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Betteco de Boer

VRIJE UNIVERSITEIT

Stabilizing bimanual coordination:
Changes in interlimb interactions

ACADEMISCH PROEFSCHRIFT

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de Vrije Universiteit Amsterdam,
op gezag van de rector magnificus
prof.dr. L.M. Bouter,
in het openbaar te verdedigen
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door

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geboren te Pretoria, Zuid-Afrika

Contents

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General introduction

In many daily tasks, we use both hands together to accomplish our goals. They can either have different roles, for instance when opening a bottle, doing the dishes, or striking a match. In these examples, one hand may have a more supportive role whereas the other hand moves more actively in achieving the task goal. Alternatively, our hands can have similar roles, for instance when lifting a heavy box with both hands or when steering a car or bike. Many of these tasks may seem very simple and they are usually executed automatically. However, if you think of executing these tasks with another person (using one hand per person) instead of your own two hands, the need for accurate cooperation between the hands becomes readily apparent. Some tasks may only deteriorate a little because one of the hands has a more supportive role, such as when striking a match or doing the dishes. However, imagine tying your shoelaces or eating with knife and fork together with another person, and you'll probably foresee many problems in coordinating your movements in time and space to achieve your goals, even when moving very slowly. These examples illustrate the benefit of having our hands coupled in order to perform bimanual tasks in everyday life. In this thesis, I will focus on the coupling between the limbs in bimanual coordination: how does coupling between the hands (or: interlimb interactions) influence bimanual coordination, how is this coupling organized, and how does it change over time?

In experimental settings, rather simple tasks have traditionally been used to study bimanual coordination. These tasks can be controlled systematically by the experimenter allowing for studying isolated aspects of the coordination task and the influence of specific task constraints. The task that has been used most profoundly, and that is also used in the experiments described in this thesis, involves rhythmic movements of the hands at the same frequency (i.e., isofrequency bimanual coordination) in two coordination patterns: in-phase and antiphase coordination. In-phase coordination reflects mirror-symmetrical movements of the hands (in our experiments simultaneous flexion and extension of the two hands in the horizontal plane), whereas antiphase coordination reflects isodirectional movements of the hands (in our experiments simultaneous flexion of one hand and extension of the other hand in the horizontal plane).

COORDINATION DYNAMICS AND PATTERN STABILITY

The characteristics of bimanual isofrequency coordination have been studied from the perspective of coordination dynamics (or dynamical systems theory). From this perspective, bimanual coordination is considered to arise from self-organizing principles:

The coordination patterns that are executed do not result from a so-called "motor program", but from interactions between the moving hands (Beek, Peper, & Stegeman, 1995). Hence, within this theoretical framework the coupling between the hands is considered as the main determinant in organizing the coordination between the limbs, in that it determines with coordination patterns can be executed stably and which patterns cannot. For isofrequency bimanual coordination only two patterns can be executed without practice: in-phase coordination and antiphase coordination (Yamanishi, Kawato, & Suzuki, 1980; Zanone & Kelso, 1992).

