than right-handers (McManus et al., 1999; Peters & Servos, 1989; Shen & Franz, 2005) and indicates that in LH individuals the asymmetry in interlimb coupling strength is weaker than in RH individuals (cf. Chapter 2).

In correspondence with the findings of Chapter 2, no effects of handedness were observed with respect to the switch pathways, suggesting that

the way in which the switches were mediated was governed by the asymmetric coupling between the hands rather than by the collective relative phase dynamics. Together, the present results indicated that the handedness-related asymmetry in interlimb coupling strength does not only determine the transient characteristics of spontaneous (unintended) phase adaptations (as revealed by Chapter 2), but also affects the way in which voluntary changes in interlimb coordination are effectuated. Interestingly, the asymmetry between the hands turned out to be larger for switches from antiphase to in-phase coordination (i.e., in the direction corresponding to spontaneous frequency-induced transitions) than for switches in the opposite direction, suggesting that either the asymmetry in coupling strength itself or the behavioral expression thereof was modulated by the intentional processes associated with the switch. Whereas in switching from anti-phase to in-phase coordination the system may exploit the intrinsic stability tendencies resulting from the interlimb coupling, these tendencies have to be opposed when switching in the reverse direction, which may call for the contribution of distinct dedicated processes (cf. Byblow, Summers, et al., 1999, 2000; Carson, Byblow, et al., 1996), possibly mediated by the supplementary motor area (cf. Byblow, Summers, et al., 1999).

Although the analysis of pre- and post-switch behavior revealed that the in-phase mode was performed more stably than the antiphase mode, the two switch conditions did not result in different switching times (τ_{sw} and τ_{sw}^*). As such, the current results do not support the general observation that switches to more stable patterns are performed more swiftly than those in the reverse direction (Byblow, et al. 2000; Carson, Byblow, et al., 1996; Serrien & Swinnen, 1999; Kelso et al., 1988; Scholz & Kelso, 1990). This deviant observation might be related to the fact that in the present study (unlike most previous studies) the pacing signal was present throughout the trial, in order to allow for adequate prescription of the different movement frequencies tested in the experiment. Possibly this pacing signal (consisting of two beeps per movement cycle) provided a perceptual anchor (e.g., Beek, Turvey, & Schmidt, 1992; Byblow et al., 1994), thereby diminishing the extent to which switching time was influenced by the difference in stability between the two patterns.⁷

⁷ Note, however, that Carson, Byblow, et al. (1996) did observe a difference in switching time between the two switch conditions both in the absence and presence of an auditory pacing signal (one beep per movement cycle).

Still, the current detailed analysis of the relative contributions of the two hands (in terms of IC) revealed that even in the absence of a difference in switching time, the way in which the switches were brought about depended on both handedness and switch condition.

The third prediction, regarding the effects of movement tempo, was not supported, given the absence of a frequency effect on the index of coupling (IC). At first blush, this difference between the current results and those obtained for unintended, relaxational transients (Chapter 2) may be interpreted as a consequence of the difference between the experimental tasks, involving intended vs. unintended transients, respectively. As argued above, (the expression of) the characteristic handedness-related asymmetry in coupling strength appears to be modulated by intentional processes (cf. Byblow, Summers, et al., 1999, 2000; Carson, Byblow, et al., 1996). On this perspective, the present results may suggest that the influences of such processes increase with increasing frequency, thereby suppressing the intrinsic amplification of the asymmetry in coupling strength (as revealed by Chapter 2). However, this interpretation should be treated with considerable caution, since specific methodological aspects of the experiment may also have affected the results in this regard.

In particular, it is conceivable that the frequency range tested in the experiment was not suitable to induce the expected effect of movement frequency. The stability of performance (as indexed by $SD\phi$) showed an optimum for the intermediate frequencies with, on average, variability being smallest for the 1.5 Hz frequency condition. This most stable frequency condition corresponded closely to the average preferred oscillation frequency for unimanual flexion-extension movements about the wrist (1.49 Hz) as determined by Peper and Beek (1998b). The frequency-related amplification of the asymmetry in coupling strength observed in Chapter 2, however, was based on frequencies ranging from 1 to 1.5 Hz applied to lower arm movements, for which an average preferred frequency of 1.10 Hz has been reported (Beek, Rikkert, & Van Wieringen, 1996). Thus, it is possible that frequency-related changes in the asymmetry of interlimb coupling strength can only be observed when movement frequency is increased considerably beyond the preferred frequency of oscillation.

In contrast to the results of Carson, Byblow, et al. (1996) and Scholz and Kelso (1990), switching time τ_{sw} also remained unaffected by the manipulation

of movement frequency. It is possible that the absence of an effect in this regard was associated with the fact that the frequency range applied in the experiment was centered around the preferred frequency of oscillation. An alternative explanation can be found in the presence of the pacing signal. As already mentioned in the preceding, such a signal may function as a perceptual anchor, thereby possibly affecting the way in which the switch is executed. However, the fact that the manipulation of movement frequency significantly affected τ_{sw}^* revealed that switching time was not characterized by a fixed perceptuo-motor anchoring strategy.

In sum, intentional switches between rhythmic coordination patterns were found to be primarily mediated by phase adaptations in the nondominant hand, and this effect was more pronounced for RH than for LH participants. These findings supported the conjecture that hand dominance is associated with an asymmetry in interlimb coupling strength (with the nondominant hand being more strongly influenced by the dominant hand than vice versa) and indicated that also intentional transient stages are (partly) governed by this asymmetry. In addition, the difference between the two switch conditions in this regard indicated that intentional processes may weaken (the expression of) the handedness-related asymmetry in coupling strength.

Acknowledgment

The authors wish to thank Carry Doeven and Pieter van der Luijt, who contributed to the design of the experiment and collected the data

Chapter 4

Laterally focused attention modulates asymmetric coupling in rhythmic interlimb coordination

Article in press:

De Poel, H. J., Peper, C. E., & Beek, P. J. (in press). Laterally focused attention modulates asymmetric coupling in rhythmic interlimb coordination. *Psychological Research*.

Used with kind permission from Springer Science and Business Media

The original article is retrievable at www.springerlink.com.

DOI: 10.1007/s00426-006-0096-9

Abstract

Peters (1989, 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 could be determined. The results revealed that the nondominant 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 nondominant limb, thereby highlighting the potential relation between inherent (handedness-related) asymmetries and voluntary attentional asymmetries. In contrast to earlier 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 co-operate 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 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., Chapters 2 and 3; Byblow, Carson, & Goodman, 1994).

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 $\phi = 0^\circ$) and the antiphase pattern (i.e., the limbs oscillate in an alternating fashion; $\phi = 180^\circ$). 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., Chapter 2; 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, $\phi > 0^\circ$ for left-handers and $\phi < 0^\circ$ 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 nondominant (ND) limb is more strongly influenced by the dominant (D) limb than vice versa (Chapters 2 and 3; Peper, Daffertshofer, & Beek, 2004; see also Byblow et al., 1994; Carson, 1993). Empirically, this asymmetry in coupling strength was evidenced by demonstrations that both spontaneous, frequency-induced (Chapter 2; Byblow et al., 1994; Byblow, Chua, & Goodman, 1995) and voluntary (Chapter 3; Carson, Byblow, Abernethy, & Summers, 1996) 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 (Chapter 2).⁸

⁸ 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).

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 processes (cf. Peper, Ridderikhoff, Daffertshofer, & Beek, 2004), 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 (Chapter 2; Peper, Daffertshofer, & Beek, 2004). 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 [nonlinear] 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 nonvisual 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. Chapter 2; Court, Bennett, Williams, & Davids, 2002; Post, Peper, & Beek, 2000; Post, Peper, Daffertshofer, & Beek, 2000; 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, Peper, & Beek, 2000; Post, Peper, Daffertshofer, & Beek, 2000; 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). Chapter 2 revealed 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. Chapter 2); 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. Chapter 2). 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. Chapter 2; Peper, Daffertshofer, & Beek, 2004) 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., Chapter 2; 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 to 100),

the other 12 as left-handed (mean LQ = -95, range -54 to -100).⁹ 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 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.

⁹ The exclusion of one LH participant following a more stringent selection criterion (i.e., $|LQ| > 70$, cf. Chapter 2) yielded qualitatively similar results.

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 \times Coordination Mode \times Frequency condition. For each participant, this resulted in a total of 76 trials, yielding an experimental session of approximately 1.5 hours (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 VU University, 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 (Chapter 2), based on the frequency specified by the metronome (f_M), using

$$\theta_{M,i} = \theta_{M,i-1} + 360^\circ \cdot (0.5 f_M / f_S) \quad [4.1]$$

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 ϕ ($\bar{\phi}$) 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, $\Delta\phi = \bar{\phi} - \phi_{\text{req}}$, with $\phi_{\text{req}} = 0^\circ$ (in-phase) or $\phi_{\text{req}} = 180^\circ$ (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.

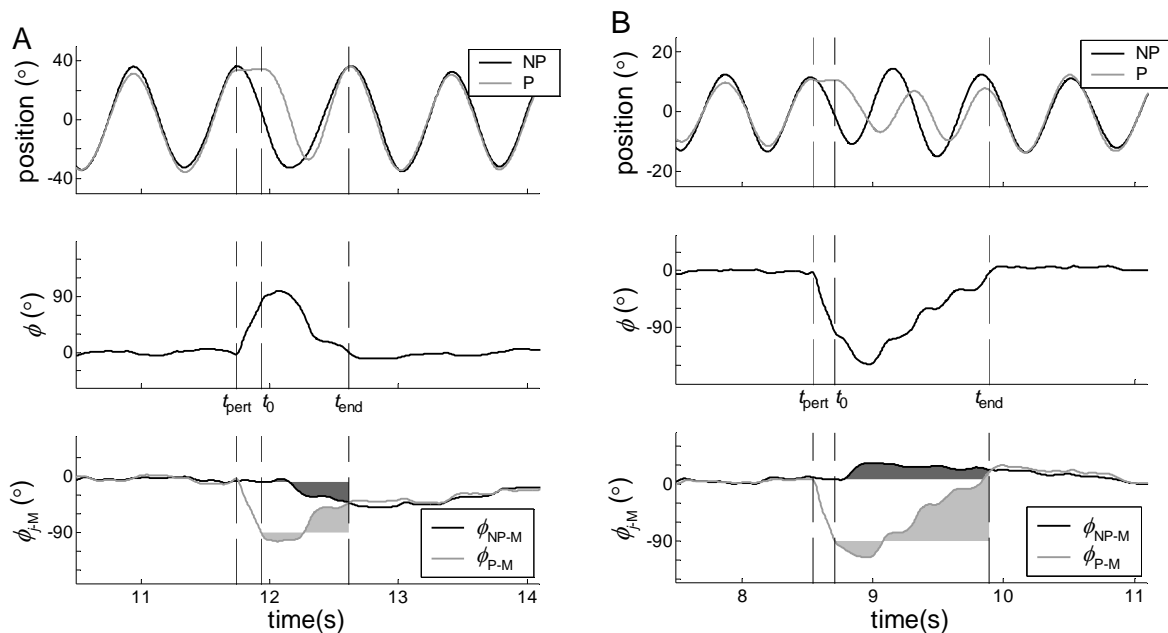


Figure 4.1. Two in-phase trials illustrating the derivation of A_P and A_{NP} . The dashed lines represent perturbation onset (t_{pert}), moment of arm release (t_0), and the end of the relaxation process (t_{end}). A: Perturbation of the right arm (movement frequency: 1.5 Hz). B: Perturbation of the 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 ϕ_{P-M} and ϕ_{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}).

Furthermore, the relative contribution of the individual arms to the relaxation back to the bimanual coordination pattern was determined, using the procedure developed in Chapter 2. 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 $|\phi_i - \phi_{pre}| < 30^\circ$ and $TCV_i \leq TCV_{pre}$. 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., $TCV_{pre,post} > 45^\circ$). On the basis of these criteria, 67 of the 1408 trials (i.e., $< 5\%$) were excluded. Binomial tests revealed significantly uneven distributions of these trials over the coordination modes, $p < .001$ (in-phase: 18, antiphase: 49), frequency, $p < 0.0001$ (1 Hz: 8, 1.5 Hz: 59), and attention conditions, $p < .05$ (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 Figure 4.1) was derived using

$$A_P = \int_{t_0}^{t_{end}} (\phi_{P-M} - \phi_0) \quad [4.2]$$

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 Figure 4.1). The relative contribution of the unperturbed arm to the relaxation process was expressed by the index of coupling (IC):

$$IC = -\frac{A_{NP}}{|A_P| + |A_{NP}|} \quad [4.3]$$

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. Figure 4.1A). 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. Figure 4.1B). 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.

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 two frequency conditions, the time series of ϕ were resampled with respect to cycle duration (Chapter 2; 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, Peper, Daffertshofer, and Beek, (2000). In brief, the data were fitted from the point where ϕ reached a value of 45° (i.e., $\phi_{t=0} = 45^\circ$), using an exponential decay function that also accounted for damped oscillations in the return signal:

$$\phi(t) = p + qe^{-\lambda t} \cos(\omega_{\text{osc}}t + \theta_{\text{osc}}) \quad [4.4]$$

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, Peper, Daffertshofer, & Beek,

2000). 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, Peper, Daffertshofer, and Beek (2000), 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 ($TCV > 45^\circ$); 4) the return signal was not a decay function within the observation interval ($\lambda < 0$); 5) the fit was unreliable (standard error of $\lambda > \text{median of } \lambda$, 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 $p < .05$. In addition, the corresponding effect sizes (f) were calculated based on the partial eta squared (η_p^2 , 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% to 15%. These trials were excluded from further analysis. For the remaining 1674 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, $t(21) = 4.47$, $p < .001$, 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 Figure 4.2). The ANOVA revealed a main effect of coordination mode, $F(1, 20) = 7.38$, $p < .05$, $f = 0.61$, which implied that the D arm lead was larger for antiphase (mean $\Delta\phi = 4.1^\circ$) than for in-phase coordination (mean $\Delta\phi = 1.7^\circ$). The significant Coordination Mode \times Frequency interaction, $F(1, 20) = 5.11$, $p < .05$, $f = 0.51$, and subsequent post-hoc simple effects analyses showed that the effect of coordination mode was only significant for performance at 1 Hz, $F(1, 20) = 3.58$, $p = .07$, $f = 0.40$, (mean $\Delta\phi = 1.1^\circ$ [in-phase] and 2.5° [antiphase]). The main effect of frequency was also significant, $F(1, 20) = 22.29$, $p < .001$, $f = 1.06$. The phase lead of the D arm increased with movement frequency (mean $\Delta\phi = 1.8^\circ$ [1 Hz] and 4.0° [1.5 Hz]), although the significant Frequency \times Handedness interaction, $F(1, 20) = 6.21$, $p < .05$, $f = 0.56$, and subsequent simple effects analyses indicated that this frequency effect was only significant for RH participants, $F(1, 9) = 27.82$, $p < .001$, $f = 1.76$, (mean $\Delta\phi = 2.2^\circ$ [1 Hz] and 5.8° [1.5 Hz]).

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, $F(1, 20) = 12.03$, $p < .005$, $f = 0.78$. Contrary to our expectations, however, this effect implied that when attention was focused on the D limb (mean $\Delta\phi = 1.7^\circ$) the D limb lead was smaller than when attention was focused on the ND limb (mean $\Delta\phi = 4.1^\circ$), as can be seen in Figure 4.2. Furthermore, the significant Attention \times Frequency interaction, $F(1, 20) = 13.81$, $p < .005$, $f = 0.83$, and subsequent post-hoc simple effects analyses revealed that

the effect of attention was only significant for performance at 1 Hz, $F(1, 20) = 23.28$, $p < .0001$, $f = 1.08$, (see Figure 4.2).

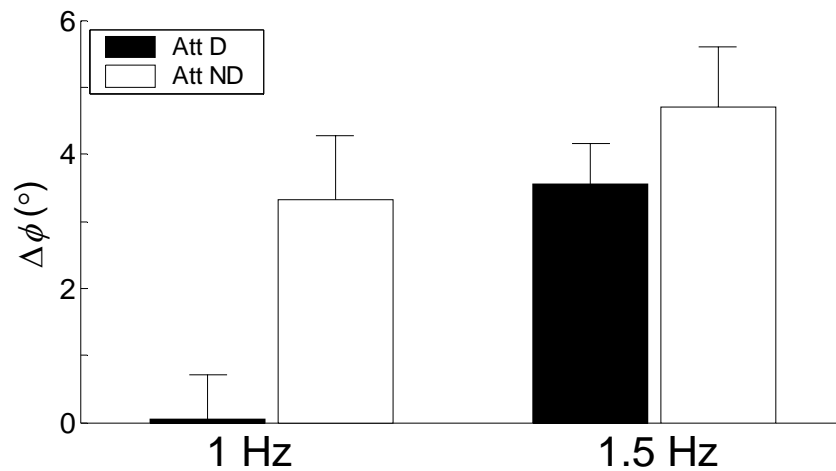


Figure 4.2. Mean phase shift ($\Delta\phi$) as a function of direction of attention and movement frequency; $\Delta\phi > 0$ denotes dominant arm lead. Att D = attention on dominant arm; Att ND = attention on nondominant arm. Error bars represent the between-subjects standard errors.

Relative phase variability (TCV)

Analysis of the variability of relative phase revealed significant effects of coordination mode, $F(1, 20) = 90.65$, $p < .001$, $f = 2.13$, frequency, $F(1, 20) = 27.11$, $p < .001$, $f = 1.16$, and the Coordination Mode \times Frequency interaction, $F(1, 20) = 16.04$, $p < .005$, $f = 0.90$. All post-hoc simple effects analyses regarding this interaction revealed significant differences, $F(1,20) > 23.48$, $p < .0001$, $f > 1.06$. 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 $TCV = 8.0^\circ$ [in-phase] and 12.3° [antiphase]) than at the lower frequency (mean $TCV = 6.9^\circ$ [in-phase] and 9.4° [antiphase]).

Perturbation analysis

Index of coupling (IC)

Statistical analysis of IC revealed a main effect of perturbed arm, $F(1, 20) = 5.08$, $p < .05$, $f = 0.50$. 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 \times Attention interaction, $F(1, 20) = 11.21$, $p < .005$, $f = 0.75$, and subsequent simple effects analyses revealed that the effect of perturbed arm was only significant when attention was focused on the D limb, $F(1, 20) = 10.51$, $p < .005$, $f = 0.72$. 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 Figure 4.3). In addition, the Coordination Mode \times Frequency interaction was significant, $F(1, 20) = 9.40$, $p < .01$, $f = 0.69$. 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 $IC = 0.23$), $F(1, 20) = 8.09$, $p < .01$, $f = 0.64$.

Stability: decay parameter (λ)

The ANOVA revealed that solely the effect of perturbed arm was significant, $F(1, 18) = 9.19$, $p < .01$, $f = 0.71$. 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.

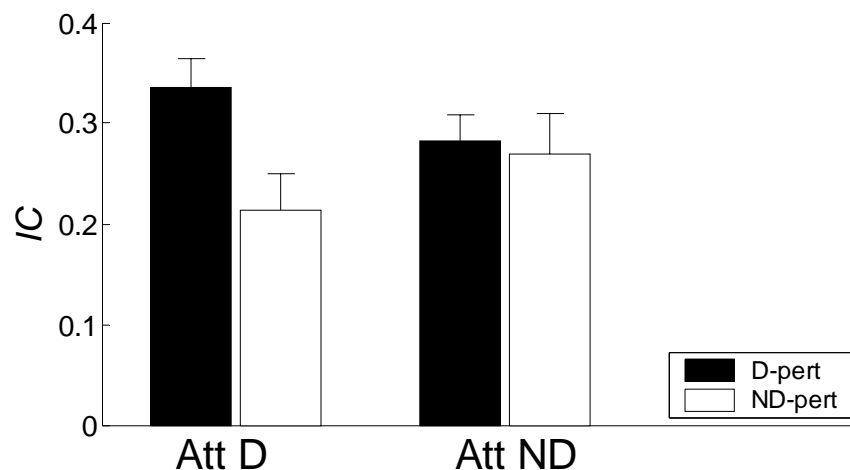


Figure 4.3. Mean values of IC (i.e., relative contribution of unperturbed arm to the relaxation process) as a function of perturbed arm and attention. Att D = attention on dominant arm; Att ND = attention on nondominant arm; D-pert = perturbation of dominant arm; ND-pert = perturbation of nondominant 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 in Chapter 2, 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 (Chapter 2; Peper, Daffertshofer, & Beek, 2004; 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 Chapters 2 and 3). 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 (Chapter 2; Post, Peper, Daffertshofer, & Beek, 2000). 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., Chapter 2; Amazeen et al., 1997; 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. Chapter 2; Treffner & Turvey, 1995) and increased with movement frequency (cf. Chapter 2; Stucchi & Viviani, 1993; Treffner & Turvey, 1996), although the latter effect was only significant for RH participants.