Bimanual isofrequency coordination between the limbs has been captured formally by the Haken-Kelso-Bunz or HKB model (Haken, Kelso, & Bunz, 1985), which consists of a pair of nonlinearly coupled nonlinear oscillators. Bimanual coordination is characterized in terms of the relative phase between the oscillators (Φ), a measure that can be used to quantify the coordination patterns and the stability properties of these patterns. Coordinative stability can be studied by examining the variability of Φ, with higher values of variability reflecting lower stability (Schöner, Haken, & Kelso, 1986). Not only does the HKB model account for the stable execution of in-phase ($\Phi = 0°$) and antiphase coordination ($\Phi = 180°$), as observed empirically (Yamanishi et al., 1980; Zanone & Kelso, 1992), it also accounts for the essential role of movement frequency. As has been shown in various experiments, in-phase coordination is more stable than antiphase coordination and increases in movement frequency induce a decrease in coordinative stability of antiphase coordination, resulting in a transition to the more stable in-phase pattern at a critical frequency (Haken et al., 1985; Kelso, 1984; Schöner et al., 1986). Furthermore, the HKB model has been extended in order to account for the influence of specific factors on the relative phase dynamics during bimanual coordination. For instance, differences in the uncoupled frequencies of the limbs (or eigenfrequencies) have been shown to induce small shifts in the relative phase between the hands and decreases in coordinative stability (e.g., Jeka & Kelso, 1995; Kelso & Jeka, 1992; Schmidt & Turvey, 1995; Sternad, Turvey, & Schmidt, 1992). Also handedness has been shown to induce an asymmetry in bimanual coordination, leading to a shift in the relative phase between the hands (de Poel, Peper, & Beek, 2007; Treffner & Turvey, 1995, 1996). By extending the HKB model, the model could account for these shifts in the relative phase and changes in coordinative stability.

However, although the HKB model and its extensions were shown to generalize to a variety of situations, the phenomenological character of the model precludes explanations of the observed behavior in terms of underlying system properties and processes (Peper, Daffertshofer, & Beek, 2004; Peper, Ridderikhoff, Daffertshofer,

& Beek, 2004). For instance, although the shift in relative phase due to a difference in eigenfrequency could be accounted for, the abstract nature of the model does not allow for interpretations regarding underlying processes of system properties responsible for the observed behavior (Peper, Nooij, & van Soest, 2004). In the course of the last couple of decades, research therefore focused more on the underpinnings of the observed behavior (e.g., Carson & Riek, 1998b; Swinnen, 2002). In this regard also a two-tiered model for rhythmic interlimb coordination was developed in which a distinction was made between a neural and an effector level, to be able to examine the functional underpinnings of the HKB model (Beek, Peper, & Daffertshofer, 2002; Peper, Ridderikhoff et al., 2004). Although this model is still descriptive at a phenomenological level, the distinction between the neural and effector level and their interaction allows for relating the observed coordinative behavior to the influence of biomechanical and neurophysiological aspects of the movement system (Peper, Daffertshofer et al., 2004; Peper, Ridderikhoff et al., 2004). As the HKB model and its extensions highlighted the importance of interlimb coupling in stabilizing bimanual coordination, insight into the functional characteristics of the coupling between the limbs will further aid our understanding of bimanual coordination. In the present thesis we therefore examined how coordinative coordination can be understood in terms of underlying sources of interlimb interaction.

INTERLIMB INTERACTIONS

In the literature several neurophysiological sources of interlimb coupling have been proposed to influence coordinative stability. First, the coupling may result from the way in which the activation of the two hands is generated by the central nervous system. Such interlimb interactions have for instance been suggested in models of coupled neural oscillators (e.g., Grossberg, Pribe, & Cohen, 1997) and timekeeper models where the internal timing mechanisms for the separate limbs were proposed to be coupled, resulting in interactions between the feedforward activation signals (motor commands) to the limbs (Helmuth & Ivry, 1996; Ivry & Richardson, 2002). In such situations, the coupling between the limbs is assumed to play a formative role in the generation of these feedforward activation signals (motor commands) to the limbs. In addition, unintended interactions between the limbs may result from neural cross-talk due to interhemispheric connections between the motor cortices via the corpus callosum and/or via uncrossed ipsilateral pathways (e.g., Cattaert, Semjen, & Summers, 1999;

Kagerer, Summers, & Semjen, 2003; Swinnen, 2002). In this situation, activation of one of the limbs also results in activation of the contralateral limb, due to spread of the neural signal via these transcallosal or ipsilateral connections. Hence, during bimanual coordination the movements of each limb may be affected due to neural cross-talk stemming from simultaneous activation of the limbs. For both central generation of the bimanual coordination pattern and the interactions due to neural cross-talk, the interlimb coupling effects are assumed to arise without any major influence from movement-related feedback.