In combination, these results corroborated the results of Chapter 2 and the theoretical argumentation of Peper, Daffertshofer, and Beek (2004) 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 Figure 4.3). 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 described in Chapter 2, 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 \times Attention interaction, $F(1, 20) = 4.68$, $p < .05$, $f = 0.67$. Subsequent post-hoc simple effects analyses indicated that IC differed over the two perturbation conditions when attention was focused on the D limb, $F(1, 10) = 6.14$, $p < .05$, $f = 0.78$ (D limb perturbed: 0.34; ND limb perturbed: 0.21), and for the neutral condition, $F(1, 10) = 5.32$, $p < .05$, $f = 0.70$ (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.¹⁰ 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' 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

¹⁰ Inclusion of the attentionally neutral condition in the ANOVA for the 12 participants that also participated in the experiment reported in Chapter 2 also revealed a main effect of attention, $F(1, 20) = 12.13$, $p < .001$, $f = 1.10$. Post-hoc simple effects analyses revealed that directing attention towards the D limb (mean $\Delta\phi = 0.8^\circ$) decreased the D limb phase lead when compared to the neutral condition (mean $\Delta\phi = 2.7^\circ$), $F(1, 10) = 8.43$, $p < .05$, $f = 0.95$, whereas the increase that was observed when attention was directed to the ND limb (mean $\Delta\phi = 4.5^\circ$) did not reach significance.

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 to 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, 2004; 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, Slotka, 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 nonvisual) 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 \times Attention interaction, $F(1, 20) = 38.00$, $p < .0001$, $f = 1.38$.¹¹ 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, $F(1, 20) = 30.10$, $p < .0001$, $f = 1.23$, and the ND arm, $F(1, 20) = 17.48$, $p < .001$, $f = 0.93$, 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, $F(1, 20) = 6.92$, $p < .05$, $f = 0.59$, and to the ND limb, $F(1, 20) = 8.40$, $p < .01$, $f = 0.65$. 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 Figure 4.3) and Rosenbaum et al. (1991; see their Figure 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).¹²

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

¹¹ Cycle amplitude (in degrees) was defined as the average of the half-cycle peak-to-peak excursions, divided by two. 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.

¹² 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 in Chapter 2) also revealed no significant difference between the amplitudes of the D and ND arm.

According to the dynamical model associated with asymmetric coupling strength (Peper, Daffertshofer, & Beek, 2004; 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 (Chapter 3; Byblow, Summers, et al., 1999; Byblow et al., 2000; Carson, Byblow, et al., 1996). 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, Beek, & Van Wieringen, 1995a, 1995c; 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, Peper, Daffertshofer, & Beek, 2000; 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, Ridderikhoff, et al., 2004).

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 cortico-spinal 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.

Chapter 5

Attentional asymmetry affects relative phase through amplitude disparity rather than asymmetric coupling

Manuscript under revision:

De Poel, H. J., Peper, C. E., & Beek, P. J. (2007). Attentional asymmetry affects relative phase through amplitude disparity rather than asymmetric coupling.

Abstract

Attentional asymmetry in rhythmic interlimb coordination induces an asymmetry in relative phase dynamics, allegedly reflecting an asymmetry in coupling strength. However, relative phase asymmetries may also be engendered by an attention-induced difference in the amplitudes (and hence the preferred frequencies) of the limb movements. We conducted three experiments to examine those (not mutually exclusive) potential effects. Controlled manipulations of amplitude disparity and attentional focus, both alone and combined, revealed that variations in amplitude disparity had the expected effects, but produced no compelling evidence for the currently prevailing interpretation that the effects of attentional asymmetry on relative phase dynamics are mediated by an asymmetry in coupling strength. Implications of these findings are discussed vis-à-vis recent empirical findings and extant models.

Introduction

In human manual behavior, perfect symmetry is the exception rather than the rule (e.g., Summers, Davis, & Byblow, 2002). For instance, in everyday life, the quality of performance in unimanual tasks and the preference of hand use in unimanual and bimanual tasks (Guiard, 1987; Peters, 1994) depend on the handedness (or hand dominance) of the performer. The unimanual advantage of the dominant hand is already apparent in simple repetitive finger tapping tasks, as this hand can tap faster and more consistently than the nondominant hand (Peters, 1980). Also in bimanual tasks, in which the movements of the two limbs are to be coordinated, performance asymmetries are observed associated with inherent asymmetries like handedness (e.g., Treffner & Turvey, 1995) and hemispheric lateralization (Serrien, Ivry, & Swinnen, 2006), but also with unilateral neuropathies (e.g., Lewis & Byblow, 2004; Steenbergen, Hulstijn, De Vries, & Berger, 1996; Olney & Richards, 1996) or (imposed) end-effector disparities due to, for instance, a difference between the limbs in terms of their inertial properties (e.g., Jeka & Kelso, 1995) or unilateral application of a prosthetic device (Donker & Beek, 2002). In addition, it has been shown that such asymmetries in coordination may be modulated by means of specific manipulations. Asymmetries in (pathological) gait, for instance, may be influenced by providing perceptual cues (Prassas, Thaut, McIntosh, & Rice, 1997; Roerdink, Lamoth, Kwakkel, Van Wieringen, & Beek, in press; Schauer & Mauritz, 2003). Similarly, focusing attention on the movement of one of the limbs has been found to affect the coordinative asymmetry in rhythmic bimanual coordination of the upper limbs (e.g., Amazeen, Amazeen, Treffner, & Turvey, 1997; Swinnen, Jardin, & Meulenbroek, 1996). The present study was aimed at pinpointing the way in which the influences of asymmetric attentional focus on rhythmic bimanual coordination are mediated by changes in interlimb coupling and/or the movement characteristics of the limbs.

For bimanual isofrequency coordination (in which the two limbs move in oscillatory fashion with identical movement frequencies), the coupling between the limb movements engenders several coordinative phenomena. For instance, without explicit practice, only two coordination patterns can be performed stably: the in-phase pattern (the limbs flex and extend simultaneously in a mirror symmetric fashion) and the antiphase pattern (the limbs move alternately). Furthermore, when movement frequency is increased, spontaneous transitions

may occur from the less stable antiphase pattern to the more stable in-phase pattern (for a review, see Kelso, 1995). These phenomena are accounted for by the well-known HKB-model (Haken, Kelso, & Bunz, 1985; Schöner, Haken, & Kelso, 1986), in which two coupled self-sustaining limit cycle oscillators yield a potential function that captures the dynamics of the relative phase between the two oscillators (i.e., the phase difference $\phi = \theta_1 - \theta_2$, with θ_i denoting the movement phase of each component), with attractors at $\phi = 0^\circ$ (in-phase) and $\phi = 180^\circ$ (antiphase). In order to derive a minimal model, the original formulation assumed identical oscillators and symmetrical coupling functions, although the authors already acknowledged the possibility of functional asymmetries in these respects.

Asymmetry in coupling strength: Handedness and attention

A typical asymmetry in isofrequency coordination is the shift in relative phase observed as an effect of handedness. That is, the right limb is, on average, leading the left limb in time for right-handers, whereas left-handers show a left limb lead (e.g., Chapter 2; Semjen, Summers, & Cattaert, 1995; Stucchi & Viviani, 1993; Swinnen, et al., 1996; Treffner & Turvey, 1995, 1996). Thus, with ϕ defined as $\theta_D - \theta_{ND}$ (with D and ND denoting the dominant and nondominant limb, respectively), in-phase coordination is characterized by $\phi > 0^\circ$ (indicating D limb lead). Furthermore, this phase shift has been shown to be larger for antiphase coordination and to increase with movement frequency (e.g., Chapter 2; Treffner & Turvey, 1995, 1996). To account for these effects, the symmetry of the original HKB-potential was broken by incorporating two additional cosine terms into the order parameter equation (Treffner & Turvey, 1995):

$$\dot{\phi} = -a \sin(\phi) - 2b \sin(2\phi) - c \cos(\phi) - 2d \cos(2\phi) \quad [5.1]$$

with the parameters c and d determining the direction and degree of the asymmetry. Because assigning nonzero values to d was sufficient to induce the observed phase shifts with respect to both 0° and 180° , c was set to zero (Treffner & Turvey, 1995).

The extra cosine terms in Equation 5.1 were suggested to reflect an asymmetry in the coupling between the limbs (Treffner & Turvey, 1995). Recently, this notion was formally elaborated by Peper, Daffertshofer, and Beek (2004), who demonstrated that the phase lead of the D limb may indeed result

from a handedness-related asymmetry in the strength of interlimb coupling, with the ND limb being more strongly influenced by the D limb than vice versa. Chapter 2 provided crucial empirical support in favor of this conception by demonstrating that the phase of the ND limb was more strongly attracted towards the phasing of the D limb (in response to a brief mechanical perturbation of the latter) than vice versa, although for left-handers this effect did not reach significance (for related results, see also Chapter 3).

Interestingly, it has been demonstrated that this asymmetry in performance can be influenced through attentional focus. When attention was directed towards the D limb, the phase lead of the D limb was found to be larger than when the ND limb was attended (Amazeen, Amazeen, Treffner, & Turvey, 1997; Amazeen, Ringenbach, & Amazeen, 2005; Franz, 2004; Pellegrini, Andrade, & Teixeira, 2005; Riley, Amazeen, Amazeen, Treffner, & Turvey, 1997; Swinnen et al., 1996). Furthermore, in line with indications that the quality of bimanual performance may benefit from an asymmetry in interlimb coupling strength (Byblow, Bysouth-Young, Summers, & Carson, 1998; Peper, Beek, & Van Wieringen, 1995a, 1995c; Summers, Davis, & Byblow, 2002), the variability of relative phase was smaller when the D limb was attended (Amazeen et al., 1997; Swinnen et al., 1996).¹³ On the basis of the proposition that effects of handedness are reflections of a difference in the degree of the attention that is focused on either limb (Peters, 1989, 1994), these results were in accordance with the asymmetric model of Treffner and Turvey (1995; i.e., Equation 5.1), which predicts larger (smaller) phase shifts and decreased (increased) variability for accrued (diminished) asymmetries in coupling strength. In accordance with the preceding, Chapter 4 provides an empirical demonstration that, indeed, the previously established handedness-related asymmetry in coupling strength diminished when attention was directed to the ND limb. This result underscored the possibility that the effects of handedness are related to an inherent asymmetry in attentional focus, as suggested by Peters (1989, 1994; see also Amazeen et al., 1997).

¹³ Note, however, that in a number of studies either or both of these effects of attentional focus were not corroborated (see Chapter 4; Franz, 2004; Pellegrini et al., 2004; Wuyts, Summers, Carson, Byblow, & Semjen, 1996).

Difference in amplitude (related to attention)

In contrast to theoretical predictions (based on Equation 5.1) and previous findings, however, Chapter 4 revealed that an asymmetric attentional focus had the inverse effect on relative phasing. That is, the D limb lead increased rather than decreased when attention was directed to the ND limb. Furthermore, the coordinative stability remained unaffected by the manipulation of attention. Although these findings may seem paradoxical at first sight, the results in Chapter 4 showed that the effects of attentional focus on the mutual coupling between the limbs were accompanied by another, possibly counteracting effect. That is, the movement amplitude attained by each limb was found to vary as a function of the direction of attention as well, yielding an attention-related difference in amplitude. More specifically, the attended limb oscillated with an amplitude that was on average 10% larger than that of the unattended limb (for related results on circle drawing, see Franz, 2004; Zelaznik & Lantero, 1996). Given recent indications that a disparity in movement amplitude invokes a phase lead of the limb performing the smaller amplitude (Amazeen et al., 2005; Buchanan & Ryu, 2006; Heuer & Klein, 2005), the larger amplitude attained by the attended limb could explain the increase (decrease) of the D limb lead when the ND (D) limb was attended, as observed in Chapter 4. The reasoning behind this interpretation is outlined in the next section.

Difference in preferred frequency (related to amplitude)

When performing repetitive unimanual movements, an increase in movement frequency is accompanied by a reduction of 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). The reverse is also true, as is exemplified by Fitts' law, which states that the maximum movement frequency decreases with increasing amplitude when moving as fast as possible (Fitts, 1954). This inverse relation has also been demonstrated for movements performed at comfortable rather than maximal speeds (Rosenbaum et al., 1991). Thus, large unimanual movement amplitudes are related to low preferred oscillation frequencies. Hence, an asymmetry in movement amplitude between the limbs in a rhythmic bimanual

coordination task is associated with a difference in preferred movement frequency.

It is well documented that such a difference in preferred movement frequency affects the relative phasing between the limbs. Empirically, this has been demonstrated by creating a difference in eigenfrequency (i.e., natural oscillation frequency) between the limbs by means of hand-held pendulums that differ in mass distribution (e.g., Schmidt & Turvey, 1995; Sternad, Turvey, & Schmidt, 1992; Sternad, Amazeen, & Turvey, 1996; Treffner & Turvey, 1995, 1996) or by studying the coordination between limbs with different (imposed) inertial properties (e.g., Jeka & Kelso 1995; Peper, Nooij, & Van Soest, 2004). These studies revealed that the limb with the higher (resultant) eigenfrequency (i.e., the ‘faster’ limb) tends to lead the limb with the lower eigenfrequency (i.e., the ‘slower’ limb) in time, yielding phase relations that are slightly, but systematically shifted away from the (intended) perfectly symmetric patterns with relative phases of 0° and 180° . These relative phase shifts and accompanying changes in coordinative stability were shown to vary as a function of the size of the eigenfrequency difference, and this effect was modulated by both the tempo of performance and the coordination pattern (in-phase or antiphase) (cf., Schmidt & Turvey, 1995; Sternad et al., 1992; Sternad et al., 1996). Furthermore, increasing the movement frequency resulted in phase wrapping between the limbs (e.g., Kelso & Jeka, 1992) and preferential routes in the spontaneous transitions from antiphase to in-phase coordination (Jeka & Kelso, 1995). These results were explained using an extension of the HKB-model (Fuchs, Jirsa, Haken, & Kelso, 1996; Kelso, DelColle, & Schöner, 1990) in which the difference in eigenfrequency between the two components (commonly referred to as $\Delta\omega$) was introduced into the HKB potential as an additional parameter, yielding

$$\dot{\phi} = \Delta\omega - a \sin(\phi) - 2b \sin(2\phi) \quad [5.2]$$

which leads to

$$\dot{\phi} = \Delta\omega - a \sin(\phi) - 2b \sin(2\phi) - c \cos(\phi) - 2d \cos(2\phi) \quad [5.3]$$

when the handedness-related terms (Equation 5.1) are also included.

Hence, because a difference between the amplitudes of the limbs (ΔA) results in a difference in preferred frequency, changes in the coordination dynamics associated with ΔA may in fact be mediated by this difference in preferred frequency (cf. $\Delta\omega$). This would imply that the attention-related

difference in amplitude counteracted the attentional modulation of the asymmetry in coupling strength with regard to its effect on the relative phase dynamics, thereby possibly obscuring the effect of the latter (Chapter 4). Thus, although Chapter 4 revealed that the change in the asymmetry in coupling strength due to attentional focus was qualitatively comparable to the effect of handedness (in support of Peters' [1989, 1994] suggestion), its influences on the relative phasing between the limbs remained to be established. It is important to do so, because if the attentionally modulated asymmetry in coupling strength indeed affects the relative phasing in the same manner as determined for handedness (i.e., in accordance with Peper, Daffertshofer, & Beek's [2004] elaboration of Equation 5.1), this would yield additional support for the suggested inherent relation between handedness and attentional focus (Peters, 1989, 1994). On the other hand, an absence of the predicted effects on the relative phase would indicate that the handedness-related and the attention-related asymmetries in coupling strength involve different processes and may, thus, not share a common source. To test these possibilities, it was therefore important to expose the (possibly) confounding influence of ΔA in a systematic manner. For this reason, three experiments were performed that aimed at dissociating between the distinct influences of ΔA (Experiment 1), the interaction between ΔA and attentional focus (Experiment 2), and the effect of attentional focus in the absence of variations in of ΔA (Experiment 3) on the relative phase dynamics.

Experiment 1

In the first experiment, a difference between the limbs' amplitudes (ΔA) was imposed, using target amplitudes that were specified for each arm separately along with online visual feedback of the actually performed amplitudes. The primary purpose was to examine whether, for bimanual oscillatory lower arm movements, ΔA indeed affected the relative phase dynamics according to the $\Delta\omega$ term in Equations 5.2 and 5.3. Recent studies provided initial support in favor of this hypothesis for bimanual in-phase pointing movements (Amazeen et al., 2005; Heuer & Klein, 2005) and for bimanual circle drawing (Buchanan & Ryu, 2006). In the present experiment, this relation was further scrutinized by systematically manipulating movement amplitudes (yielding a large range of ΔA), as well as the (coupled) movement

frequency and the coordination pattern. In this way, the following predictions were tested.

Given the inverse relation between preferred frequency and amplitude, Equation 5.3 predicts that the limb moving at the smallest amplitude (i.e., the limb with the highest preferred frequency) leads the other limb in time, and that the stability of performance decreases with increasing $|\Delta A|$. Furthermore, according to Equation 5.3 these effects will be amplified for higher (coupled) movement frequencies and will be larger for antiphase than for in-phase coordination. Note that these predictions correspond to the characteristics of isofrequency coordination in the presence of an eigenfrequency difference (cf. e.g., Sternad et al., 1996; Treffner & Turvey, 1996).

Methods

Participants

Ten healthy volunteers (4 women and 6 men, aged 21-37 years) participated in the study. They were all right-handed, as indicated by a Dutch version of the Edinburgh handedness inventory (Oldfield, 1971; mean laterality quotient [LQ] = 82, range 43 to 100). Participants gave their informed consent prior to taking part in the experiment.

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). Computer-generated auditory pacing stimuli of alternating high-pitched (400-Hz) and low-pitched (200-Hz) beeps (duration: 50 ms) were presented through headphones (Sennheiser HD 520 II).

For the manipulation and feedback of the movement amplitudes, light-emitting diodes (LEDs) were presented on two vertically oriented LED bows (one for each arm). Each LED bow consisted of a slightly curved display comprising a series of 448 LEDs that covered a vertical distance of 94 cm. The two LED bows were placed 150 cm in front of the participant and were

positioned next to each other (resulting in a 15 cm lateral distance between the two LED arrays) so that participants could monitor the amplitude feedback of both arms from a single point of gaze. The centers of the LED bows were approximately at eye level.

Task and experimental conditions

Participants performed bimanual oscillatory movements with the lower arms in the in-phase and antiphase coordination modes at two movement frequencies (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 flex and extend the arms simultaneously, while in the antiphase condition the arms had to flex and extend alternately. Five ΔA conditions were presented, in which the amplitude ratio between the D and the ND arm was 1:2, 3:4, 1:1, 4:3, or 2:1. Accordingly, the prescribed amplitudes (D:ND) were 14°:28°, 18°:24°, 21°:21°, 24°:18°, and 28°:14° (with amplitude defined as half the peak-to-peak movement range).

In order to solely manipulate the required movement amplitudes, rather than other spatial features of the performance, target amplitude was prescribed in a manner that was independent of the spatial center of oscillation of the arm. To this end, each target amplitude (i.e., 14°, 18°, 21°, 24°, or 28°) was specified by an illuminated target LED (in all cases this was the center LED of the corresponding LED bow). In addition, two illuminated LEDs specified a tolerance range of $\pm 3^\circ$. During task performance, the actually performed amplitude of each half cycle was determined online for each arm (using a peak-detection algorithm) and was presented (with a delay of 28.3 ms) on the LED bow by means of a fourth LED. The feedback was refreshed each half cycle and the scaling of the feedback was in degrees, thus corresponding to that of the performed amplitude. If the performed amplitude was larger (smaller) than the target amplitude, the feedback LED was displayed higher (lower) than the target LED. This online feedback procedure enabled participants to perform the required amplitudes, without performing aiming movements at spatial targets. Although they were instructed to keep the amplitude within the tolerance range, occasional outliers were allowed. Directly upon completion of a trial, the trial was discarded and rerun if the mean performed amplitude fell outside the

tolerance range (target amplitude $\pm 3^\circ$) and/or the amplitude variability (*SD*) exceeded 3° , which occurred in only a few trials for two participants.

Procedure

Participants were instructed to start each trial by first coordinating the arm movements with the pacing signal and subsequently matching the amplitudes with the target amplitudes. Once this was achieved, the experimenter waited for three more movement cycles and then started the recording of 30 experimental cycles. The trials were grouped in five amplitude blocks, which consisted of two coordination mode blocks (in-phase and antiphase). The order of the amplitude and coordination mode blocks was counterbalanced over participants. Within each coordination mode block, both frequency conditions were presented four times in a random order. This resulted in a total of 80 trials for each participant, yielding an experimental session of approximately 75 minutes (including breaks).

Prior to the experimental trials, participants performed several practice trials. First, a unimanual trial (with the D arm) was executed in order to familiarize the participant with the amplitude feedback. Subsequently, two to three practice trials were performed in each of the following conditions: 1:1, 1 Hz, in-phase; 4:3, 1.5 Hz, in-phase; and 1:2, 1.5 Hz, antiphase. In addition, participants performed one practice trial at the beginning of each amplitude block to get acquainted with the new amplitude condition. All procedures described in this article fully complied with the ethical guidelines of the American Psychological Association and were approved by the Ethics Committee of the Faculty of Human Movement Sciences of the VU University, Amsterdam.