On the other hand, movement afference from the hands may also induce coupling between the limbs, as has been shown for kinesthetic tracking of another limb's movements (Stinear & Byblow, 2001, 2002; Viviani, Baud-Bovy, & Redolfi, 1997). In these experiments, one hand was moved passively while participants followed these movements with their other hand in a certain coordination pattern. Because participants could not see their hands, tracking performance was based on kinesthetic afference. Results showed that participants were indeed able to do so, with in-phase coordination being less variable than antiphase coordination. Also when moving both hands actively the importance of kinesthetic afference was evident: when the afferent signals of one of the limbs was influenced through tendon vibration, bimanual coordination was affected significantly (Steyvers, Verschueren, Levin, Ouamer, & Swinnen, 2001). The role of kinesthetic signals in bimanual coordination may be related to the manner in which coordinative stability is perceived, given that in perceptual judgment tasks involving visual of kinesthetic stimuli it has been shown that, for equal levels of variability, phase coordination is judged to be more stable than antiphase coordination (Bingham, Zaal, Shull, & Collins, 2001; Wilson, Bingham, & Craig, 2003; Wilson, Collins, & Bingham, 2005). Finally, besides the central generation of a specific coordination pattern and intentional use of kinesthetic afference to execute certain coordination patterns, interlimb interactions have also been proposed to result from unintentional influences of movement-elicited afference stemming from another limb (Baldissera, Cavallari, Marini, & Tassone, 1991; Serrien, Li, Steyvers, Debaere, & Swinnen, 2001; Swinnen, Dounskaia, Verschueren, Serrien, & Daelman, 1995). Results in this regard have shown changes in active limb activation due to passive movements of another limb (Serrien et al., 2001; Swinnen et al., 1995). Due to changes in the movement-elicited afferences stemming from the passively moving limb, stability characteristics of bimanual coordination patterns were found to be affected.

Empirical support has been reported for these different forms of interlimb interaction, but how do they contribute to stability characteristics of bimanual coordination? To

address this question, Ridderikhoff, Peper, and Beek (2005) developed a methodology to study these general sources of interlimb interaction concurrently in order to assess their relative contributions to coordinative stability. According to this method, three sources of interlimb interaction can be assessed by comparing several tasks involving specific combinations of passive and active movements (these tasks are described in greater detail in Chapters 2, 4, and 5). The method is neurophysiologically motivated, without addressing the underlying processes and mechanisms. As such, the interlimb interactions were defined at a general functional level and differ with regard to two functional aspects: the intentionality to perform a specific pattern and the dependence on movement-elicited afference (cf. Table 1.1). First, integrated timing reflects interaction processes related to feedforward timing of the efferent signals when intending to perform a specific bimanual movement pattern. Note however that the resulting interlimb interactions themselves do not necessarily reflect intentional processes, for instance when the interactions hinder performance of a particular coordination pattern or in the case of neural cross-talk. Second, error correction reflects the correction of relative phasing errors based on kinesthetic afference, in order to stabilize the intended bimanual coordination pattern. Third, phase entrainment pertains to the unintentional entraining influences stemming from contralateral afference, resulting in unintended attraction towards specific phase relations between the limbs.

Using this methodology to examine the stabilizing contributions of the three sources of interaction, it has been shown that the differential stability of in-phase and antiphase coordination results from interactions related to integrated timing and error correction

Table 1.1

Sources of interlimb interaction underlying bimanual coordination

Interlimb interaction		*Afference-dependence*	*Intentionality of coordination*
Integrated timing	Generation of an integrated control signal for both limbs, specifying the bimanual pattern	No	Yes
Error correction	Correction of relative phase errors based on kinesthetic afference, to stabilize a bimanual pattern	Yes	Yes
Phase entrainment	Phase entrainment by contralateral afference towards specific phase relations between the limbs	Yes	No