Data analysis

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. Instances of peak flexion and extension were obtained using a custom-made peak-picking algorithm. For each half cycle, movement amplitude (in degrees) was calculated as the peak-to-peak flexion-extension excursion divided by two. The relative phase (ϕ) between the arms was calculated for each full cycle as

$\phi_i = 360^\circ(t_{D,i} - t_{ND,i}) / (t_{D,i+1} - t_{D,i})$, where $t_{D,i}$ and $t_{ND,i}$ indicate the time of the i th peak of the dominant arm and the nondominant arm, respectively. This procedure was performed twice using either only the flexion peaks or only the extension peaks. The resulting data were pooled to obtain circular mean and variability measures (see below).¹⁴ Thus, for in-phase coordination, $\phi > 0$ indicated a phase lead of the D arm (i.e., right arm lead, since in this experiment all participants were right-handed), and $\phi < 0$ indicated a phase lead of the ND arm.

Using circular statistics (Mardia, 1972), the performance was evaluated on the basis of the mean relative phase (ϕ) and its variability, as obtained for the 2nd to the 29th cycle of each trial. 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 et al., 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.

Unless specified otherwise, dependent variables were submitted to a repeated measures analysis of variance (ANOVA) with within-subjects factors amplitude ratio (1:2, 3:4, 1:1, 4:3, 2:1), coordination mode (in-phase, antiphase), and frequency (1, 1.5 Hz). The significance level was set at $p < .05$. The corresponding effect sizes (f) were calculated based on the partial eta squared (η_p^2 ; Cohen, 1988). In case the assumption of sphericity was violated, the degrees of freedom were adjusted using the Huynh–Feldt procedure. Significant interactions were further scrutinized by analyzing appropriate simple effects (Keppel, 1991; $p < .05$), which were completed, if necessary, by post-hoc paired-samples t -tests (using a modified Bonferroni α -level correction procedure that takes the correlation between conditions into account; see Uitenbroek, 1997). Significant main effects of factors with more than two levels (here: amplitude ratio) were also submitted to post-hoc paired-samples t -tests. For comparisons based on one-sample t -tests, Cohen's d was reported as a measure of effect size (Cohen, 1988).

¹⁴ Continuous relative phase was also calculated (following Chapters 2 and 4) and yielded comparable (statistical) results.

Results

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. The mean frequencies of the left and the right arm differed 3% or less, indicating that the movements were 1:1 frequency locked. The prescribed frequencies were adequately performed, with averages and corresponding standard deviations of 1.006 Hz ($SD = 0.014$) and 1.506 Hz ($SD = 0.012$).

Ratio	Requirements		Performance						
	A_{req}		A		CE_A		SD_A		ΔA
	D	ND	D	ND	D	ND	D	ND	
1:2	14	28	15.4	26.2	1.4	-1.8	1.13	1.62	-10.8
3:4	18	24	17.8	23.5	-0.2	-0.5	1.03	1.40	-5.7
1:1	21	21	20.8	20.8	-0.2	-0.2	1.07	1.15	0.0
4:3	24	18	23.6	18.1	-0.4	0.1	1.23	1.12	5.5
2:1	28	14	27.3	14.5	-0.7	0.5	1.57	1.28	12.8

Table 5.1. Required amplitude (A_{req}), mean performed amplitude (A), constant error (CE_A), and amplitude variability (SD_A) for the dominant (D) and nondominant (ND) arm, as well as the mean performed amplitude difference (ΔA), as obtained for each amplitude ratio (Ratio; D:ND) in Experiment 1. All values are in degrees.

Movement amplitude

Table 5.1 summarizes the performed amplitudes (A). In order to analyze the amplitude performance, the constant error of the amplitude ($CE_A = A - A_{\text{req}}$) was calculated. The values of CE_A , averaged across coordination mode and frequency conditions, were subjected to a one-sample t -test against $CE_A = 0^\circ$. This revealed that CE_A was significantly larger than 0° (implying overestimation) for the smallest amplitude (i.e., 14°), $t(79) = 6.81$, $p < .00001$, $d = 0.76$, while CE_A was significantly smaller than 0° (implying underestimation) for the three largest amplitudes (i.e., 21° , 24° , and 28°), $t(79) < -3.71$, $p < .001$, $d < -0.41$. Nevertheless, the CE values were small (see Table 5.1), indicating that the performance of the amplitudes was reasonably adequate.

Shift in mean relative phase ($\Delta\phi$)

The mean phase shift ($\Delta\phi$) was expressed with respect to the required relative phase (ϕ_{req}), that is, $\Delta\phi = \phi - \phi_{\text{req}}$, with $\phi_{\text{req}} = 0^\circ$ (in-phase) or $\phi_{\text{req}} = 180^\circ$ (antiphase). Figure 5.1A shows that this phase shift was strongly dependent on the imposed amplitude ratio. When the D arm performed the larger amplitude, the mean phase shift was negative (indicating ND arm lead), but became increasingly positive (indicating D arm lead) when the amplitude of the D arm decreased relative to that of the ND arm. These changes culminated in a significant effect of amplitude ratio, $F(4, 36) = 23.89$, $p < .00001$, $f = 1.63$, in the ANOVA on $\Delta\phi$. According to the corresponding post-hoc analyses, only the differences between 1:2 and 3:4 and between 4:3 and 2:1 were not significant. Furthermore, the effect of frequency, $F(1, 9) = 7.62$, $p < .05$, $f = 0.92$, and the Amplitude Ratio \times Frequency interaction, $F(4, 36) = 9.43$, $p < .001$, $f = 1.02$, indicated that the effect of amplitude ratio was more pronounced for the higher frequency, specifically for the conditions in which the amplitude of the D arm was smaller than that of the ND arm (see Figure 5.1A). Indeed, post-hoc simple effects analyses revealed that $\Delta\phi$ was amplified at the higher frequency for the 1:1, 3:4, and 1:2 (D:ND) amplitude ratios.

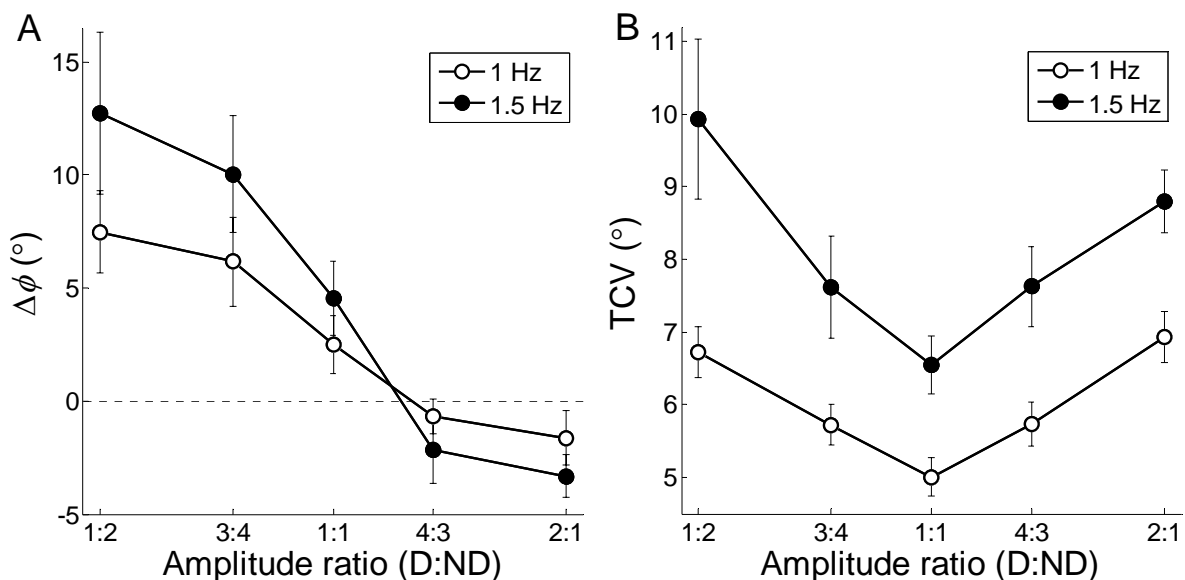


Figure 5.1. Mean shift in relative phase ($\Delta\phi$; Panel A) and relative phase variability (TCV; Panel B) as a function of amplitude ratio and movement frequency. Error bars represent the between-subjects standard errors.

In Figure 5.1A the $\Delta\phi$ curves are not symmetrically organized around $\Delta\phi = 0^\circ$, but are shifted upward. One-sample t -tests revealed that $\Delta\phi$ was significantly different from $\Delta\phi = 0^\circ$ for all amplitude conditions, $|t|(39) > 2.54$, $p < .05$, $|d| > 0.40$. Since this implied that $\Delta\phi > 0^\circ$ in the 1:1 amplitude condition, this indicated a significant bias towards D (i.e., right) arm lead.

Relative phase variability (TCV)

The ANOVA conducted on *TCV* revealed the commonly observed effects of coordination mode, $F(1, 9) = 24.55$, $p < .001$, $f = 1.65$, frequency, $F(1, 9) = 35.78$, $p < .001$, $f = 1.99$, and the Coordination Mode \times Frequency interaction, $F(1, 9) = 14.34$, $p < .01$, $f = 1.26$. Variability increased with frequency and antiphase performance (mean *TCV* = 6.3° [1 Hz]; 9.4° [1.5 Hz]) was more variable than in-phase performance (mean *TCV* = 5.9° [1 Hz]; 7.0° [1.5 Hz]), while post-hoc simple effects analysis of the interaction revealed that the latter effect did not reach significance in the 1 Hz condition. Furthermore, the effect of amplitude ratio was significant, $F(4, 36) = 12.77$, $p < .00001$, $f = 1.19$. Variability was lowest for the 1:1 condition and increased with the difference between the amplitudes (see Figure 5.1B). Post-hoc comparisons revealed that only the differences between 1:2 and 2:1, and between 3:4 and 4:3 were not significant, indicating that the effect was symmetric around the 1:1 ratio. The Amplitude Ratio \times Coordination Mode interaction, $F(4, 36) = 2.86$, $p < .05$, $f = 0.56$, was also significant. Simple effect analysis revealed that the effect of coordination mode was significant for all but the 2:1 amplitude condition (mean *TCV* for the ratios 1:2 to 2:1, in-phase: 7.3° , 5.9° , 5.1° , 6.0° , 7.8° ; antiphase: 9.2° , 7.5° , 6.6° , 7.5° , 8.3°).

Discussion

The findings confirmed the hypothesis that a difference in the amplitudes performed by the individual arms (ΔA) affected the relative phase dynamics in a manner that can be accounted for by the $\Delta\omega$ term in Equation 5.3, consistent with the inverse relation between the unimanual movement amplitude and preferred frequency. Accordingly, the obtained relative phase shifts (cf. Figure 5.1A) corresponded to the predicted effects. A significant shift in relative phase away from the required 0° and 180° phase relations was observed, in that the arm performing the smaller amplitude (corresponding to the higher uncoupled

frequency) was leading the other arm in time (Amazeen et al., 2005, Buchanan & Ryu, 2006, Heuer & Klein, 2005). This phase shift increased with the difference in amplitude (see Figure 5.1A), although post-hoc analyses indicated that the phase shifts obtained for the 1:2 and 2:1 conditions were not significantly different from the phase shifts obtained for the 3:4 and 4:3 conditions, respectively. Furthermore, as predicted, these effects on the relative phase were amplified at the higher movement frequency (Figure 5.1A) and the variability of relative phase (TCV) increased significantly with the difference in amplitude (Figure 5.1B). The prediction that the effect of ΔA would be more pronounced for antiphase than for in-phase coordination, however, was not supported. It is conceivable that much larger variations in ΔA are required to induce this effect at the examined movement frequencies. Future research may usefully aim at further examining the effects of ΔA , for instance by testing predictions based on Equations 5.2 and 5.3 (with ΔA being inversely related to $\Delta\omega$ regarding phase wrapping and phase transition routes; cf. Jeka & Kelso, 1995; Kelso & Jeka, 1992).

Although the obtained TCV values were symmetric around the 1:1 amplitude ratio, the $\Delta\phi$ curve was shifted upward, indicating D arm lead. This effect was amplified for the higher movement frequency. These results, as obtained for our right-handed participants, are in agreement with the effects of the handedness-related parameter d in Equation 5.3 and are therefore in accordance with the asymmetric relative phase dynamics that encompass a handedness-related asymmetry in coupling strength (Chapter 2; Peper, Daffertshofer, & Beek, 2004; Treffner & Turvey, 1995)

In sum, it can be concluded that a difference in amplitude between the limbs influences the asymmetry in relative phasing as well as the coordinative stability, in a manner that can be accounted for by the $\Delta\omega$ term in Equation 5.3. Thus, it is possible that in Chapter 4 the expected influences of the attentional modulations of interlimb coupling strength were indeed obscured by counteracting effects of attention-related imbalances in amplitude, as was already anticipated in that chapter. In other words, despite the demonstrated effect of amplitude disparity, it remains possible that laterally focused attention affected the relative phasing between the limbs in a manner similar to handedness, that is, through an asymmetry in coupling strength. To address this question, we conducted a second experiment in which the effects of attentional

focus and a difference in amplitude on the relative phase dynamics were dissociated.

Experiment 2

The aim of the second experiment was to examine whether asymmetrically focused attention and amplitude disparity (ΔA) have opposite effects on the relative phase dynamics. To this end, we used the same manipulation of ΔA as in Experiment 1, with additional manipulation of the direction of attention. Given that laterally focused attention has been shown to alter the asymmetry in coupling strength (Chapter 4) that may correspond to modulations of parameter d in Equation 5.3 (Chapter 2; Peper, Daffertshofer, & Beek, 2004), it was predicted that, for any given ΔA (i.e., provided that ΔA is equal over the attention conditions), the relative phase is influenced by attentional focus. Specifically, based on Equation 5.3 the phase advance of the leading limb (i.e., the limb moving with the smaller amplitude) was predicted to be larger (smaller) when attention was directed towards this (the other) limb (as illustrated in Figure 5.2). To test this prediction, both the direction of attention and the movement amplitudes were manipulated.

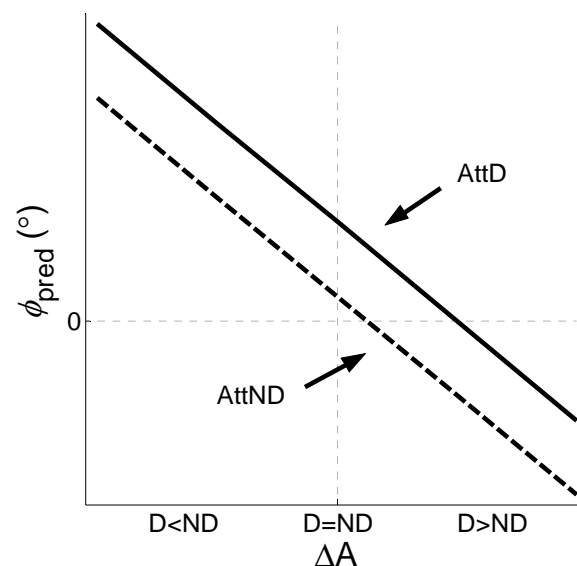


Figure 5.2. Schematic illustration of the predicted effects of ΔA and attentional focus on the relative phasing between the limbs ($\Delta\phi$). AttD = dominant limb attended; AttND = nondominant limb attended.

Recently, Amazeen et al. (2005) independently manipulated these factors to examine their effects on the relative phase dynamics. To this end, participants performed bimanual Fitts' tasks, in which the direction of attention was assumed to vary with the difficulty of each subtask, as manipulated by variations in the widths of spatial targets. However, it has been shown that manipulations of target width alter the kinematic characteristics of the movement, which, theoretically, may also affect the relative phase dynamics. More specifically, when moving to a smaller target, a limb behaves more like a softening spring (i.e., enhanced slowing down in the vicinity of the target; e.g., Buchanan et al., 2006; Guiard, 1993; Mottet & Bootsma, 1999) corresponding to enhanced negative nonlinear (i.e., Duffing) stiffness of the limit cycle oscillator, which is accompanied by increased linear stiffness (ω) when normalized to cycle time (Mottet & Bootsma, 1999). A difference in the component dynamics in this regard introduces nonzero values of $\Delta\omega$ in Equation 5.3 (Daffertshofer et al., 1999; Fuchs et al., 1996), which theoretically yields a tendency towards a phase lead of the limb with the most stringent spatial constraints (i.e., largest [non]linear stiffness). Thus, it is conceivable that these accompanying kinematic variations, rather than attentional focus, (partly) induced the changes in the relative phase dynamics that resulted from manipulations of the relative difficulty of the two subtasks. To avoid the potentially confounding influence of such task-related differences between the limbs, in the present experiment the direction of attention was not manipulated by means of task difficulty but rather through instruction (cf. Chapter 4; Franz, 2004; Swinnen et al., 1996; Wuyts et al., 1996). Because Experiment 1 had revealed that the effects of ΔA were comparable for in-phase and antiphase coordination, solely in-phase coordination was examined.

Methods

Participants

Ten participants (3 women and 7 men, aged 21-37 years) took part in Experiment 2. Two of them were labeled as left-handed (with LQs of -100 and -54), while eight were right-handed (mean LQ = 81, range 43 to 100; Oldfield, 1971). Participants gave their informed consent prior to taking part in the experiment.

Apparatus

The apparatus was the same as in Experiment 1 for participants 1-5. Due to technical problems, for participants 6-10 an alternative but similar apparatus was used, involving a different set of potentiometers (Sakae, type FCP40A-5k; accuracy 0.1°; sampling rate: 300 Hz) in an otherwise identical setup.

Procedure

Apart from the additional manipulation of attention, the task, the instructions, and the amplitude conditions were the same as in Experiment 1. In contrast to Experiment 1, only in-phase movements were examined at a movement frequency of 1.25 Hz. The procedure with regard to the manipulation of the direction of attention was as follows. A trial was started by first coordinating the arm movements with the pacing signal and matching the amplitudes with the target amplitudes. Once this was achieved, the experimenter waited for three more movement cycles and then started the recording of 36 experimental cycles. Directly after the completion of the eighth cycle, the participant received a verbal cue ('left' or 'right') from the experimenter indicating which arm to attend to. Upon this cue, the participant turned his or her head slightly towards the indicated arm and concentrated on and visually monitored the movements of this arm for the rest of the trial (cf. Chapter 4; Franz, 2004; Swinnen et al., 1996; Wuyts et al., 1996), while being instructed to maintain the prescribed amplitude difference. A cardboard cylinder (attached to the headphones) that encircled the face prevented vision of the contralateral arm, so that participants could only see the attended arm. The experimenter ascertained that no head rotations away from the indicated arm were made during the rest of the trial. The presentation of practice trials was comparable to that in Experiment 1, but now only included in-phase movements at 1.25 Hz.

The experimental trials were grouped in five 'amplitude blocks'. Within these blocks, each attention condition was performed four times in a randomized order. Thus, each participant performed 40 trials in total, which lasted approximately 45 minutes (including one break).

Data analysis

Data analysis was the same as for Experiment 1. The mean and variability of ϕ and A were determined for the 12th to the 35th cycle, and, in addition, for the epoch prior to the attention manipulation (i.e., from the 2nd to the 8th cycle).

These ‘pre-attention’ measures were calculated to examine whether the initial conditions were comparable to the results obtained for Experiment 1. The statistical procedures were similar to those described for Experiment 1.

Results

Movement Frequency

The difference in mean frequency between the left and the right arm (as obtained over the complete trials) was $< 3\%$, indicating proper 1:1 frequency locking. The prescribed frequency of 1.25 Hz was adequately performed: 1.254 Hz ($SD = 0.007$).

‘Pre-attention’ performance

The results of the ‘pre-attention’ performance were comparable to the results obtained for Experiment 1. The mean relative phase (ϕ_{pre}) as calculated for the epoch prior to the attention signal was subjected to a repeated measures ANOVA with the factor amplitude ratio (1:2, 3:4, 1:1, 4:3, 2:1), which yielded a significant effect, $F(4, 36) = 4.78, p < .05, f = 0.73$. Table 5.2 shows that ϕ_{pre} decreased towards ND arm lead ($\phi_{\text{pre}} < 0$) for amplitude ratios larger than 1 (i.e., $D > ND$). Post-hoc paired-samples t -tests indicated that ϕ_{pre} was significantly lower for the 2:1 ratio than for the 1:2, 3:4, and 1:1 ratios (see Table 5.2). The repeated measures ANOVA with the factor amplitude ratio (1:2, 3:4, 1:1, 4:3, 2:1) conducted on the pre-attention relative phase variability (TCV_{pre}) also revealed a significant effect, $F(4, 36) = 9.16, p < .0001, f = 1.01$. Post-hoc paired-samples t -tests showed that the variability for the ratios 1:2 and 2:1 was significantly higher than for the other amplitude conditions, and that 2:1 was more variable than 1:2 (see Table 5.2). The remainder of this section presents the results obtained while attention was focused on either the D or ND arm.

Movement amplitude

Because the applied tolerance ranges for movement amplitude still allowed small variations in amplitude, the actually performed amplitude (A) was analyzed in detail to examine whether it varied as a function of the manipulation of attention. First of all, one-sample t -tests of the constant error of the amplitude (CE_A) against $CE_A = 0^\circ$ yielded significant underestimation for the smallest amplitude, $t(39) = 3.22, p < .01, d = 0.51$, and overestimation for the largest

amplitude, $t(39) = -2.10$, $p < .05$, $d = -0.33$, which was comparable to the results obtained for CE_A in Experiment 1. In addition, the performed amplitude (A) was subjected to a repeated measures ANOVA with the factors arm (D, ND), attention (AttD, AttND), and prescribed amplitude (14° , 18° , 21° , 24° , 28°). In accordance with the amplitude manipulation, the effect of prescribed amplitude was significant, $F(4, 36) = 265.72$, $p < .00001$, $f = 5.41$. Furthermore, the significant effect of arm, $F(1, 9) = 5.26$, $p < .05$, $f = 0.76$, revealed a difference in amplitude between the D arm (mean $A = 20.8^\circ$) and the ND arm (mean $A = 21.2^\circ$). Moreover, significant effects were obtained for the Arm \times Attention, $F(1, 9) = 10.10$, $p < .01$, $f = 1.06$, and Arm \times Attention \times Prescribed Amplitude interactions, $F(4, 36) = 19.62$, $p < .00001$, $f = 1.47$. Post-hoc simple effects analyses demonstrated that for the three largest prescribed amplitudes (i.e., 21° , 24° , and 28°) the actually attained amplitude varied systematically as a function of attention: For both the D and ND arm A was larger when the corresponding arm was attended (AttD or AttND, respectively; see Figure 5.3).

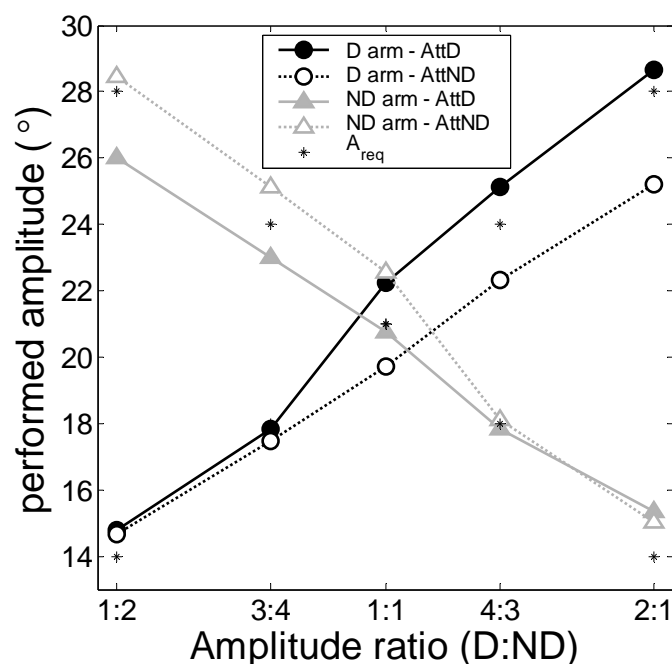


Figure 5.3. Mean performed amplitude as a function of amplitude ratio and attentional focus. Circles denote amplitude of the dominant (D) arm, triangles that of the nondominant (ND) arm, with attentional focus on the D arm (AttD; closed symbols, solid lines) or ND arm (AttND; open symbols, dashed lines). Required amplitudes (A_{req}) are indicated by *. For presentational reasons, error bars were omitted.

Ratio	Pre-attention						Attention					
	CE_A		SD_A		ϕ_{pre}	TCV_{pre}	CE_A		SD_A		ϕ	TCV
	D	ND	D	ND			D	ND	D	ND		
1:2	0.1	-0.6	0.95	1.57	5.6	6.6	0.7	-0.8	1.08	1.63	5.6	6.6
3:4	-0.3	-0.3	1.07	1.38	4.3	5.8	-0.3	0.1	1.13	1.47	3.7	6.5
1:1	-0.1	0.0	1.04	1.17	1.7	5.4	0.0	0.7	1.08	1.17	1.8	5.5
4:3	-0.4	-0.2	1.25	1.15	-1.3	5.9	-0.3	-0.0	1.28	1.13	-0.4	6.1
2:1	-0.5	0.5	1.50	1.19	-2.3	7.5	-1.1	1.2	1.56	1.17	-2.6	7.4

Table 5.2. Constant error (CE_A) and variability (SD_A) of the performed amplitudes for the dominant (D) and nondominant (ND) arm, as well as mean relative phase (ϕ) and its variability (TCV) for each amplitude ratio (Ratio; D:ND) as obtained for the pre-attention and attention stages in Experiment 2. All values are in degrees and are collapsed over the attention conditions.

The amplitude variability (SD_A) was also subjected to a repeated measures ANOVA with the factors arm (D, ND), attention (AttD, AttND), and prescribed amplitude (14°, 18°, 21°, 24°, 28°). Amplitude variability was lower for the D arm (mean $SD_A = 1.22^\circ$) than for the ND arm (mean $SD_A = 1.32^\circ$), as indicated by the significant effect of arm, $F(1, 9) = 24.59$, $p < .001$, $f = 1.65$. The effect of prescribed amplitude, $F(4, 36) = 48.10$, $p < .00001$, $f = 2.31$, and subsequent post-hoc paired-samples t -tests revealed that the two largest amplitudes (i.e., 24° and 28°) were performed significantly more variably than the others, with 28° being more variable than 24° performance (cf. Table 5.2). Furthermore, the Arm \times Attention \times Prescribed Amplitude interaction was significant, $F(4, 36) = 2.66$, $p < .05$, $f = 0.54$. Post-hoc simple effects analysis showed that this interaction was due to the fact that for either arm the largest amplitude was performed less variably when this arm was attended (D arm: mean $SD_A = 1.48^\circ$ [AttD]; 1.63° [AttND]; ND arm: mean $SD_A = 1.70^\circ$ [AttD]; 1.57° [AttND]).

Mean relative phase (ϕ)

Because in this experiment only in-phase coordination was examined, ϕ was equal to $\Delta\phi$. In accordance with the results of Experiment 1, the repeated measures ANOVA with the factors attention (AttD, AttND) and amplitude ratio (1:2, 3:4, 1:1, 4:3, 2:1) revealed an effect of amplitude ratio, $F(4, 36) = 8.89$, $p <$

.01, $f = 0.99$. For the 1:2 amplitude ratio, ϕ was significantly higher than for the 1:1, 4:3, and 2:1 ratios, while for the 2:1 ratio ϕ was significantly lower than for all other ratios (Table 5.2; see also Figure 5.4), as indicated by post-hoc simple effects analysis. Furthermore, a significant effect was obtained for the Attention \times Amplitude Ratio interaction, $F(4, 36) = 3.51$, $p < .05$, $f = 0.62$. A significant simple effect of amplitude ratio was obtained for both amplitude conditions, whereas subsequent paired-samples t -tests indicated that when attention was focused on the ND arm, the effect of amplitude ratio on ϕ was more pronounced for the conditions in which the ND arm performed the smaller amplitude (4:3 and 2:1), as illustrated in Figure 5.4. However, post-hoc simple effects analysis did not yield significant differences between the attention conditions for any amplitude ratio individually.

Finally, the ϕ curve in Figure 5.4 was significantly shifted upwards (indicating D arm lead), given that only ϕ as obtained for the 4:3 ratio was not significantly different from $\phi = 0^\circ$, as indicated by one-sample t -tests (cf. Experiment 1; for the other ratios: $|t| > 2.69$, $p < .05$, $|d| > 0.60$).

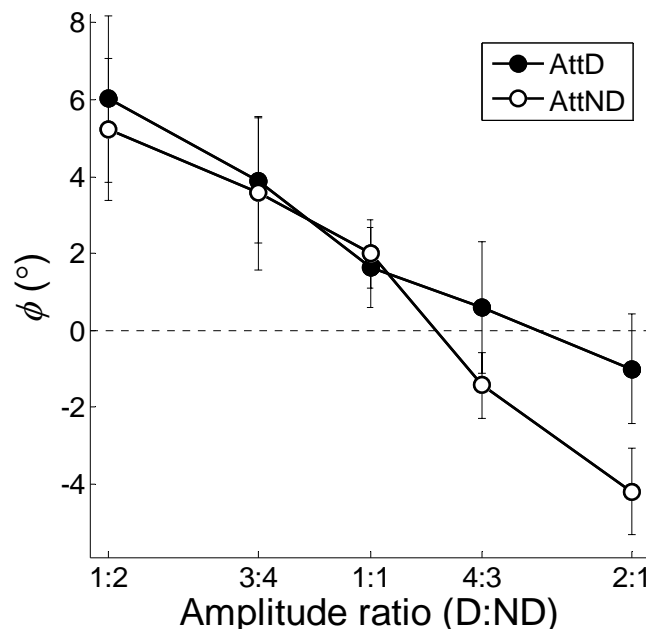


Figure 5.4. Mean relative phase (ϕ) as a function of amplitude ratio and attentional focus, as obtained for Experiment 2. AttD = dominant arm attended; AttND = nondominant arm attended. Error bars represent the between-subjects standard errors.

Phase variability (TCV)

The repeated measures ANOVA on *TCV* with the factors attention (AttD, AttND) and amplitude ratio (1:2, 3:4, 1:1, 4:3, 2:1) yielded only a significant effect of amplitude ratio, $F(4, 36) = 14.58, p < .00001, f = 1.27$. Post-hoc paired samples *t*-tests showed that variability was significantly lower for the 1:1 amplitude ratio than for all other amplitude conditions. Furthermore, for the 2:1 condition, *TCV* was significantly higher than in the other conditions, including the 1:2 condition (see Table 5.2). *TCV* for the 1:2 condition, however, did not differ statistically from that obtained for the 3:4 condition.

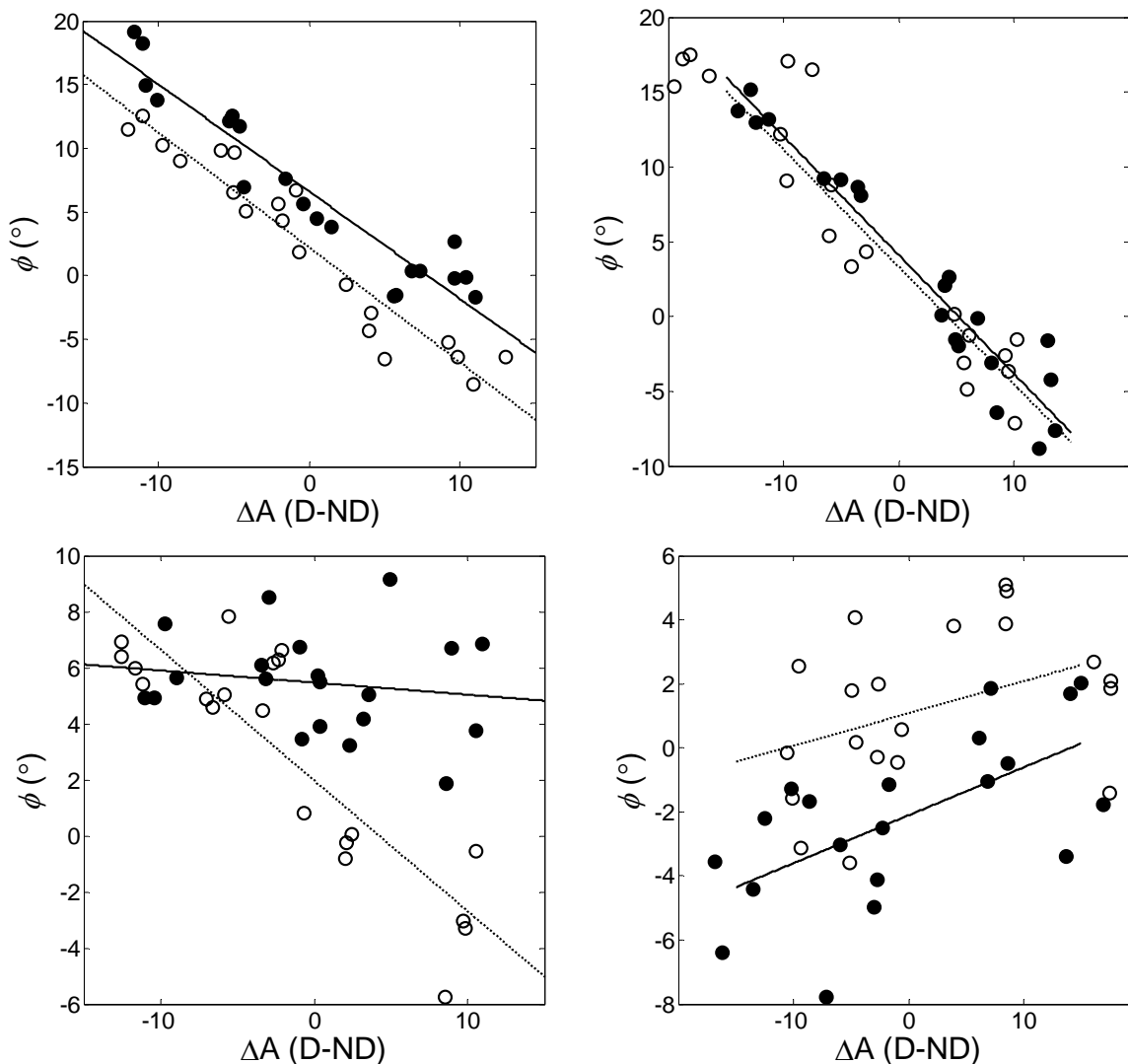


Figure 5.5. Mean relative phase (ϕ) as a function of performed amplitude difference (ΔA) for each trial. The panels present typical examples as obtained for four of the ten participants (solid circles: dominant arm attended; open circles: nondominant arm attended). Linear regression lines are also plotted (solid lines: dominant arm attended; dashed lines: nondominant arm attended).

Regression analysis of ϕ with respect to ΔA

According to our hypothesis (illustrated in Figure 5.2) ϕ was expected to be larger (indicating enhanced D arm lead) when attention was focused on the D arm, for the whole range of ΔA values. To examine this prediction, for each individual participant, the values of ϕ were plotted against the actually performed ΔA as obtained for each trial, and linear regression functions were computed for each attention condition (see Figure 5.5 for typical examples). With a few exceptions (2 out of 20), the correlations (absolute values ranging from .399 to .965) were significant ($p < .05$). Whereas attentional focus was predicted to affect the intercept of the linear regression curves (cf. Figure 5.2), neither the intercept (range -6.2° to 7.9°) nor the slope (range -0.9° to 0.2°) was significantly affected by the direction of attention (AttD, AttND), as was revealed by paired-samples t -tests.

Discussion

In spite of the fact that for each arm movement amplitude was prescribed, the actually performed amplitudes still varied as a function of attentional focus (see Figure 5.3). That is, while the performance of the smallest two amplitudes (i.e., 14° and 18°) did not depend on which arm was attended, the other three amplitudes (i.e., 21° , 24° , and 28°) were performed larger (smaller) when the arm performing that amplitude was attended (not attended). Because each condition included at least one of the three amplitudes that exhibited an effect of attention, this attention effect played into the actually performed amplitude relations for all amplitude ratios. For the 1:1 amplitude condition, the attended arm moved with a larger amplitude than the unattended arm (cf. Chapter 4; Franz, 2004), involving an attention-related ΔA of on average 4.3° , corresponding to 20% of the prescribed amplitude (21°). In the conditions with unequal amplitudes, ΔA varied with attentional focus in a similar vein. Specifically, the larger of the two amplitudes was amplified when the corresponding arm was attended, whereas it was reduced when the other arm was attended. Here, the additional attention-related ΔA was on average 2.8° , corresponding to 33% of the prescribed ΔA 's. Thus, the actually performed amplitude difference was influenced by attentional focus in a manner consistent with that observed in Chapter 4, implying that, even though movement amplitude was now explicitly prescribed, the actual amplitude difference was still affected by the attention manipulation. As a

consequence, caution was in order when interpreting the results regarding the relative phase and its variability, since the prerequisite that ΔA was equal for both attention conditions was violated.

In accordance with the results of Experiment 1, the phase relation (ϕ) was primarily determined by the imposed ΔA , resulting in a phase lead of the arm that performed the smaller amplitude. The significant Attention \times Amplitude Ratio interaction (cf. Figure 5.4) suggested that for the conditions in which the D arm performed the larger amplitude (i.e., 4:3 and 2:1), attentional focus also affected ϕ (in a manner in line with our predictions; see Figure 5.2), although the corresponding post-hoc analysis did not yield significant differences between the attention conditions. Note, however, that Figure 5.4 suggests no effect of attention for the other amplitude conditions (including the 1:1 ratio) and that no effect of attention was obtained for relative phase variability. At the same time, it should be acknowledged that the interpretation of these results regarding the influences of attentional focus was hindered by the observed attention-related changes in amplitude, given their impact on the relative phasing between the arms (as demonstrated in Experiment 1). Therefore, in an attempt to obviate the effect of variations in amplitudes on relative phasing, we analyzed the linear regressions between the relative phase and the actually performed ΔA for each participant individually, to determine whether the corresponding intercepts varied as a function of attentional focus (as illustrated in Figure 5.2). This analysis revealed no significant effects of attention.

In sum, no strong conclusions could be drawn from Experiment 2 with regard to the prediction that the attentional modulation of the asymmetry in coupling strength (cf. Chapter 4) affects the relative phasing according to modulation of parameter d in Equation 5.3. However, it is possible that the predicted effects were obscured by the counteracting effect induced by the variations in amplitude. That is, although the persistent modulations of movement amplitude appear to be a genuine behavioral collateral of attentional focus (cf. Chapter 4; Franz, 2004; Zelaznik & Lantero 1996), this aspect of the attention manipulation hindered the analysis of the influences of another characteristic of the manipulation (viz., the asymmetry in coupling strength; Chapter 4) on the relative phase dynamics. Furthermore, the present task involved the instruction to maintain a particular amplitude difference. This may have required some degree of monitoring of the unattended limb (e.g., based on proprioceptive signals), thereby potentially affecting the manipulation of

attentional focus. Given these considerations, it was mandatory that variations in movement amplitude were eliminated completely, in order to examine the potential effect of the attention-related asymmetry in coupling strength on the relative phasing in isolation. This was achieved in a third experiment.

Experiment 3

An optimal test of the effects of the attentionally modulated asymmetry in coupling strength on the relative phase dynamics required a paradigm that precluded any covarying influence of the attention-related changes in amplitude. To this end, a third experiment was performed in which participants rotated their hands in circles with a fixed radius, by means of rotating rigid cranks around their axes. In this way, all potential variations in movement amplitude (A) related to the manipulation of attention were eliminated, allowing us to examine the effects the attentional modulations of interlimb coupling strength in isolation. Only in-phase circling movements were examined, because the synchrony of this coordination pattern implies that (at any moment in time) the arms attain (approximately) identical movement phases, thereby precluding potential variations in the relative phasing between the arms induced by differences between them associated with the biomechanical aspects of various phases in the movement cycle.

Methods

Participants

Sixteen participants (8 women and 8 men, aged 24-37 years) took part in the experiment. Two participants were labeled as left-handed (with LQs of -100 and -54), while fourteen were right-handed (mean LQ = 87, range 43 to 100; Oldfield, 1971). Participants gave their informed consent prior to taking part in the experiment.

Apparatus

Participants performed bimanual circling movements in the horizontal plane by means of two cranks. The circling radius (i.e., crank length) was fixed at 6 cm. (This particular crank length was based on the circle sizes applied in relevant circle drawing studies; e.g., Buchanan & Ryu, 2006; Wuyts et al., 1996; Zelaznik & Lantero, 1996). Each crank had a handle at the distal end that could

revolve on its own vertical axis, so that the crank could be circled without changing the grip on the handle (see Figure 5.6B). A black cardboard circle (with a radius of 6 cm) was attached to each crank lever in order to prevent visual information about its orientation. The circling axes of the two cranks were 75 cm apart and the participant was seated on a height-adjustable chair in between the two tables on which the cranks were mounted. Using an Optotrak camera system (Northern Digital, Waterloo, ON, Canada), 3D position data of the four active markers that were placed on the outer sides of the handles (two markers per handle, see Figure 5.6B) were recorded at a sample rate of 300 Hz. Computer-generated auditory pacing stimuli (pitch 200 Hz; duration: 50 ms) were presented through headphones (Sennheiser HD 520 II).