(Ridderikhoff, Peper, & Beek, 2005, 2006, 2007). Whereas integrated timing is the main source of interaction that contributes to this differential stability (Ridderikhoff, Peper et al., 2005), also error correction is slightly more effective for in-phase than antiphase coordination (Ridderikhoff, Peper et al., 2005; Ridderikhoff et al., 2007). Phase entrainment on the other hand has been found to contribute equally to the stability of both coordination patterns (Ridderikhoff, Peper et al., 2005; Ridderikhoff et al., 2006). For integrated timing and error correction, attentional costs of the interlimb interactions have been found to be larger during antiphase than in-phase coordination and about equal for the two patterns for phase entrainment. Moreover, attentional demands were larger for error correction than for integrated timing – probably reflecting the processing of afferent information in the working memory to effectuate error correction (Ridderikhoff, Peper, & Beek, 2008). Furthermore, error correction has been found to act as a secondary stabilizing mechanism, which becomes more prominent in stabilizing the coordination pattern when integrated timing is not sufficient to ensure coordinative stability (Ridderikhoff, Peper et al., 2005; Ridderikhoff et al., 2008). Finally, error correction has been found to be more effective in combination with the generation of an integrated bimanual activation pattern. Presumably the generation of integrated bimanual control signals acts as a reference frame, in terms of expected sensory predictions, to allow for more effective error corrections based on kinesthetic afference (Ridderikhoff et al., 2007).

Changes in bimanual coordination at various time scales

Because the stability properties of rhythmic bimanual coordination are not fixed but change at various time scales, the present thesis examined how changes in bimanual coordinative stability and accuracy can be understood in terms of the underlying interlimb interactions. To this end, various sources of change are addressed, and the associated changes in coordinative stability are examined in terms of the stabilizing contributions of integrated timing, error correction, and phase entrainment.

At short time scales, particular characteristics of the hand movements have been shown to influence bimanual stability and accuracy. For instance, accuracy and stability of bimanual coordination have been found to be affected by changes in task conditions like movement frequency (e.g., Kelso, 1984; Peper & Beek, 1998b; Post, Peper, & Beek, 2000; Schöner et al., 1986), movement amplitude (e.g., Post, Peper, & Beek, 2000; Ryu & Buchanan, 2004; Spijkers & Heuer, 1995), differences between the eigenfrequencies of

the individual limbs (e.g., Jeka & Kelso, 1995; Schmidt & Turvey, 1995; Sternad et al., 1992), and laterally focused attention (e.g., de Poel, Peper, & Beek, 2008; Swinnen, Jardin, & Meulenbroek, 1996). Also at longer time scales bimanual coordination is influenced by a variety of factors. For instance, stability properties change as a function of development across childhood (e.g., Fitzpatrick, Schmidt, & Lockman, 1996; Robertson, 2001), aging in the elderly (e.g., Summers, Lewis, & Fujiyama, 2010; Temprado, Vercruysse, Salesse, & Berton, 2010; Wishart, Lee, Murdoch, & Hodges, 2000), learning a new bimanual coordination pattern (e.g., Fontaine, Lee, & Swinnen, 1997; Zanone & Kelso, 1992, 1997), and rehabilitation, for instance after stroke (e.g., Cauraugh, Lodha, Naik, & Summers, 2010). Although most of these changes in coordinative stability are well documented, it is unknown how they are engendered by changes in the underlying interlimb interactions. In the present thesis, changes in bimanual coordination are addressed at various time scales by examining associated changes in stabilizing contributions of the underlying sources of interlimb interaction, using the methodology of Ridderikhoff, Peper, et al. (2005) described above. For short time scales the effects of movement frequency and movement amplitude are studied in relation to the interlimb interactions, whereas at longer time scales the effects of learning and development are examined.

OUTLINE OF THE THESIS

In Chapters 2 and 3 the way in which changes in coordinative stability result from the identified interlimb interactions are addressed at short time scales, whereas Chapters 4 and 5 focus on changes at longer time scales. Chapter 2 addresses the effects of frequency on bimanual coordinative stability and the underlying interlimb interactions. Movement frequency may be considered an essential feature when studying bimanual coordination, because it enhances the stability difference between in-phase and antiphase coordination, eventually resulting in the transition from antiphase to in-phase coordination. For this reason, bimanual performance was examined for three different frequencies, with the highest frequency being equal to the critical frequency, i.e., the frequency at which the transition from antiphase to in-phase occurs. Chapter 3 provides new insights into the influences of movement amplitude on the (unintentional) phase entrainment between the limbs. To this end, the effects of variations in the movement amplitudes as such were compared to effects resulting from changing the amplitude relation between the limbs. Chapter 4 addresses the acquisition of a new bimanual coordination pattern, thereby examining the changes in bimanual coordination and the underlying interactions over a

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longer time span. In this study, participants learned a bimanual pattern that lies exactly in between in-phase and antiphase coordination ($\Phi = 90°$) and we examined the stabilizing contributions of integrated timing, error correction, and phase entrainment to this new coordination pattern as well as its mirror-symmetrical partner ($\Phi = 270°$). Also the effects of attentional focus were examined, by comparing learning with a focus directed to the movement themselves (i.e., an internal focus of attention) and learning with a focus directed to the effects of the movements (i.e., an external focus of attention). In Chapter 5 changes on an even longer time scale were studied by comparing four age groups (viz. children ranging from 6 to 15 years, and young adults). The development of temporally coordinated flexion-extension movements of the hands were examined in terms of the three sources of interlimb interaction. Inspired by the developmental characteristics of the myelination of the corpus callosum, development of temporal coupling of the hands was contrasted with the development of spatial coupling of the hands as observed in a bimanual drawing task. Finally, in Chapter 6 the main findings of this thesis are summarized, and the changes in bimanual coordination and in the underlying interlimb interactions at shorter and longer time scales are compared and further discussed.

2

Frequency-induced changes in interlimb interactions: Increasing manifestations of closed-loop control

In bimanual coordination, interactions between the limbs result in attraction to in-phase and antiphase coordination. Increasing movement frequency leads to decreasing stability of antiphase coordination, often resulting in a transition to the more stable in-phase pattern. It is unknown, however, how this frequency-induced loss of stability is engendered in terms of the interlimb interactions underwriting bimanual coordination. The present study was conducted to help resolve this issue. Using an established method (based on comparison of various unimanual and bimanual tasks involving both passive and active movements), three sources of interlimb interaction were dissociated: (1) integrated timing of feedforward signals, (2) afference-based correction of relative phase errors, and (3) phase entrainment by contralateral afference. Results indicated that phase entrainment strength remained unaffected by frequency and that the stabilizing effects of error correction and integrated timing decreased with increasing frequency. Their contributions, however, reflected an interesting interplay as frequency increased. For moderate frequencies coordinative stability was predominantly secured by integrated timing processes. However, at high frequencies, the stabilization of the antiphase pattern required combined contributions of both integrated timing and error correction. In sum, increasing frequency was found to induce a shift from predominantly open-loop control to more closed-loop control. The results may be accounted for by means of an internal forward model for sensorimotor integration in which the sensory signals are compared to values predicted on the basis of efference copies.