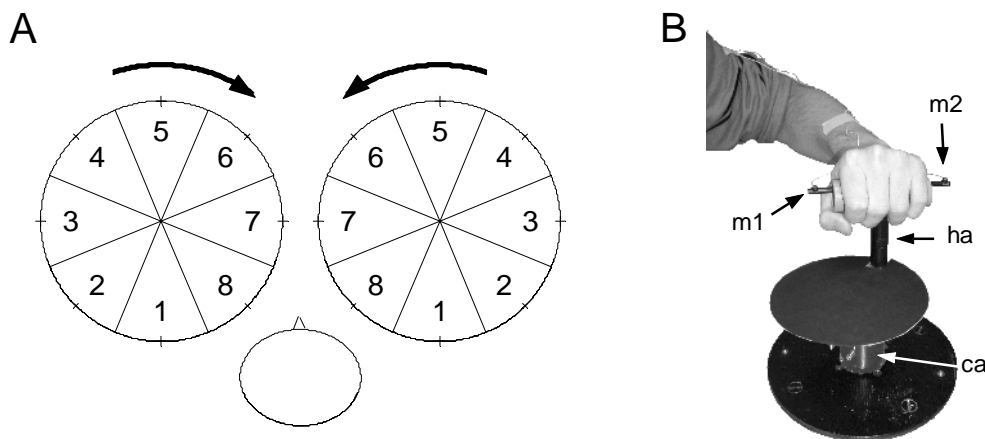


Figure 5.6. Panel A: Schematic top view of the experimental setup as applied in Experiment 3. Note that the size of the circles is not true to scale. The arrows indicate the direction of circling. The eight cycle phases used in the analysis of the local dynamics (see Results) are indicated for both arms. Panel B: Front view of the left crank, illustrating the grip on the handle, with m1 and m2 indicating the marker positions; ca = circling axis; ha = handle axis.

Procedure

Participants performed bimanual circling movements in an inward circling in-phase mode, by moving the right limb counterclockwise and simultaneously moving the left limb clockwise in a mirror-symmetric fashion, as indicated by the arrows in Figure 5.6A. The auditory pacing signal prescribed the movement frequency at 1 Hz (cf. Swinnen et al., 1996). Participants were instructed to produce a complete circle for each metronome pulse, but were not required to synchronize a specific movement phase with the metronome. The direction of

attention was manipulated in the same way as in Experiment 2: In each trial, the participant (wearing the cardboard cylinder) first initiated the coordinated arm movements, while subsequently the recording of 36 experimental cycles was started. After the completion of the eighth cycle, the participant received verbally the attention cue ('left' or 'right'). Four trials were performed for each attention condition. The order of these trials was randomized. Prior to the experimental trials, two to three practice trials were performed in order to accustom participants to circling the cranks as smoothly as possible.

Data analysis

Based on the obtained position data of the markers, the center of the grip was determined for each recorded sample. Subsequently, the rotational angle (θ) of the lever was calculated based on the location of the grip center. Because circling movements do not involve unambiguous turning points (in contrast to the oscillatory movements in Experiments 1 and 2), a continuous measure of relative phase was required rather than the point estimates used in our previous analyses. To this end, the continuous relative angle (RA) was computed using $RA = \theta_D - \theta_{ND}$ (cf. Mechsner, Kerzel, Knoblich, & Prinz, 2001; Tomatsu & Ohtsuki, 2005), which reflected the relative phasing of the bimanual circling movements (for a related procedure, see Carson, Thomas, Summers, Walters, & Semjen, 1997). Prior to calculation of RA , the position signal for the ND arm was converted by changing the sign of the displacement along the horizontal axis, in order to normalize the angular data in terms of direction. The circular mean and TCV (Mardia, 1972) of RA were calculated from the 12th to the 35th cycle.

Results

Global dynamics

The movement frequency of 1 Hz was adequately performed (mean = 1.009 Hz; $SD = 0.031$) and the difference in mean frequency of the left and the right arm (as obtained over the complete trials) was $< 7\%$ for all trials, thereby indicating that 1:1 frequency locking was achieved. A paired samples t -test revealed no significant difference in mean RA between D and ND arm attention (1.2° and 0.9° , respectively). In addition, a Wilcoxon signed rank test demonstrated that the RA s as obtained for the two attention conditions did not differ. The variability of RA (as indexed by TCV) also exhibited no effect of

attention (mean $TCV = 17.9^\circ$ and 18.0° when attention was focused on the D and ND arm, respectively), as indicated by a paired samples t -test.

Visual inspection of the angular velocity profiles for each arm, however, suggested that movement speed varied systematically as a function of the phase of the cycle. This implied that the relative phasing between the arms may also have varied within each movement cycle. For this reason, RA and TCV were also analyzed locally for 8 different phases of the movement cycle, as described in the next paragraph.

Local dynamics

The circle of the D arm was divided into 8 equidistant, nonoverlapping cycle phases of 45° as defined in Figure 5.6A. Accordingly, the time series of RA were cut into 192 segments ($24 \text{ cycles} \times 8 \text{ cycle phases}$). For each segment, the mean and TCV of RA were calculated. Subsequently, for each trial, these measures were averaged over the 24 movement cycles, yielding one value of mean RA and TCV for each of the 8 cycle phases. These values were subjected to repeated measures ANOVAs with the factors attention (AttD, AttND) and cycle phase (1 to 8). For mean RA , the effect of cycle phase, $F(3.1, 46.8) = 5.16$, $p < .01$, $f = 0.59$, as well as the Cycle Phase \times Attention interaction, $F(2.5, 37.6) = 29.57$, $p < .00001$, $f = 1.40$, were significant. Figure 5.7A shows that the RA varied as a function of cycle phase, and that this effect was, roughly, mirror symmetric for the two attention conditions. The post-hoc analysis demonstrated significant simple effects of cycle phase for both attention conditions. The corresponding post-hoc paired-samples t -tests showed that when the D arm was attended the RA values were largest (indicating D arm lead) in phase 8, and smallest (indicating ND arm lead) in phase 5, whereas when the ND arm was attended RA was largest in phase 4 and smallest in phase 1. In other words, when both arms were at the proximal part of the circle (i.e., close to the body, cf. phase 1 and 8, see Figure 5.6A) the attended arm tended to lead, while the unattended arm tended to lead when both arms were at the distal part of the circle (cf. phase 4 and 5, see Figure 5.6A). However, further analysis of this interaction in terms of the simple effects of attention for each cycle phase revealed no significant results.

For TCV the ANOVA also revealed a main effect of cycle phase, $F(3.7, 56.1) = 19.96$, $p < .00001$, $f = 1.15$. Figure 5.7B reveals the existence of two areas with reduced variability. Post-hoc paired-samples t -tests indicated that the

variability at phases 7 and 8 of the cycle (i.e., both limbs medio-proximal and medial, respectively, see Figure 5.6A) was significantly lower than at all other phases, followed by phases 3 and 4, that were significantly less variable than phases 5 and 6. The significant Cycle Phase \times Attention interaction, $F(5.6, 84.5) = 6.74$, $p < .0001$, $f = 0.67$, and subsequent post-hoc analyses indicated significant *TCV* differences between the D and ND arm attention conditions at phases 2, 4, 6, and 7.

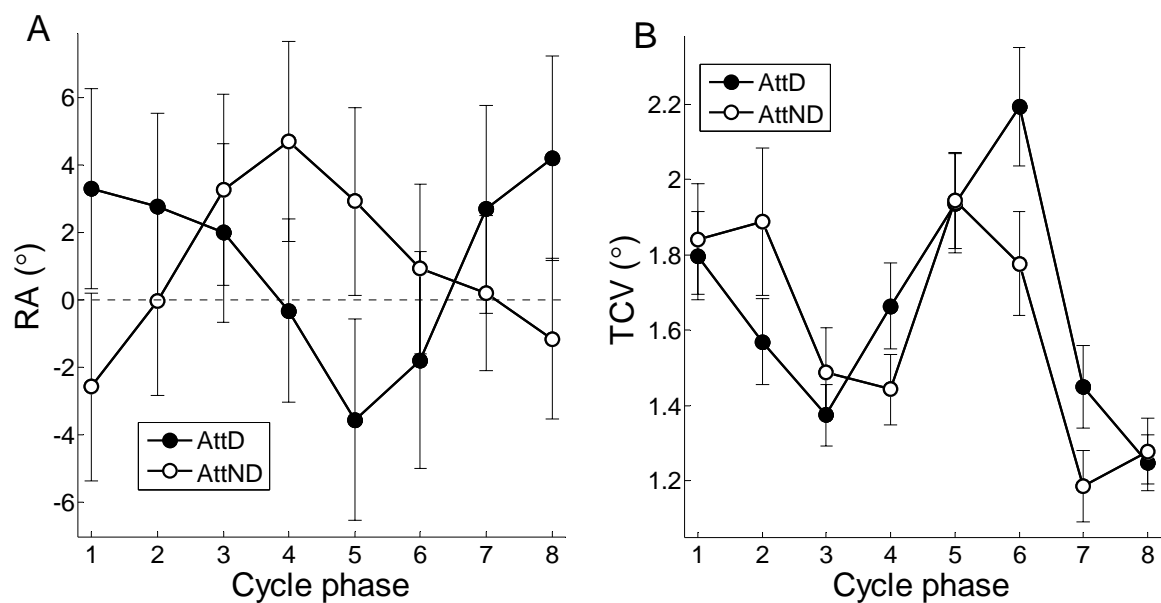


Figure 5.7. Mean relative angle (*RA*; Panel A) and mean relative angle variability (*TCV*; Panel B) as a function of the cycle phase (of the dominant arm) and attentional focus. AttD = dominant arm attended; AttND = nondominant arm attended. Error bars represent the between-subjects standard errors.

Discussion

In this third experiment variations in movement amplitude (*A*) were eliminated in order to examine the effects of laterally focused attention on the phase relation between the limbs in absence of attention-induced variations in movement amplitudes (see Experiment 2). When the data were averaged over the movement cycles (global dynamics), the results indicated no effects of attentional focus. Neither the mean phase relation (as indexed by *RA*) nor its variability (as indexed by *TCV*) differed over the attention conditions. These findings are inconsistent with previous studies (Amazeen et al., 1997; Amazeen et al., 2005; Franz, 2004; Swinnen et al., 1996) and do not support the assertion

that laterally focused attention influences the (global) relative phase dynamics through an asymmetry in coupling strength (Chapter 4; Amazeen et al., 1997).

On the other hand, the manipulation of attention seemed to have an effect at specific phases of the movements. When both arms were in the proximal part of the circle (viz. phase 1 and 8), the attended arm tended to lead, while the unattended arm tended to lead when the arms were in the distal part of the circle (viz. phase 4 and 5; see Figure 5.7A). An explanation for such differential local effects may be sought in the phenomenon of ‘anchoring’. It has been argued that particular points in the movement cycle (i.e., ‘anchor’ points) may serve as control points for the production of cyclical movements (Beek, 1989). For one-dimensional flexion-extension movements the points of maximum flexion and extension are regarded as anchor points, because at these points movement variability is typically reduced when coordinated with perceptual stimuli (e.g., Byblow, Carson, & Goodman, 1994; Carson, 1996; Fink, Foo, Jirsa, & Kelso, 2000; Maslovat, Chua, & Franks, 2006). Moreover, movement variability has been demonstrated to be larger for maximum extension than for maximum flexion, although this differential variability is also influenced by musculo-skeletal factors (Carson, 1996) and point of gaze (Roerdink, Peper, & Beek, 2005). Note that the occurrence of anchoring phenomena does not necessarily result from the presence of an external (pacing) signal, because an anchor may also be provided intrinsically by (perception of) the movement phase (cf. Beek, 1989).

This interpretation of the local dynamics was supported by signs of reduced coordinative variability (as indexed by *TCV*) at specific phases of the movement cycle (see Figure 5.7B). Because the variability was smallest in phases 7 and 8, this region may represent a primary anchor point. The results regarding *RA* revealed that in the vicinity of this anchor point the attended arm tended to lead. This may suggest that laterally focused attention influences the relative phase dynamics in a manner that is consistent with the effects of modulation of parameter d in Equation 5.3, but only in the vicinity of the primary anchor point. Because anchor points have been proposed to serve as specific control points in the movement cycle (Beek, 1989), the observed effect of directed attention may underscore that in particular at these anchor points attention-demanding control or interaction processes are active (e.g., error correction or feedforward control; cf. Ridderikhoff, Peper, & Beek, 2005, 2006). These findings indicate that the coordination dynamics may vary across

movement phases, and that analysis of local dynamics may provide additional insights into coordinative control (e.g., Byblow et al., 1994; Van Mourik, Daffertshofer, & Beek, 2007).

General Discussion

The present series of experiments were conducted to pinpoint the way in which attentional asymmetries affect the relative phasing between the limbs in bimanual isofrequency coordination. Consistent with the assumption that the effects of handedness are related to the amount of attention that is directed to each limb (Peters, 1989, 1994), previous studies had indicated that focusing attention on the movements of either limb influenced the relative phasing in a manner comparable to handedness (Amazeen et al., 1997; Riley et al., 1997; Swinnen et al., 1996). Because these effects of handedness appeared to result from an asymmetry in the strength of the interlimb interactions (Chapter 2; Peper, Daffertshofer, & Beek, 2004), the similarity between the effects of the two factors may indicate that the attentional modifications of the phase relation between the limbs were also induced by changes in the asymmetry of interlimb coupling strength (Chapter 2; Amazeen et al., 1997; Peper, Daffertshofer, & Beek, 2004). Although Chapter 4 revealed that laterally focused attention indeed modulated the degree of asymmetry in interlimb coupling strength, the expected corresponding changes in relative phasing were not observed. The interpretation of these results was, however, hindered by additional attention-related variations in movement amplitude that were postulated to entail counteracting effects on the relative phase dynamics, thereby possibly obscuring the effects of the attention-induced changes in interlimb coupling strength. The three experiments presented in this chapter were therefore aimed at dissociating between the changes in the relative phase dynamics induced by (attention-related) differences in the movement amplitudes of the two limbs (ΔA) and those resulting from changes in the asymmetry in coupling strength due to laterally focused attention.

Asymmetry due to attentional focus: Amplitude vs. coupling strength

Based on indications that the preferred frequency and amplitude of unimanual oscillatory movements are inversely related (e.g., Rosenbaum et al., 1991) and that, accordingly, a difference in amplitude (ΔA) may be related to a

difference in preferred frequency ($\Delta\omega$), predictions regarding the effects of ΔA were derived from (an extension of) the HKB-model of rhythmic interlimb coordination (Haken et al., 1985) that incorporates the detuning term $\Delta\omega$ (Equations 5.2 and 5.3; Fuchs et al., 1996; Kelso et al., 1990; Treffner & Turvey, 1996). The results of Experiment 1 confirmed these predictions regarding the mean relative phase and its variability. The major finding was that the arm performing the smallest amplitude was leading in time (see also Amazeen et al., 2005; Buchanan & Ryu, 2006; Heuer & Klein, 2005). This result confirmed the relation between the attention-related difference in amplitude and the shift in relative phase as proposed in Chapter 4, given that in that study the arm that was attended produced a larger amplitude and tended to lag the unattended arm (that was oscillating at a smaller amplitude). Thus, theoretically (based on Equation 5.3) it was indeed possible that this corollary had obscured the predicted effect of attentional modulation of the asymmetry in coupling strength (as observed in Chapter 4) on the relative phase dynamics.

The results of the simultaneous manipulation of ΔA and attentional focus in Experiment 2, however, did not reveal clear effects of attentional focus on the relative phase. Importantly, even though amplitude was prescribed explicitly, the interpretation of the results was still hindered by the persistent attention-related amplitude variations, which may again have obscured the possible influences of the asymmetry in coupling strength (as in Chapter 4). For this reason, a final experiment was conducted, in which any potential effects of ΔA were eliminated. Although in this experiment the attentional focus appeared to have influenced the relative phasing between the limbs at specific phases of the movement cycle (see next section), the global relative phasing was not affected. The latter finding contradicted the proposed effect of attentional modulations of the asymmetry in coupling strength on the coordination dynamics (Chapter 4; Amazeen et al., 1997; Treffner & Turvey, 1995). Thus, although it has been shown that focusing attention on the D or ND arm influences the asymmetry in coupling strength (Chapter 4), the current results indicate that this does not induce asymmetries in the overall relative phase. Hence, these findings strongly suggest that the asymmetry in relative phasing due to attentional focus (as observed by, e.g., Amazeen et al., 1997) is not mediated by an asymmetry in coupling strength, but rather by accompanying asymmetries at the component level, specifically by an attention-related difference in movement amplitude. Furthermore, the absence of the predicted effects of attentional focus on the

relative phase dynamics militates against the interpretation that the two sources of coupling asymmetry (i.e., handedness and attentional focus) are expressions of a common process and is, therefore, at odds with the proposition that the effects of handedness may be related to an inherent asymmetry in attentional focus (Peters, 1989, 1994).

At first blush, the present explanation seems to contradict previous studies that reported no effect of attentional focus on the relative phasing (Stucchi & Viviani, 1993; Wuyts et al., 1996) or reported the opposite result, in that the D limb lead increased (decreased) when the D (ND) limb was attended (Amazeen et al., 1997; Amazeen et al., 2005; Franz, 2004; Pellegrini et al., 2004; Riley et al., 1997; Swinnen et al., 1996). However, it is important to note that in most of these studies the amplitudes of the individual limb movements were not controlled in the experiment and/or not systematically considered in the analysis (for notable exceptions, see Amazeen et al., 2005; Franz, 2004) and that it is not unlikely that some of these results were confounded by a difference in amplitude. For example, in the bimanual pendulum swinging studies of Amazeen et al. (1997) and Riley et al. (1997), the direction of attention was manipulated through prescribing spatial accuracy constraints (i.e., target width) and movement amplitude for either the left or the right limb. However, because the preferred amplitude (i.e., 25° , as reported by Amazeen et al., 1997) was larger than those prescribed for the attended hand (i.e., 11° and 22°), their experiments probably involved a difference between the amplitudes of the two limbs. Given the current results, it seems likely that the observed phase leads (which were indeed larger when the attended hand attained the 11° rather than the 22° amplitude) were in fact caused by the smaller amplitude performed by the attended limb.

Global vs. local dynamics

The current predictions regarding the relative phase dynamics were based on Equation 5.3 and the corresponding elaboration of Peper, Daffertshofer, and Beek (2004; see also Chapter 2), which capture the overall coordination dynamics. That is, the mean relative phasing and its variability are defined as global measures, without taking variations within the movement cycles into account (cf. Haken et al., 1985). As such, the present results regarding the global coordination dynamics did not support the predicted relation between the

attention-related asymmetry in coupling strength and the relative phasing between the arms (see previous section). On a more local level, however, attentional focus seemed to invoke systematic variations in relative phasing as a function of the movement phase, suggesting that the attended arm tended to lead in the vicinity of the primary anchor point (located close to the body for inward in-phase cycling movements; see Experiment 3). Hence, at this anchor point (which may serve as a primary control point; e.g., Beek, 1989) the attentional focus modified the phase relation in the predicted direction. Although at the current stage, it cannot be readily interpreted in relation to Equation 5.3, this observed tendency underscores that analysis of the coordination dynamics at various phases of the movement cycle may provide vital information about coordinative control, and illustrates that it is important to complement global relative phase analysis with analyses at other levels, to address phase-dependent control and interaction processes during (bi)manual coordination tasks (e.g., Beek, 1989; Ridderikhoff et al., 2006).

Implications for modeling

According to Equation 5.3, a shift in relative phasing ($\Delta\phi$) only occurs when $\Delta\omega \neq 0$, $c \neq 0$, and/or $d \neq 0$. Parameters a and b , however, do not contribute to asymmetries in the relative phase dynamics, because they support attraction towards the (symmetric) stable solutions of exactly $\phi = 0^\circ$ and $\phi = 180^\circ$ (see Chapter 2; Peper, Daffertshofer, & Beek, 2004). Hence, although asymmetric contributions of the coupling influences between the arms (i.e., from the attended arm onto the unattended arm, and vice versa) to parameters a and/or b affect the overall strength of attraction to in-phase and antiphase coordination (and, thus, coordinative stability), they do not induce a phase shift away from those patterns (for an explicit account in this regard, see Chapter 2). Furthermore, given Equation 5.3, coordinative stability is predicted to increase (indexed by lower variability of ϕ) with $|d|$. Based on the finding that laterally focused attention affected the asymmetry in coupling strength (Chapter 2), together with the present observation that this modulation affected neither the relative phasing between the arms nor its variability, it can be concluded that attentional focus did not affect parameter d , and that, therefore, the attention-related asymmetry in coupling strength appeared to reside solely in the parameters a and/or b . Hence, although it has been argued that d may be

influenced by attentional asymmetries (Amazeen et al., 1997; Riley et al., 1997), the present study failed to provide convincing support for this relation, indicating that 1) an asymmetry in coupling strength *per se* does not necessarily induce a shift in relative phase and 2) handedness and attentional focus have distinct influences on the relative phase dynamics, associated with distinct parameter modulations in Equation 5.3.