2

INTRODUCTION

The stability of rhythmic bimanual coordination is influenced by movement frequency. Whereas both in-phase and antiphase coordination can be executed stably at low frequencies, increasing frequency results in loss of stability of the antiphase pattern, often followed by a transition to the more stable in-phase pattern (Haken et al., 1985; Kelso, 1984; Schöner et al., 1986). In consequence of these findings, frequency has been identified as a primary 'control parameter' for inducing qualitative changes (i.e., phase transitions) in movement patterns, not only in bimanual coordination but also in other forms of interlimb coordination, including bipedal (Diedrich & Warren, 1995) and quadrupedal gait (Hoyt & Taylor, 1981), and social coordination (Schmidt, Carello, & Turvey, 1990). Especially in the context of bimanual coordination frequency-induced transitions have been studied extensively in terms of the underlying nonlinear dynamics, for instance by demonstrating signs of an imminent loss of stability (viz. critical fluctuations and critical slowing down, Kelso, Scholz, & Schöner, 1986; Scholz, Kelso, & Schöner, 1987).

However, in terms of motor control, the precise underpinnings of the frequency-induced loss of stability remain unknown, although it has recently been shown that the stability-related changes with movement frequency are related to egocentric as well as allocentric constraints (Li, Levin, Forner-Cordero, Ronsse, & Swinnen, 2009). Since the stability of bimanual coordination is governed by interlimb interactions (Byblow, Carson, & Goodman, 1994; Peper, Ridderikhoff et al., 2004; Schmidt, Shaw, & Turvey, 1993; Swinnen, 2002), it is reasonable to assume that changes in stability must originate from changes in these interactions. In the present study we therefore sought to uncover how changes in movement frequency influence the interlimb interactions underwriting bimanual coordination. In particular, using the method developed by Ridderikhoff, Peper et al. (2005), we examined how the contributions of three functionally defined sources of interlimb interaction were affected by movement frequency.

Based on pertinent behavioral and neurophysiological literature, Ridderikhoff, Peper et al. (2005) distinguished three functional sources of interlimb interaction: (1) integrated timing of feedforward signals, (2) afference-based error correction of relative phase errors, and (3) phase entrainment by contralateral afference. The first source (integrated timing) reflects interaction processes pertaining to the timing of the efferent signals that specify the bimanual movement pattern, i.e., irrespective of adjustments that may occur as a result of afferent feedback. How this specification of the bimanual pattern is instantiated is still a matter of debate. For instance, integrated timing may result from

interactions between two (or more) timing mechanisms regulating the timing of the individual limbs, or from a single timing mechanism sending parallel signals to multiple limbs. Most notably, the specification of the timing pattern has been suggested to result from cerebellar timing mechanisms involved in bimanual coordination (e.g., Helmuth & Ivry, 1996), from a system of coupled neural oscillators that specifies the bimanual coordination pattern (e.g., Daffertshofer, Peper, & Beek, 2005; Grossberg et al., 1997), or from a single circuit specifying the required timing and phase relation between the limbs (Turvey, Schmidt, & Rosenblum, 1989). The second source (error correction) comprises afference-based correction processes that result in adjustments of the relative phasing between the limbs. This source may involve supraspinal correction processes that monitor and adjust the timing of the coordinated limb movements (Baldissera et al., 1991; Carson & Riek, 1998b). This implies that error correction associated with the timing of a single limb (irrespective of its coordination with other limbs), such as responses to loading that do not differ for unimanual or bimanual movements (Baldissera, Cavallari, & Esposti, 2006), are not comprised by this source of interlimb interaction, as they are not aimed at improving the coordination between the limbs. The third source (phase entrainment) is based on peripheral reflexes that result from afferent input from the contralateral limb, inducing attraction towards specific phase relations between the limbs (in-phase and antiphase; Baldissera et al., 1991; Serrien et al., 2001; Swinnen et al., 1995). Whereas the correction of relative phase errors involves the intentional use of movement-elicited afference (i.e., to correct for detected phasing errors), phase entrainment is the result of unintentional entraining effects of these afferent signals.