Focusing attention on either limb invokes a difference between the movement amplitudes of the limbs (i.e., ΔA ; cf. Chapter 2; Franz, 2004; see also Experiment 2), which (as demonstrated in Experiment 1) influences the relative phase dynamics according to the effects of associated changes in $\Delta\omega$ in Equation 5.3 (see also Amazeen et al., 2005; Buchanan & Ryu, 2006). In addition, it is possible that the attention-related asymmetry in coupling strength (as observed in Chapter 2) originated from this (attention-related) difference in amplitude. After all, since the coupling between the two components has been modeled as a function of the state variables (i.e., position and velocity) of two limit cycle oscillators, theoretically, larger amplitudes result in larger coupling influences exerted on the other oscillator (Haken et al., 1985; Peper & Beek, 1999). Hence, a difference between the limbs' amplitudes may induce an asymmetry in the interlimb coupling strength. This interpretation is consistent with the neurophysiological observation that larger movements enhance both the efferent (e.g., motor neurons) and afferent (e.g., muscle spindles) firing frequencies, yielding stronger neural signals (Kandel, Schwartz, & Jessel, 1991). It is conceivable that such stronger neural signals lead to stronger contralateral effects, for instance, through neural cross-talk via the corpus callosum, ipsilateral corticospinal pathways, or interlimb spinal reflex pathways (for a review see Carson, 2005). Indeed, when one of the limbs was moved passively, the invoked afference-based phase entrainment was found to be stronger when the passive hand was moved with a larger amplitude (Ridderikhoff et al., 2005).

Hence, it is possible that the two attention-related phenomena (viz., amplitude difference and modulation of the asymmetry in coupling strength) are in fact intimately related. The observation that the handedness-related asymmetry in coupling strength demonstrated in Chapter 2 was *not* associated with a difference in amplitude (see Footnote 5 in Chapter 4) underscores the present interpretation that the asymmetries in coupling strength associated with handedness and attentional focus stem from different sources. Whether attention-induced asymmetries in coupling strength indeed originate from an

asymmetry in amplitude awaits further examination. On this account, the coupling influences from the limb performing the larger amplitude on that performing the smaller amplitude should be stronger than in the reverse direction. Using the methodology applied in Chapters 2 and 4 this hypothesis can be readily tested.

Conclusion

Although focusing attention on either limb has been demonstrated to affect the degree of asymmetry in interlimb coupling strength (Chapter 4), the present study provided no compelling grounds for assuming that these modulations entered into the relative phase dynamics according to a change in parameter d in Equation 5.3. Alternatively, a difference between the amplitudes of the arm movements, which varied systematically with attentional focus (see also Chapter 4), appeared to account for the observed effects on the relative phasing between the arms. The discrepancy between these results and those resulting from an asymmetry in coupling strength due to hand dominance indicates that these two instances of coupling asymmetry do not share a common source, which poses considerable challenges to the idea that effects of handedness are in fact expressions of an inherent difference in the amount of attention that is directed to either limb (as proposed by Peters, 1989, 1994). In modeling terms, the coupling asymmetries associated with handedness and attentional focus do not only differ with regard to the parameters that appear to be modulated, but also with respect to their potential relation to the state variables of the oscillating components. Whereas it is possible that the changes in coupling strength due to attentional asymmetries stem from the associated variations in movement amplitude, this relation has not been corroborated for hand dominance. On a more general note, the present study emphasized that the analysis of rhythmic bimanual performance in terms of the compound effects at the level of the relative phasing alone is not always sufficient and may even hamper interpretation of the data, thereby underscoring the importance of complementary analyses of both the coupling and the component dynamics.

Chapter 6

Epilogue

In the preceding chapters, four studies were presented that addressed the hypothesis that asymmetries in the performance of rhythmic isofrequency bimanual performance (e.g., the phase lead of the dominant limb) result from asymmetries in the strength of the interactions between the participating limbs. This hypothesis was proposed in previous studies that examined the effects of both handedness and asymmetries in attentional focus. Unfortunately, however, those studies were typically focused on the collective behavior (i.e., the relative phasing between the limbs), and/or did not address the alleged underlying asymmetry in coupling strength head-on. Using novel experimental approaches (both in terms of manipulations and analyses), the work in this thesis revealed that the movements of the two limbs indeed influenced each other to different degrees as a function of handedness and laterally focused attention. However, the asymmetries in coupling strength that were associated with these two factors appeared to affect the relative phasing between the limbs in essentially different ways.

In Chapters 2-4, analysis of the relative phase dynamics was complemented with examination of the phase adaptations made by both limbs during a variety of transient stages of coordination. In particular, using graded measures of phase adaptation, we examined the relative contribution of each limb to spontaneous (Chapter 2) and voluntary (Chapter 3) switches between coordination patterns, as well as to the re-establishment of the coordination pattern in response to a mechanical perturbation of one of the limbs (Chapters 2 and 4). Chapters 2 and 3 specifically examined the effects of handedness by considering both right-handers and left-handers. In conformity with previous reports, the dominant limb was slightly leading the nondominant limb in time (see also Chapters 4 and 5). A novel, yet theoretically predicted, finding was that these phase shifts were accompanied by a handedness-related asymmetry in interlimb coupling strength in that, during transient behavior, the nondominant limb was more strongly influenced by the dominant limb than vice versa. This asymmetry in coupling strength was more pronounced for right-handers than for left-handers. Similar handedness-related coupling asymmetries were reported in Chapter 4. Thus, the results of Chapters 2-4 provided clear support for the contention that the typical phase lead of the dominant limb results from an asymmetry in coupling strength. In addition, Chapter 3 indicated that this ‘intrinsic’ handedness-related effect may be modulated by intentional processes

associated with voluntary switches between coordination patterns, thereby underscoring that the asymmetry in coupling strength is not fixed but adaptive.

Besides the influence of handedness on the interlimb interactions, Chapter 4 demonstrated that, as predicted, focusing attention on either limb had a similar effect on the asymmetry in coupling strength. Initially, this was taken as support for the proposition that effects of handedness in bimanual coordination may actually be reflections of an attentional bias (Peters, 1989, 1994). However, even though attentional focus modulated the asymmetry in coupling strength as predicted, the phase lead of the dominant limb decreased rather than increased when this limb was attended. This unexpected finding was explained by the accompanying observation that the attended limb moved with a larger amplitude than the unattended limb, which, theoretically, results in a phase lead of the limb performing the smallest amplitude. The latter relation was subsequently confirmed by the empirical results of Experiment 1 in Chapter 5. Nevertheless, Chapter 5 provided no compelling support for the assertion that focusing attention on either limb affected the relative phase dynamics through modulation of the asymmetry in the interlimb coupling strength.

Despite the attentional modulation of the asymmetry in coupling strength (as observed in Chapter 4), no effect of attentional focus on coordinative stability was found in Chapters 4 and 5. These findings were inconsistent with the prediction based on the asymmetric potential proposed by Treffner and Turvey (1995; i.e., Equation 2.1) that coordinative stability is enhanced by an asymmetry in interlimb coupling strength. In retrospect, however, this is not surprising. That is, although asymmetric attentional focus did affect the asymmetry in coupling strength in the predicted direction (Chapter 4), this did not result in a shift in the relative phasing between the limbs (Chapter 5). Hence, focusing attention on either limb did not influence the coordination dynamics according to the proposed potential (Equation 2.1). As a consequence, the corresponding effects on the stability of relative phasing may no longer be expected either. The absence of both predicted effects (i.e., regarding the phase shift and coordinative stability, respectively) lends further support to the present interpretation that the observed asymmetric effects of laterally focused attention on the relative phase dynamics were *not* mediated by an asymmetry in coupling strength.

In summary, although the identified effects of handedness and attentional focus on the asymmetry in coupling strength were comparable, these two factors

were shown to have distinct influences at the level of the collective behavior (i.e., the relative phase dynamics). It was emphasized that this level of analysis requires complementary analyses at the level of the individual components (here: regarding movement amplitude) and the coupling between them, in order to adequately interpret the observed behavioral phenomena. Furthermore, the discrepancy between the effects of handedness and asymmetric attentional focus did not support the suggested relation between these two factors in bimanual coordination (Peters, 1989, 1994), which served as a starting point for the research reported in Chapters 4 and 5, as well as for other studies (e.g., Amazeen, Amazeen, Treffner, & Turvey, 1997). This calls for (re)considerations of the theoretical and functional significance of the asymmetry in coupling strength, which are discussed in the following sections.

Handedness-related asymmetry in coupling strength

The results of Chapters 2 and 3 corroborated the prevailing interpretation that the commonly observed phase lead of the dominant limb is an expression of a handedness-related asymmetry in coupling strength (Peper, Daffertshofer, & Beek, 2004; Treffner & Turvey, 1995). Although the experiments in question involved bimanual tasks in which the subtasks assigned to the two limbs were identical, it is conceivable that the asymmetry in coupling strength is advantageous for bimanual tasks in general. Since in everyday bimanual tasks the dominant hand usually performs the more demanding subtask, it is reasonable to assume that its performance ‘dictates’ to some extent the subordinate actions of the nondominant hand. This aspect of bimanual coordination is likely to be most pronounced if the dominant hand has a stronger influence on the nondominant hand than vice versa, as indeed was found to be the case.

The preceding discussion is reminiscent of findings in studies of multifrequency coordination indicating that the timing of the ‘slow’ hand is integrated into the leading temporal structure of the ‘fast’ hand (e.g., Summers, Rosenbaum, Burns, & Ford, 1993; Summers & Kennedy, 1992; Summers & Pressing, 1994). Also in this situation an asymmetry in coupling strength appears to subserve an asymmetry in the functional dependencies between the hands. Although effects of handedness in these tasks have been reported (Byblow, Bysouth-Young, Summers, & Carson, 1998; Summers, Davis, &

Byblow, 2002; see also Peters, 1981, 1985), it appears that the asymmetry in coupling with regard to the subtask disparity is more prevailing than that of handedness (see Peper, Beek, & Van Wieringen, 1995a, 1995c; Verheul & Geuze, 2003). This suggests that the asymmetry in coupling strength may vary as a function of the subtask requirements, but also that the handedness-related asymmetry may be beneficial when the nondominant limb performs a subordinate role and its movements are attuned to those of the dominant limb.

Asymmetries due to laterally focused attention

An intriguing finding was that the movement amplitudes of the limbs differed as a function of the direction of attention. It appeared that a limb oscillated at a larger amplitude when it was attended than when the other limb was attended (Chapter 4), even when the limbs' amplitudes were prescribed (Chapter 5). This attention-related amplitude dependency seems to be a common characteristic of repetitive movements (cf. Franz, 2004; Zelaznik & Lantero, 1996). In Chapters 4 and 5, this phenomenon provided an explanation for the observed shifts in the relative phasing between the limbs. A question that remains to be answered, however, is why different amplitudes were adopted when attention was asymmetrically divided over the two limbs. To address this question, it is useful to first recall a statement by Peters (1994):

“When the bimanual organization essentially assigns an equal status to the movements of the two hands . . . an asymmetry in the movements of the two hands is not expected. An asymmetry is expected only when there is a differential focusing of attention and an unequal allocation of ‘effort’ (Kahneman, 1973).” (p. 606)

From this point of view, focusing attention on the movements of a particular limb may involve a difference in the amount of effort that is dedicated to each limb's performance. It is possible that participants increased the amplitude of the movements of the attended limb (see Chapter 5) in order to improve control. After all, a larger movement amplitude generates stronger kinesthetic feedback signals (Kandel, Schwartz, & Jessell, 1991), which may thus enhance the control of the limb in question.

In Chapters 4 and 5 two basic methods to manipulate attentional focus were discussed. One of them entailed superimposition of additional task-related requirements for (one of) the limbs (e.g., Amazeen et al., 1997), while the other

involved instructions to visually attend the movements of one of the limbs and to concentrate on these movements (cf. Franz, 2004; Swinnen, Jardin, & Meulenbroek, 1996; Wuyts, Summers, Carson, Byblow, & Semjen, 1996). The latter method was used in the experiments reported in the present thesis. Although this manipulation avoided the potentially confounding influences of inherent task-related differences between the components, it did not allow for systematic control of variations in the *degree* of attentional asymmetry. Hence, one may question whether this instructional manipulation invoked sufficiently large differences in the amount of attention directed to each limb. In other words, could the absence of the expected effect of attentional focus on the relative phasing (see Chapter 5) be related to a deficiency in the effectiveness of the adopted manipulation?

The results presented in this thesis indicate that this was not the case, because distinct effects of attentional focus were observed. Manipulation of attentional focus affected both the asymmetry in coupling strength and the movement amplitude of each limb (Chapters 4 and 5). Moreover, attentional focus affected the relative phasing, which appeared to be induced by the attention-related amplitude difference. Additionally, in the study presented in Chapter 4, performance of the attended limb was slightly more consistent in the temporal domain¹⁵ (although this result was not reported), suggesting a difference in the amount of attention that was invested in the performance of each of the subtasks. In sum, the observed effects of attentional focus indicate that the manipulation of attention was effective. Consistent with the conclusions of Wuyts et al. (1996), the results of Chapters 4 and 5 suggest that attentional asymmetries affect the coordination dynamics primarily through attention-related differences between the dynamics of the two oscillating components.

¹⁵ In particular, repeated measures ANOVAs with the factors limb (D, ND) and attention (AttD, AttND) performed on the standard deviation of the movement frequency (SD_f) of each limb, revealed a significant Limb \times Attention interaction, $F(1, 19) = 21.19$, $p < .001$, $f = 0.92$. Post-hoc simple effects analysis revealed that for the D limb, SD_f was larger when the ND limb was attended (mean $SD_f = 0.052$ Hz [AttD]; 0.054 Hz [AttND]), while for the ND limb SD_f was larger when the D limb was attended (mean $SD_f = 0.054$ [AttD]; 0.052 [AttND]).

Coupling vs. component dynamics

In this thesis, substantial support was obtained for the notion that a handedness-related asymmetry in the degree to which the limbs influence each other results in an asymmetry in the relative phase dynamics (Treffner & Turvey, 1995), in accordance with the derivation presented by Peper, Daffertshofer, and Beek (2004; see Chapter 2). This asymmetry was also found to be affected by laterally focused attention, but, contrary to theoretical predictions, the so induced asymmetry in coupling strength did not appear to affect the relative phasing between the limbs. Moreover, asymmetric attentional focus also induced a difference between the limbs with respect to their movement amplitudes. Based on this combination of results, it was therefore suggested in Chapter 5 that an amplitude disparity between the limbs may induce an asymmetry in the degree to which they influence each other. This is a plausible inference, given the adopted theoretical framework, as will be elucidated next.

For this purpose, it is necessary to briefly consider the system of coupled oscillators that underlies the dynamics of the relative phase between these oscillators (i.e., the HKB model; Haken, Kelso, & Bunz, 1985). In this autonomous system, the movements of the individual limbs are modeled as two self-sustaining limit-cycle oscillators which are coupled as a function of the state variables (i.e., position x and velocity \dot{x}) of both oscillators, following the general expression

$$\ddot{x}_1 + f_1(x_1, \dot{x}_1) = I_{12, \alpha_1, \beta_1}(x_1, x_2, \dot{x}_1, \dot{x}_2) \quad [6.1a]$$

$$\ddot{x}_2 + f_2(x_2, \dot{x}_2) = I_{21, \alpha_2, \beta_2}(x_2, x_1, \dot{x}_2, \dot{x}_1) \quad [6.1b]$$

In Equations 6.1, x_i , \dot{x}_i , and \ddot{x}_i ($i = 1$ or 2) reflect the position, velocity, and acceleration of the individual oscillators, respectively; the left hand sides describe the equations of motion of the individual oscillators; the functions I_{12} and I_{21} describe the coupling between the two oscillators, with the parameters α_i and β_i determining the degree to which one oscillator is coupled to the other (i.e., through its state variables x_i and \dot{x}_i ; Haken et al., 1985).

Derivation of the relative phase dynamics of this model (with specific functional forms for both the component oscillators and the coupling between them), revealed that the coupling strength depends on 1) the coupling parameters α_i and β_i , and 2) the amplitudes of the individual oscillators. (For the full

equations of the model and the subsequent derivation of the amplitude-dependent coupling, the interested reader is referred to Haken et al., 1985; see also Peper & Beek, 1999.) As a consequence, an asymmetry in the strength of coupling may be induced through a difference between I_{12} and I_{21} in terms of the coupling parameters α_i and β_i (assuming that the form of the coupling functions is identical in both directions; cf. Haken et al., 1985, see also Chapter 2), but also through systematic differences between the oscillators with regard to their amplitudes. Although previous studies provided little evidence for such an amplitude-dependent coupling (Peper & Beek, 1998a, 1998b, 1999; Post, Peper, & Beek, 2000, but see also Kudo, Park, Kay, & Turvey, 2006), the relation between amplitude disparity and asymmetric coupling strength, as postulated in Chapter 5, is fully consistent with the HKB model. Hence, examination of the effects of amplitude disparities on the coupling strength asymmetry may shed light on the current discussion whether interlimb coupling strength, and hence coordinative stability, depends on movement amplitudes (e.g., Kudo et al., 2006; Peper & Beek, 1999).

These considerations underscore the intricate relation between the behavior (or control) of the individual limbs and the coupling between them in bimanual coordination. This relation is also a central theme in the neurophysiological literature on bimanual coordination. The current consensus is that bimanual control is achieved through a widely dispersed network of neural processes (e.g. Cardoso de Oliveira, 2002; Carson, 2005; Donchin, Cardoso de Oliveira, & Vaadia, 1999; Swinnen, 2002), in which coupling processes are intimately connected to unimanual control processes. For instance, entrainment effects based on the afferent feedback of the contralateral limb are more pronounced for larger movement amplitudes of the latter limb (Ridderikhoff, Peper, & Beek, 2005), indicating that this form of interlimb interaction depends on actual performance characteristics of the individual limbs.

Because theoretically (the asymmetry in) the degree to which the limbs influence each other depends on both the movement amplitudes of the individual limbs and the processes involved in the coupling between them, some caution is in order when interpreting indications of asymmetries in coupling strength. The designs and analyses presented in this thesis were instrumental in dissociating the influences of handedness and asymmetric attentional focus on the asymmetry in coupling strength. In particular, the absence of an amplitude

disparity in Chapter 2 (see Footnote 11) indicates that the handedness-related asymmetry in coupling strength is not induced by a difference between the oscillating components, but that it stems from an asymmetry in the coupling parameters α_i and β_i in I_{12} and I_{21} (Equations 6.1). Thus, the results presented in the present thesis suggest that the observed attention-related asymmetry in coupling strength resulted from an asymmetry in movement amplitude, whereas handedness affected the interaction processes as such. Importantly, the empirical dissociation of both factors militated against Peters' suggestion that handedness effects are simply reflections of an attentional bias.

In sum, according to Equation 6.1 and the subsequent discussion, the individual performance of each limb during a rhythmic bimanual task is affected by the coupling influences stemming from the other limb, while (asymmetries in) the strength of this coupling is partly dependent on (differences between) the characteristics of the limbs' movements. Although this issue may seem trivial at first glance, it offers new entry points for the study of the interlimb interactions (and their neurophysiological underpinnings) during rhythmic bimanual coordination. In this respect, the insights gained in the present thesis may serve as a starting point for future research, aimed at delineating the influence of component dynamics on the interlimb coupling and their corresponding influences on the relative phase dynamics. This may lead to new predictions regarding the functional significance of an asymmetry in coupling strength that can be examined for the performance of a variety of rhythmic bimanual tasks requiring coordination between two dissimilar subtasks (cf. Chapter 1). A first step in this respect may be taken by testing the hypothesis that the limb moving at a smaller amplitude is more strongly influenced by the limb performing the larger amplitude than vice versa (see Chapter 5).

Coda

Bimanual coordination is characterized by interactions between the limbs. The work presented in this thesis shows that crucial information about the influences of these interlimb interaction processes may be gained in adequately designed studies of rhythmic isofrequency coordination. Three main conclusions stood out in particular. First, the experiments identified distinct asymmetries in coupling strength (i.e., differences in the degree to which the limbs influence each other), which appeared to result either from asymmetries in the gain of the

Epilogue

coupling processes themselves, or from differences between the movement characteristics of the two individual components. Second, the experiments revealed that handedness and laterally focused attention have distinct and irreducible effects on bimanual coordination. Finally, the study as a whole demonstrated that besides analysis of the collective behavior (i.e., the relative phase dynamics), complementary levels of analysis are essential to fully capture the intricate relation between interlimb coupling and coordinative stability.

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.
- Amunts, K., Schlaug, G., Schleicher, A., Steinmetz, H., Dabringhaus, A., Roland, P. E., et al. (1996). Asymmetry in the human motor cortex and handedness. *NeuroImage*, *4*, 216-222.
- Bagesteiro, L. B., & Sainburg, R. L. (2002). Handedness: Dominant arm advantages in control of limb dynamics. *Journal of Neurophysiology*, *88*, 2408-2421.
- 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. (1989). *Juggling dynamics*. Amsterdam: Free University Press.
- Beek, P. J., & Beek, W. J. (1988). Tools for constructing dynamical models of rhythmic movement. *Human Movement Science*, *7*, 301-342.
- Beek, P. J., Peper, C. E., & Stegeman, D. F. (1995). Dynamical models of movement coordination. *Human Movement Science*, *14*, 573-608.
- 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.
- Beek, P. J., Turvey, M. T., & Schmidt, R. C. (1992). Autonomous and nonautonomous dynamics of coordinated rhythmic movements. *Ecological Psychology*, *3*, 65-95.
- Buchanan, J. J., Park, J. H., & Shea, C. H. (2006). Target width scaling in a repetitive aiming task: Switching between cyclical and discrete units of action. *Experimental Brain Research*, *175*, 710-725.
- 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., Bysouth-Young, D. F., & Summers, J. J. (1999). Stabilisation of bimanual coordination through visual coupling. *Human Movement Science*, *18*, 281-305.
- 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., & Goodman, D. (1994). Performance asymmetries in multifrequency coordination. *Human Movement Science*, *13*, 147-174.
- 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.

References

- Cardoso de Oliveira, S. (2002). The neuronal basis of bimanual coordination: Recent neurophysiological evidence and functional models. *Acta Psychologica, 110*, 139-159.
- Carson, R. G. (1993). Manual asymmetries: Old problems and new directions. *Human Movement Science, 12*, 479-506.
- Carson, R. G. (1996). Neuromuscular-skeletal constraints upon the dynamics of perception-action coupling. *Experimental Brain Research, 110*, 99-110.
- Carson, R. G. (2005). Neural pathways mediating bilateral interactions between the upper limbs. *Brain Research Reviews, 49*, 641-662.
- 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.
- Carson, R. G., Byblow, W. D., & Goodman, D. G. (1994). The dynamical substructure of bimanual coordination. In S. Swinnen, H. Heuer, J. Massion & P. Casaer (Eds.), *Interlimb coordination: Neural, dynamical, and cognitive constraints* (pp. 319-337). San Diego: Academic Press.
- Carson, R. G., Goodman, D., Kelso, J. A. S., & Elliott, D. (1996). Phase transitions and critical fluctuations in rhythmic coordination of ipsilateral hand and foot. *Journal of Motor Behavior, 28*, 56-57.
- Carson, R. G., Thomas, J., Summers, J. J., Walters, M. R., & Semjen, A. (1997). The dynamics of bimanual circle drawing. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology, 50*, 664-683.
- Cattaert, D., Semjen, A., & Summers, J. J. (1999). Simulating a neural cross-talk model for between-hand interference during bimanual circle drawing. *Biological Cybernetics, 81*, 343-358.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences*. Hillsdale, NJ: 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.
- Debaere, F., Wenderoth, N., Sunaert, S., Van Hecke, P., & Swinnen, S. P. (2004). Changes in brain activation during the acquisition of a new bimanual coordination task. *Neuropsychologia, 42*, 855-867.
- 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.
- Deutsch, D. (1983). The generation of 2 isochronous sequences in parallel. *Perception & Psychophysics, 34*, 331-337.
- Donchin, O., Cardoso de Oliveira, S., & Vaadia, E. (1999). Who tells one hand what the other is doing: The neurophysiology of bimanual movements. *Neuron, 23*, 15-18.
- Donker, S. F., & Beek, P. J. (2002). Interlimb coordination in prosthetic walking: Effects of asymmetry and walking velocity. *Acta Psychologica, 110*, 265-288.
- Fink, P. W., Foo, P., Jirsa, V. K., & Kelso, J. A. S. (2000). Local and global stabilization of coordination by sensory information. *Experimental Brain Research, 134*, 9-20.
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology, 47*, 381-391.

- Franz, E. A. (1997). Spatial coupling in the coordination of complex actions. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology*, *50*, 684-704.
- 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., Eliassen, J. C., Ivry, R. B., & Gazzaniga, M. S. (1996). Dissociation of spatial and temporal coupling in the bimanual movements of callosotomy patients. *Psychological Science*, *7*, 306-310.
- 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. (1996). Extending the HKB model of coordinated movement to oscillators with different eigenfrequencies. *Biological Cybernetics*, *74*, 21-30.
- Gerloff, C., & Andres, F. G. (2002). Bimanual coordination and interhemispheric interaction. *Acta Psychologica*, *110*, 161-186.
- 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.
- Guiard, Y. (1993). On Fitts' and Hooke's laws: Simple harmonic movement in upper-limb cyclical aiming. *Acta Psychologica*, *82*, 139-159.
- 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.
- Haken, H., Peper, C. E., Beek, P. J., & Daffertshofer, A. (1996). A model for phase transitions in human hand movements during multifrequency tapping. *Physica D*, *90*, 179-196; *92*, 260 (erratum).
- 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.
- Heuer, H., Spijkers, W., Kleinsorge, T., Van der Loo, H., & Steglich, C. (1998). The time course of cross-talk during the simultaneous specification of bimanual movement amplitudes. *Experimental Brain Research*, *118*, 381-392.
- 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.
- Kagerer, F. A., Summers, J. J., & Semjen, A. (2003). Instabilities during antiphase bimanual movements: Are ipsilateral pathways involved? *Experimental Brain Research*, *151*, 489-500.
- Kahneman, D. (1973). *Attention and effort*. Englewood Cliffs, NJ: Prentice-Hall.
- Kandel, E. R., Schwartz, J. H., & Jessell, T. M. (1991). *Principles of neural science* (3rd ed.). London: Prentice Hall International.

References

- Kay, B. A., Kelso, J. A., 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. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge, MA: MIT press.
- Kelso, J. A. S. (1984). Phase-transitions and critical behavior in human bimanual coordination. *American Journal of Physiology*, *246*, 1000-1004.
- Kelso, J. A., 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, NJ: Erlbaum.
- Kelso, J. A. S., & Jeka, J. J. (1992). Symmetry-breaking dynamics of human multilimb coordination. *Journal of Experimental Psychology-Human Perception and Performance*, *18*, 645-668.
- Kelso, J. A. S., Scholz, J. P., & Schöner, G. (1988). Dynamics governs switching among patterns of coordination in biological movement. *Physics Letters A*, *134*, 8-12.
- Keppel, G. (1991). *Design and analysis: A researcher's handbook* (3rd ed.). Upper Saddle River, NJ: 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.
- Kobayashi, M., Hutchinson, S., Schlaug, G., & Pascual-Leone, A. (2003). Ipsilateral motor cortex activation on functional magnetic resonance imaging during unilateral hand movements is related to interhemispheric interactions. *NeuroImage*, *20*, 2259-2270.
- Kopell, N. (1988). Toward a theory of modelling central pattern generators. In A. H. Cohen, S. Rossignol, & S. Grillner (Eds.), *Neural control of rhythmic movements in vertebrates* (pp. 369-413). New York: Wiley Interscience.
- Kudo, K., Park, H., Kay, B. A., & Turvey, M. T. (2006). Environmental coupling modulates the attractors of rhythmic coordination. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 599-609.
- Kugler, P.N., Kelso, J.A.S., & Turvey, M.T. (1980). Coordinative structures as dissipative structures I: Theoretical lines of convergence. In G.E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 3- 47). Amsterdam: North Holland.
- Lee, T. D., Almeida, Q. J., & Chua, R. (2002). Spatial constraints in bimanual coordination: influences of effector orientation. *Experimental Brain Research*, *146*, 205-212.
- Lewis, G. N., & Byblow, W. D. (2004). Bimanual coordination dynamics in poststroke hemiparetics. *Journal of Motor Behavior*, *36*, 174-188.
- Mardia, K. V. (1972). *Statistics of directional data*. London: Academic Press.
- Marteniuk, R. G., Mackenzie, C. L., & Baba, D. M. (1984). Bimanual movement control: information processing and interaction effects. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology*, *36*, 335-365.
- Maslovat, D., Chua, R., & Franks, I. M. (2006). Anchoring strategies for learning a bimanual coordination pattern. *Journal of Motor Behavior*, *38*, 101-117.
- McManus, I. C. (2002). *Right hand, left hand: The origins of asymmetry in brains, bodies, atoms and cultures*. London: Weidenfeld & Nicolson.
- McManus, I. C., Porac, C., Bryden, M. P., & Boucher, R. (1999). Eye-dominance, writing hand, and throwing hand. *Laterality*, *4*, 173-192.

- Mechner, F., Kerzel, D., Knoblich, G., & Prinz, W. (2001). Perceptual basis of bimanual coordination. *Nature*, *414*, 69-73.
- Mottet, D., & Bootsma, R. J. (1999). The dynamics of goal-directed rhythmical aiming. *Biological Cybernetics*, *80*, 235-245.
- Nathan, P. W., Smith, M. C., & Deacon, P. (1990). The corticospinal tracts in man: Course and location of fibers at different segmental levels. *Brain*, *113*, 303-324.
- Netz, J., Ziemann, U., & Homberg, V. (1995). Hemispheric asymmetry of transcallosal inhibition in man. *Experimental Brain Research*, *104*, 527-533.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97-113.
- Olney, S.J., & Richards, C. (1996). Hemiparetic gait following stroke. Part I: Characteristics. *Gait & Posture*, *4*, 136-148.
- 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. (1998a). Distinguishing between the effects of frequency and amplitude on interlimb coupling in tapping a 2:3 polyrhythm. *Experimental Brain Research*, *118*, 78-92.
- Peper, C. E., & Beek, P. J. (1998b). Are frequency-induced transitions in rhythmic coordination mediated by a drop in amplitude? *Biological Cybernetics*, *79*, 291-300.
- Peper, C.E., & Beek, P.J. (1999). Modeling rhythmic interlimb coordination: The roles of movement amplitude and time delays. *Human Movement Science*, *18*, 263-280.
- 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). Frequency-induced transitions in bimanual tapping. *Biological Cybernetics*, *73*, 301-309.
- Peper, C. E., Beek, P. J., & Van Wieringen, P. C. W. (1995c). 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. (2004). 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: A multidisciplinary approach* (pp. 297-323). Amsterdam: Kluwer.
- Peper, C. E., Nooij, S. A. E., & van Soest, A. J. (2004). Mass perturbation of a body segment: 2. Effects on interlimb coordination. *Journal of Motor Behavior*, *36*, 425-441.
- Peper, C. E., Ridderikhof, A., Daffertshofer, A., & Beek, P. J. (2004). Explanatory limitations of the HKB model: Incentives for a two-tiered model of rhythmic interlimb coordination. *Human Movement Science*, *23*, 673-697.
- Peters, M. (1980). Why the preferred hand taps more quickly than the non-preferred hand: Three experiments on handedness. *Canadian Journal of Psychology-Revue Canadienne De Psychologie*, *34*, 62-71.
- Peters, M. (1981). Attentional asymmetries during concurrent bimanual performance. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology*, *33*, 95-103.
- Peters, M. (1985). Constraints in the performance of bimanual tasks and their expression in unskilled and skilled subjects. *Quarterly Journal of Experimental Psychology Section a: Human Experimental Psychology*, *37*, 171-196.
- Peters, M. (1989). Do feedback processing, output variability, and spatial complexity account for manual asymmetries? *Journal of Motor Behavior*, *21*, 151-155.

References

- 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 Press.
- 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.
- Peters, M., & Servos, P. (1989). Performance of subgroups of left-handers and right-handers. *Canadian Journal of Psychology-Revue Canadienne de Psychologie*, *43*, 341-358.
- Post, A. A., Peper, C. E., & Beek, P. J. (2000). 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. (2000). Relative phase dynamics in perturbed interlimb coordination: Stability and stochasticity. *Biological Cybernetics*, *83*, 443-459.
- Prassas, S., Thaut, M., McIntosh, G., & Rice, R. (1997). Effect of auditory rhythmic cueing on gait kinematic parameters of stroke patients. *Gait & Posture*, *6*, 218-223.
- Provins, K. A. (1997). Handedness and speech: A critical reappraisal of the role of genetic and environmental factors in the cerebral lateralization of function. *Psychological Review*, *104*, 554-571.
- Ridderikhoff, A., Peper, C. E., & Beek, P. J. (2005). Unraveling interlimb interactions underlying bimanual coordination. *Journal of Neurophysiology*, *94*, 3112-3125.
- Ridderikhoff, A., Peper, C. E., & Beek, P. J. (2006). Bilateral phase entrainment by movement-elicited afference contributes equally to the stability of in-phase and antiphase coordination. *Neuroscience Letters*, *399*, 71-75.
- 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.
- Roerdink, M., Lamoth, C. J. C., Kwakkel, G., Van Wieringen, P. C. W., & Beek, P. J. (in press). Gait coordination following stroke: Effects of walking velocity and auditory pacing. *Physical Therapy*.
- Roerdink, M., Peper, C. E., & Beek, P. J. (2005). Effects of correct and transformed visual feedback on rhythmic visuo-motor tracking: Tracking performance and visual search behavior. *Human Movement Science*, *24*, 379-402.
- Rogers, M. A., Bradshaw, J. L., Cunnington, R. C., & Phillips, J. G. (1998). Inter-limb coupling in coordinated bimanual movement: Attention and asymmetries. *Laterality*, *3*, 53-75.
- 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.
- Schauer, M., & Mauritz, K. H. (2003). Musical motor feedback (MMF) in walking hemiparetic stroke patients: randomized trials of gait improvement. *Clinical Rehabilitation*, *17*, 713-722.
- 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.
- Schmidt, R. C., & Turvey, M. T. (1995). Models of interlimb coordination-equilibria, local analyses, and spectral patterning - Comment on Fuchs and Kelso (1994). *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 432-443.

- Scholz, J. P., & Kelso, J. A. S. (1990). Intentional switching between patterns of bimanual coordination depends on the intrinsic dynamics of the patterns. *Journal of Motor Behavior*, *22*, 98-124.
- 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., Cassidy, M. J., & Brown, P. (2003). The importance of the dominant hemisphere in the organization of bimanual movements. *Human Brain Mapping*, *18*, 296-305.
- 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.
- Serrien, D. J., & Swinnen, S. P. (1999). Intentional switching between behavioral patterns of homologous and nonhomologous effector combinations. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 1253-1267.
- 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. (1994). Hand preference, practice order, and spatial assimilations in rapid bimanual movement. *Journal of Motor Behavior*, *26*, 123-134.
- 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.
- Singh, L. N., Higano, S., Takahashi, S., Kurihara, N., Furuta, S., Tamura, H., et al. (1998). Comparison of ipsilateral activation between right and left handers: A functional MR imaging study. *NeuroReport*, *9*, 1861-1866.
- Spijkers, W., & Heuer, H. (1995). Structural constraints on the performance of symmetrical bimanual movements with different amplitudes. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology*, *48*, 716-740.
- Steenbergen, B., Hulstijn, W., de Vries, A., & Berger, M. (1996). Bimanual movement coordination in spastic hemiparesis. *Experimental Brain Research*, *110*, 91-98.
- 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.
- Sternad, D., Turvey, M. T., & Schmidt, R. C. (1992). Average phase difference theory and 1:1 phase entrainment in interlimb coordination. *Biological Cybernetics*, *67*, 223-231.
- Steyvers, M., Verschueren, S. M. P., Levin, O., Ouamer, M., & Swinnen, S. P. (2001). Proprioceptive control of cyclical bimanual forearm movements across different movement frequencies as revealed by means of tendon vibration. *Experimental Brain Research*, *140*, 326-334.
- Stinear, J. W., & Byblow, W. D. (2004). An interhemispheric asymmetry in motor cortex disinhibition during bimanual movement. *Brain Research*, *1022*, 81-87.
- 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.

References

- Summers, J. J., & Kennedy, T. M. (1992). Strategies in the production of a 5:3 polyrhythm. *Human Movement Science, 11*, 101-112.
- Summers, J. J., & Pressing, J. (1994). Coordinating the two hands in polyrhythmic tapping. In S. P. Swinnen, H. Heuer, J. Massion, & P. Casaer (Eds.), *Interlimb coordination: Neural, dynamical, and cognitive constraints* (pp. 571–593). San Diego: Academic Press.
- Summers, J. J., Rosenbaum, D. A., Burns, B., & Ford, S. (1993). Production of polyrhythms. *Journal of Experimental Psychology: Human Perception and Performance, 19*, 416–428.
- Swinnen, S. P. (2002). Intermanual coordination: From behavioural principles to neural-network interactions. *Nature Reviews Neuroscience, 3*, 348-359.
- Swinnen, S. P., Dounskaia, N., Levin, O., & Duysens, J. (2001). Constraints during bimanual coordination: the role of direction in relation to amplitude and force requirements. *Behavioural Brain Research, 123*, 201-218.
- 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.
- Swinnen, S. P., Jardin, K., Verschueren, S., Meulenbroek, R., Franz, L., Dounskaia, N., et al. (1998). Exploring interlimb constraints during bimanual graphic performance: Effects of muscle grouping and direction. *Behavioural Brain Research, 90*, 79-87.
- Swinnen, S. P., Young, D. E., Walter, C. B., & Serrien, D. J. (1991). Control of asymmetrical bimanual movements. *Experimental Brain Research, 85*, 163-173.
- Tomatsu, S., & Ohtsuki, T. (2005). The effect of visual transformation on bimanual circling movement. *Experimental Brain Research, 166*, 277-286.
- 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.
- Tuller, B., & Kelso, J. A. S. (1989). Environmentally-specified patterns of movement coordination in normal and split-brain subjects. *Experimental Brain Research, 75*, 306-316.
- Uitenbroek, D. G. (1997). *SISA Binomial*. Southampton: D.G. Uitenbroek. Retrieved January 11, 2006, from the World Wide Web: <http://home.clara.net/sisa/binomial.htm>
- Van Mourik, A., Daffertshofer, A., & Beek, P. J. (2007). Extracting dynamics from the stochastics of rhythmic forearm movements. Unpublished manuscript.
- Van Riper, C. (1935). The quantitative measurement of laterality. *Journal of Experimental Psychology, 8*, 372-382.
- Verheul, M. H. G., & Geuze, R. H. (2003). 'Side-effects': Intrinsic and task-induced asymmetry in bimanual rhythmic coordination. *Experimental Brain Research, 152*, 185-197.
- Verheul, M. H. G., & Geuze, R. H. (2004). Bimanual coordination and musical experience: The role of intrinsic dynamics and behavioral information. *Motor Control, 8*, 270-291.
- Verschueren, S. M. P., Swinnen, S. P., Cordo, P. J., & Dounskaia, N. V. (1999). Proprioceptive control of multijoint movement: Bimanual circle drawing. *Experimental Brain Research, 127*, 182-192.

- 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.
- Volkman, J., Schnitzler, A., Witte, O. W., & Freund, H. J. (1998). Handedness and asymmetry of hand representation in human motor cortex. *Journal of Neurophysiology*, *79*, 2149-2154.
- Wuyts, I. J., Byblow, W. D., Summers, J. J., Carson, R. G., & Semjen, A. (1998). Intentional switching between patterns of coordination in bimanual circle drawing. In J. P. Piek (Ed.), *Motor control and human skill: a multidisciplinary perspective* (pp. 191-208). Champaign IL: Human Kinetics.
- 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.
- Wyke, M. (1971). Effects of brain lesions on performance of bilateral arm movements. *Neuropsychologia*, *9*, 33-42.
- Yamanishi, J. I., Kawato, M., & Suzuki, R. (1979). Studies on human finger tapping neural networks by phase-transition curves. *Biological Cybernetics*, *33*, 199-208.
- Yamanishi, J. I., Kawato, M., & Suzuki, R. (1980). Two Coupled oscillators as a model for the coordinated finger tapping by both hands. *Biological Cybernetics*, *37*, 219-225.
- Zanone, P. G., & Kelso, J. A. (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.

Summary

The majority of the manual tasks that we perform involve some degree of coordination between limb movements. In such instances of interlimb coordination the two limbs do not move independently, but interact. These interlimb interactions become readily apparent when simultaneously performing different (sub)tasks with each of the limbs, like patting the head with one hand and rubbing the tummy with the other. In the focal task of this thesis (i.e., rhythmic bimanual coordination with the two upper limbs moving at the same frequency) the interlimb interactions result in attraction to particular coordination patterns rendering them intrinsically stable. For this type of coordination, previous studies demonstrated that handedness and laterally focused attention (i.e., focusing on one limb at the expense of the other) induce asymmetries in the overall coordinative performance. These effects were accounted for by an asymmetric version of the well-known HKB-potential, which describes the stability properties of the phase difference between limbs (i.e., the relative phase dynamics) induced by the coupling between the limbs. Given these findings, handedness and laterally focused attention were proposed as potential sources of asymmetry in the interlimb interactions. The work reported in this thesis examines the relation between (the stability of) interlimb coordination and asymmetries in the strength of interlimb interactions.

The first experiment, presented in Chapter 2, examined the hypothesis that the effects of handedness on bimanual isofrequency coordination, in particular the phase advance of the dominant limb, result from an asymmetry in interlimb coupling strength with the nondominant limb being more strongly influenced by the dominant limb than vice versa. Phase adjustments in both limbs in response to mechanical perturbation of the bimanual coordination pattern and during frequency-induced phase transitions confirmed this hypothesis for both right- and left-handed participants. In the right-handers these adaptations were made predominantly by the nondominant limb in both situations, whereas this tendency did not reach significance in the left-handers, implying that the asymmetry in coupling strength was less pronounced in the latter group. In the right-handers, the degree of asymmetry also depended on movement frequency.

Chapter 3 reports an experiment in which right- and left-handers made voluntary switches from in-phase to antiphase coordination and vice versa, at four different frequencies. As in the study reported in Chapter 2, the results revealed that the intentional switches were primarily mediated by phase adaptations in the nondominant hand, indicating a handedness-related asymmetry in coupling strength. Again, the asymmetry was less pronounced in left-handers than in right-handers, albeit that in this study the asymmetry was significant for both groups of participants. Furthermore, the asymmetry was larger for switches from antiphase to in-phase coordination (i.e., in the same direction as spontaneous transitions) than for switches in the reverse direction, suggesting that (the expression of) the handedness-related asymmetry in coupling strength was weakened by intentional processes associated with the required voluntary switches.

In line with the suggestion of Peters (1989, 1994) that expressions of handedness in bimanual coordination reflect an inherent attentional bias, previous findings showed that attentional asymmetries affect bimanual coordination in a manner similar to handedness. Motivated by these studies, the experiment reported in Chapter 4 examined whether attentional asymmetries modulated the underlying asymmetry in coupling strength. Both left-handers and right-handers performed in-phase and antiphase coordination, while focusing attention on either limb. Using the same method as in Chapter 2 (i.e., mechanical perturbations), the degree to which the limbs were influenced by each other was determined. As in Chapter 2, the results revealed that the nondominant limb was more strongly affected by the dominant limb than vice versa. Moreover, consistent with Peters' proposition, the handedness-related asymmetry in coupling strength was reduced when attention was focused on the nondominant limb. In contrast to previous findings, however, the commonly observed phase lead of the dominant limb was decreased rather than increased when attention was focused on this limb. This unexpected result was explained in terms of the additional finding that attentional focus also induced a difference in amplitude between the limbs, which was argued to result in a difference in their respective preferred frequencies and, thus, in a phase advance of the limb moving with the smaller amplitude.

The validity of this explanation was examined in Chapter 5, which reports three experiments in which amplitude disparity and attentional focus were manipulated in a controlled fashion, both alone and in conjunction. Whereas

variations in amplitude disparity had the expected effects, the results revealed no compelling evidence for the suggestion that the effects of attentional asymmetry on relative phase dynamics are mediated by an asymmetry in coupling strength. These findings indicate that attentional focus affects interlimb coordination through differences between the dynamics of the two components (here: via amplitude disparity), thereby militating against Peters' suggestion that the effects of directed attention on interlimb coordination are comparable to those of handedness.

The final chapter discusses the thesis' main findings and implications. Although both handedness and asymmetric attentional focus were associated with an asymmetry in interlimb coupling strength, these asymmetries appeared to have distinct effects on interlimb coordination. This implies that previous applications of the prevailing dynamical model – that was developed to account for the effects of handedness on the relative phase dynamics – in the context of attentional asymmetries, were based on invalid assumptions. Furthermore, it is underscored that, theoretically, asymmetries in the strength of the interlimb interactions as such may reside in the coupling processes themselves, but may also result from differences between the limbs' movements. All in all, the thesis demonstrated that besides analysis of the collective behavior (i.e., the relative phase dynamics), complementary levels of analysis are essential to fully capture the intricate relation between interlimb coupling and coordinative stability.

Samenvatting

Asymmetrische koppelingssterkte tussen de ledematen bij ritmische bimanuele coördinatie

Tijdens de uitvoering van de meeste bimanuele taken worden de bewegingen van beide handen in meer of mindere mate op elkaar afgestemd. Dit betekent dat de handen niet onafhankelijk van elkaar bewegen, maar elkaar beïnvloeden. Deze zogenoemde tussenledemaatinteracties komen duidelijk naar voren wanneer we simultaan twee verschillende handbewegingen proberen uit te voeren, zoals het bekende ‘tikken op het hoofd en rondjes draaien op de buik’. Met de interacties tussen de ledematen als voornaamste aandachtspunt, richt dit proefschrift zich op bimanuele coördinatietaken waarbij de handen of armen ritmisch met hetzelfde tempo bewegen. Bij een dergelijke bimanuele taak zorgen de tussenledemaatinteracties ervoor dat bepaalde coördinatiepatronen gemakkelijk (stabiel) kunnen worden uitgevoerd, terwijl andere coördinatiepatronen heel wat oefening vereisen voordat zij ook maar enigszins stabiel kunnen worden uitgevoerd. Het meest stabiele gedrag wordt vertoond bij het simultaan heen en weer bewegen van de ledematen (in-fasecoördinatie), gevolgd door het alternerend heen en weer bewegen (tegenfasecoördinatie). Het Haken-Kelso-Bunz- of HKB-model beschrijft deze en andere coördinatieverschijnselen in termen van de relatieve fase tussen de twee bewegingen, gemodelleerd als niet-lineaire oscillatoren, waarbij de – eveneens niet-lineaire – koppeling tussen de ledematen een belangrijke rol speelt.

Hoewel de bewegingen van beide ledematen volgens het standaard HKB-model perfect symmetrisch zijn, hetgeen op het eerste gezicht ook zo lijkt te zijn, heeft een aantal studies aangetoond dat er veeleer sprake is van asymmetrie: de uitvoering van de coördinatiepatronen vertoont asymmetrieën als functie van handvoorkeur en het richten van de aandacht op een van de handen (zoals het licht doch systematisch voorlopen van de ene hand ten opzichte van de andere). Deze effecten konden worden beschreven door een aangepaste versie van het HKB-model, waarin de sterkte van de koppeling tussen de twee ledematen asymmetrisch werd voorgesteld in plaats van symmetrisch. Handvoorkeur en asymmetrisch gerichte aandacht werden aldus gepostuleerd als mogelijke bronnen van asymmetrie in de koppelingssterkte.

Daarnaast voorspelt dit model dat zo'n asymmetrie in de koppelingssterkte bevorderlijk is voor de stabiliteit van de coördinatie. In dit proefschrift wordt onderzocht of (de stabiliteit van) de uitvoering van de coördinatiepatronen inderdaad samenhangt met asymmetrieën in de sterkte van de interacties tussen de ledematen.

In het eerste experiment, beschreven in Hoofdstuk 2, wordt specifiek ingegaan op de hypothese dat effecten van handvoorkeur op bimanuele ritmische coördinatie – met name het licht voorlopen van de dominante hand – kunnen worden beschreven door een asymmetrie in de sterkte van de koppeling tussen de ledematen, waarbij de niet-dominante hand sterker wordt beïnvloed door de dominante hand dan omgekeerd. Hiertoe werd geanalyseerd hoe veranderingen in de tussenledemaatcoördinatie werden bewerkstelligd door aanpassingen in de fasering van de afzonderlijke ledematen. Zowel tijdens spontane overgangen tussen coördinatiepatronen (als gevolg van het geleidelijk opvoeren van het bewegingstempo) als na mechanische verstoringen bleek de fasering van de niet-dominante hand het meest te worden aangepast, conform de onderzoekshypothese. Dit gold voor rechtshandige proefpersonen en in mindere mate voor linkshandige proefpersonen (waarvoor het effect net niet significant was). Dit wijst op een minder uitgesproken asymmetrie in koppelingssterkte bij de linkshandigen. Voor de rechtshandigen bleek de mate van asymmetrie in de interacties afhankelijk te zijn van het bewegingstempo.

In Hoofdstuk 3 wordt een experiment gerapporteerd waarin rechts- en linkshandige proefpersonen intentioneel switchten van het in-fase- naar het tegenfasepatroon, en andersom. De resultaten waren vergelijkbaar met die van Hoofdstuk 2: ook wanneer men opzettelijk (in plaats van spontaan, zoals in Hoofdstuk 2) van coördinatiepatroon veranderde, kwam de overgang voornamelijk tot stand door faseveranderingen in de beweging van de niet-dominante hand, hetgeen duidt op een handvoorkeurgerelateerde asymmetrie in de koppelingssterkte. Ook hier was de asymmetrie minder uitgesproken voor linkshandigen dan voor rechtshandigen – deze keer was het effect echter significant voor beide groepen. Verder bleek dat de koppelingsasymmetrie sterker was wanneer men switchte van tegenfase naar in-fase (d.w.z., in dezelfde richting als spontane overgangen) dan in omgekeerde richting. Dit suggereert dat (het tot uitdrukking komen van) deze asymmetrie werd afgezwakt door cognitieve processen die samenhangen met het intentioneel switchen tussen coördinatiepatronen.

In Hoofdstuk 4 worden de effecten van het richten van de aandacht op een van beide ledematen onderzocht. Het uitgangspunt hierbij was het idee van Peters (1989, 1994) dat de bij bimanuele coördinatietaken gevonden effecten van handvoorkeur een gevolg zijn van het feit dat de meeste aandacht wordt gericht op de bewegingen van de dominante hand. In overeenstemming met dit idee hadden eerdere onderzoeken reeds aangetoond dat aandachtsgerelateerde asymmetrieën de uitvoering van bimanuele coördinatiepatronen op een vergelijkbare wijze beïnvloeden als handvoorkeur en derhalve (volgens deze studies) beschreven kunnen worden met hetzelfde asymmetrische model. In de betreffende studies waren de tussenledemaatinteracties als zodanig echter niet onderzocht. In Hoofdstuk 4 werd daarom onderzocht of het asymmetrisch richten van aandacht (d.w.z., op de dominante of niet-dominante ledemaat) de onderliggende asymmetrie in koppelingssterkte inderdaad in dezelfde richting moduleert als handvoorkeur. Zowel rechts- als linkshandige proefpersonen voerden in-fase- en tegenfasecoördinatiepatronen uit terwijl ze hun aandacht richtten op de dominante dan wel op de niet-dominante ledemaat. Zoals in Hoofdstuk 2, werd met behulp van mechanische verstoringen nagegaan in welke mate de twee ledematen elkaar beïnvloeden. Wederom werd gevonden dat de beweging van de niet-dominante ledemaat sterker werd beïnvloed door (een verstoring van) de beweging van de dominante ledemaat dan vice versa. Bovendien bleek dat, overeenkomstig de suggestie van Peters en de daaruit voortvloeiende voorspellingen, de handvoorkeurgerelateerde asymmetrie in koppelingssterke afnam wanneer de aandacht werd gericht op de niet-dominante ledemaat. In tegenstelling tot eerdere bevindingen bleek dat de gebruikelijke fasevoorsprong van de dominante ledemaat afnam in plaats van toenam wanneer de aandacht was gericht op deze ledemaat. Dit onverwachte resultaat kon echter worden verklaard aan de hand van een ander effect van het lateraal richten van de aandacht. Het bleek namelijk dat dit eveneens een uitwerking had op de uitgevoerde bewegingsamplitudes van de twee ledematen. De amplitude van de ledemaat, waarop de aandacht was gericht, was significant groter dan die van de andere ledemaat. Een verschil in amplitude impliceert een verschil in voorkeurstempo tussen de ledematen, wat theoretisch gezien leidt tot een fasevoorsprong van de beweging met de kleinste amplitude (uitgevoerd door de niet-geattendeerde ledemaat). Met andere woorden, gerichte aandacht heeft zowel invloed op de asymmetrie in koppelingssterkte als op de amplitude van de bewegingen van de afzonderlijke ledematen. Theoretisch gezien beïnvloeden

deze twee potentiële effecten (die elkaar overigens niet uitsluiten) de uiteindelijke uitvoering van het coördinatiepatroon in tegengestelde richting.

Om de bovenstaande hypothese verder te testen, werden drie experimenten uitgevoerd, die beschreven worden in Hoofdstuk 5, waarin de effecten van een amplitudeverschil en het richten van de aandacht zowel onafhankelijk van elkaar als in samenhang werden onderzocht. De resultaten van deze experimenten lieten zien dat een verschil tussen de twee ledematen met betrekking tot de uitgevoerde bewegingsamplitudes inderdaad leidde tot de verwachte effecten op de coördinatie (d.w.z., een fasevoorsprong van de ledemaat met de kleinste amplitude). Wanneer de bewegingsamplitudes werden gefixeerd, werd er echter geen duidelijke evidentie gevonden voor de hypothese dat de relatieve fasering wordt beïnvloed door een aandachtsgerelateerde asymmetrie in de koppelingssterkte. Deze bevindingen toonden aan dat het richten van de aandacht op een van de twee ledematen weliswaar de coördinatie tussen de ledematen beïnvloedt, maar dat dit veeleer komt door een aandachtsgerelateerd verschil tussen de beide ledematen (in dit geval een amplitudeverschil) dan door een asymmetrie in de koppelingssterkte. Dit is in tegenspraak met Peters' suggestie, omdat de effecten van lateraal gerichte aandacht op de bimanuele coördinatie niet vergelijkbaar bleken met die van handvoorkeur.

In Hoofdstuk 6, de epiloog, worden de belangrijkste bevindingen alsmede de implicaties van het gepresenteerde onderzoek besproken. De onderzoeksresultaten illustreren dat, naast de analyse van de coördinatie op het collectieve niveau (de relatieve fase), complementaire analyseniveaus (zoals de dynamica van de ledematen en hun interacties) nodig zijn om de complexe relatie tussen bimanuele koppeling en coördinatieve stabiliteit adequaat te doorgronden. Hoewel zowel handvoorkeur als lateraal gerichte aandacht bleek samen te hangen met een asymmetrie in de sterkte van de koppeling tussen de ledematen, bleek ook dat beide factoren een wezenlijk verschillende invloed hadden op de uitvoering van het bimanuele coördinatiepatroon. Deze bevinding is in strijd met de interpretatie dat de effecten van handvoorkeur en asymmetrisch gerichte aandacht op bimanuele coördinatie door hetzelfde asymmetrische dynamische model kunnen worden beschreven. Het onderzoek toont aan dat asymmetrieën in de sterkte van de interacties kunnen voortvloeien uit de koppelingsprocessen zelf, maar ook het resultaat kunnen zijn van verschillen tussen de bewegingen van de afzonderlijke ledematen.

Dankwoord

Voor u ligt het eindresultaat van vier jaar promotieonderzoek. Een proefschrift met mijn naam eronder. Ik mag zeggen dat ik best wel trots op mijzelf ben, maar ik ben ook trots op een heleboel anderen. Ik wil iedereen bedanken die mij (al dan niet bewust en op wat voor manier dan ook) heeft geholpen en ondersteund tijdens deze, voor mij bijzonder uitdagende periode. Een aantal mensen wil ik hier wat meer expliciet mijn dank betuigen.

Allereerst wil ik Peter Beek en Lieke Peper bedanken voor de kans die ze mij hebben geboden dit onderzoek te doen, alsmede voor de goede en prettige begeleiding die ik heb mogen genieten. Zonder jullie kennis, vaardigheid, inzet, en geduld was dit proefschrift niet tot stand gekomen. Peter, als promotor heb jij de vorderingen tijdens het project steeds goed onder de loep gehouden. Jouw inbreng, overzicht, kennis, en ervaring waren essentieel voor het welslagen van dit project, hetgeen voor mij gaandeweg steeds duidelijker naar voren kwam. Verder hoop ik ooit jouw vaardigheid in het je schriftelijk dan wel verbaal uitdrukken te kunnen benaderen: ik stond er versteld van hoe goed jij soms kon verwoorden wat ik eigenlijk bedoelde.

Lieke, ik kan me niet voorstellen hoe de afgelopen vier jaren zouden zijn gelopen zonder jou als dagelijks begeleider. De goede balans tussen begeleiden en samenwerken, je snelle replek op toegestuurde stukken en mailtjes, je enthousiaste opmerkingen en opbouwende kritische commentaar, en jouw (behoefte aan) duidelijkheid heb ik erg gewaardeerd en waren van cruciaal belang voor mijn functioneren in dit project. Jouw bijdrage aan dit proefschrift en aan mijn ontwikkeling als wetenschapper is daarom ook onmiskenbaar groot, alsook mijn dank daarvoor.

Bert Clairbois en Bert Coolen dank ik voor hun onmisbare technische ondersteuning bij dit onderzoek en alle (mentale) hulp bij (het weer opstarten van) de ABSA-meetopstelling. Ook wil ik Hans de Koning bedanken voor zijn enthousiaste en acute inzet bij het laatste experiment.

Een stimulerende en plezierige werkomgeving is minstens net zo belangrijk als de werkzaamheden zelf. Dank daarvoor aan alle collega's op de Faculteit der Bewegingswetenschappen, met name mijn (oud-) B656-kamergenoten Stefan van Drongelen, Sietske Aaldersberg en Gert Faber; neighbours Rita Ferraz de Oliveira, Olaf Binsch, and Floor Hettinga, and the

snoeppot; Martijn Niessen en Stella Donker, de treinreis van en naar Utrecht (inclusief de regelmatige vertragingen) werd een stuk aangenamer wanneer ik een van jullie tegenkwam op het station of in de coupé; Rolf van de Langenberg, Claudine Lamoth, Anke van Mourik, Nicolette van den Dikkenberg, Joost Dessing, Andreas Daffertshofer, Tjeerd Boonstra, Hemke van Doorn, Rob Withagen, Johan Koedijker, Paulion van Hof, Luc Selen, Alistair Vardy, John Stins, Niek van Ulzen, Arne Ridderikhoff: bedankt voor alle (inhoudelijke) gesprekken en al het andere daar omheen.

Johan, jou wil ik daarbij nog bedanken voor de broodnodige ‘anti RSI’ sparring-sessies op de 4^e. Deze waren zeer effectief om frustraties en tegenslagen weg te slaan, onze (wetenschappelijke) gedachten te ordenen – leuke dubbeltaak –, of om zomaar de gedachten even te verzetten. Hoe belangrijk dit eigenlijk was begint steeds meer tot me door te dringen.

Melvyn, met jou op de kamer was het bijna een tweede thuis. Niet alleen onze roots waren overeenkomstig, maar ook onze wetenschappelijke interesses en ideeën bleken soms akelig nauw aan elkaar verwant. Onze talloze (inhoudelijke) discussies, monologen en andere vormen van communicatie zijn van zeer grote waarde geweest voor dit proefschrift en zijn schrijver. It was very pleasant to make knowledge with you!

Bjorn, Tim en Harmen, mijn paranimfen. Helaas mogen er maar twee op het podium, maar jullie weten wel beter. Bedankt voor jullie reflectie en relativering aangaande mijn promotieonderzoek, maar ook voor alles wat daar totaal niets mee te maken heeft.

Henk en Ma(rry), bedankt voor jullie interesse en steun in alles wat ik doe. Het feit dat jullie altijd (zelfs in mindere tijden) voor me klaar staan en naar me willen luisteren (hoe moeilijk ik soms ook te volgen ben) betekent heel veel voor mij.

Tenslotte, lieve Marja. Zonder jouw aanmoediging, ondersteuning, en afleiding had ik het een stuk moeilijker gehad. Bedankt voor al je liefde, begrip, en geduld. (8!)

List of publications

Papers in international journals

De Poel, H. J., Peper, C. E., & Beek, P. J. (2007). Attentional asymmetry affects relative phase through amplitude disparity rather than asymmetric coupling. (*manuscript currently in revision*)

De Poel, H. J., Peper, C. E., & Beek, P. J. (in press). Laterally focused attention modulates asymmetric coupling in rhythmic interlimb coordination. *Psychological Research*.

De Poel, H. J., Peper, C. E., & Beek, P. J. (2007). Handedness-related asymmetry in coupling strength in bimanual coordination: Furthering theory and evidence. *Acta Psychologica*, 124, 209-237.

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.

Abstracts

De Poel, H.J., Peper, C.E., & Beek, P.J. (2006). Rhythmic bimanual coordination: Modulation through asymmetries in interlimb coupling and component dynamics. In: *Proceedings IFKB Meeting 2006* (p. 7). Amsterdam, the Netherlands.

De Poel, H.J., Peper, C.E., & Beek, P.J. (2006). Asymmetries in bimanual coordination: Effects of handedness, directed attention and amplitude. In: *Proceedings of the 9th European Workshop on Ecological Psychology* (p. 15). Groningen, the Netherlands.

De Poel, H.J., Peper, C.E., & Beek, P.J. (2005). Asymmetries caused by handedness and attention affect the coordination between the upper limbs. In: *Proceedings of the 10th Winter Conference of the Dutch Psychonomics Society (NVP)* (p. 43). Egmond aan Zee, the Netherlands.

Publications

De Poel, H.J., Peper, C.E., & Beek, P.J. (2005). Handedness-related asymmetries in bimanual coordination dynamics originate from an asymmetry in coupling strength. In: Heft, H., Marsh, K.L., & Rosenblum, L.D (Eds.), *Proceedings of the 13th International Conference on Perception and Action* (pp. 61-61). Monterey, CA, USA.

De Poel, H.J., & Peper, C.E. (2004). Are coordinative asymmetries due to handedness the result of asymmetrical coupling strength? In: Cesari, P. (Ed.), *Proceedings of the 8th European Workshop on Ecological Psychology* (pp. 22-23). Verona, Italy.

Otten, E., De Poel, H.J., & Hof, A.L. (2001). Stepping away from stance: Horizontal force profiles and their origin. In: Duysens, J., Smits-Engelsman, C.M., & Kingma, H. (Eds.), *Control of Posture and Gait* (pp. 307-310). Maastricht, the Netherlands.