Ridderikhoff, Peper et al. (2005) developed an experimental protocol to examine the relative contributions of these sources of interlimb interaction to the stability of rhythmic bimanual coordination. Using this protocol, they concluded that integrated timing constitutes a primary source of coordinative stability and that the stability difference between in-phase and antiphase results predominantly from this source of interlimb interaction. Error corrections were only observed if the pattern could not be stabilized by means of integrated timing. Phase entrainment was found to stabilize in-phase and antiphase coordination to a similar degree (see also Ridderikhoff et al., 2006). In addition, the protocol was successfully applied to determine the attentional load associated with the three sources of interaction (Ridderikhoff et al., 2008). In the present study the same protocol was used to examine how changes in coordinative stability in response to frequency variations result from modulations in the interlimb interactions. That is, we examined how the stabilizing contributions of these sources of interaction change as a function of movement frequency. In doing so, we were particularly interested in the

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potential interplay between integrated timing and error correction, as the role of error correction is likely to become more important as the stability of bimanual coordination is challenged (see next section).

Unraveling interlimb interactions

By comparing five tasks involving bimanual or unimanual rhythmic flexion-extension movements about the wrist, the contributions of the three sources of interactions can be dissociated, as has been described by Ridderikhoff, Peper et al. (2005). These tasks differ with regard to the degree in which the three sources of interaction are assumed to be involved (see Table 2.1). By means of systematic pairwise comparisons of two tasks that differ in only one source of interlimb interaction, the contribution of all three sources of interlimb interaction to the coordination pattern can be investigated.

In task UN (unimanual coordination) unimanual wrist cycling movements are executed at a tempo specified by a pacing signal. In task UNm, the same task is performed, while the contralateral hand is moved passively by means of a motor (i.e., UNm: task UN with motor). These passive movements are shifted with respect to the pacing signal (by +30°, 0°, or -30°). Since participants are instructed to ignore these passive movements, shifts in the phasing of the actively moving hand result from unintentional phase entrainment by afferent signals from the contralateral hand. Because in task UN none of the sources of interlimb interaction are involved, comparison of UNm and UN serves to tease apart the contribution of phase entrainment.

During kinesthetic tracking participants are instructed to track the passively moving hand with their actively moving hand, either in the presence of a distracting phase-shifted auditory signal (task KTa) or without such an auditory signal (task KT). In order to track their passively moving hand, participants have to reduce the relative phasing error between the hands, using the afferent signals from the passive hand. Hence, in these tasks, the afferent signals from the contralateral hand not only induce unintended phase entrainment, but are also used for error corrections. In contrast to phase entrainment, these error corrections are intentional, as movement-elicited afference is used to establish a required phase relation between the hands. The influence of error correction can be assessed by comparing KTa to UNm, as this source of interaction is present in the former but not in the latter task. Note that these two tasks involve identical configurations of passive movements and the auditory signal, and only differ in instruction. In addition, the robustness of the error correction process can be assessed in terms of its susceptibility to the distracting influences of the auditory signal. To this end, KT is compared to KTa.

In task AB (active bimanual coordination) participants perform oscillatory wrist movements with both hands at a frequency prescribed by a pacing signal. In theory, the role of integrated timing can be examined by comparing AB and KT: during KT only error correction and phase entrainment are present, whereas AB also involves integrated timing. As previous results (Ridderikhoff, Peper et al., 2005) indicated that error correction serves as a secondary mechanism that hardly comes into play as long as integrated timing provides sufficient coordinative stability (see next), the contribution of integrated timing may also be examined by comparing AB to UNm.

Using a subtraction design, these strategic comparisons can provide insight into the degree to which coordinative stability depends on the specific sources of interaction. In addition to these comparative assessments, the coordinative stability, the overall strength of interlimb coupling, and the degree of error correction can be estimated for each individual task (i.e., for AB, KT, KTa, and UNm) using established dependent variables. To examine how the contributions of the three sources of interlimb interaction are affected by movement frequency, the five tasks were compared for three different frequencies.

Table 2.1
Tasks and sources of interlimb interaction

	Task description	Interactions		
		IT	EC	PE
AB	Active bimanual coordination at a tempo specified by an auditory pacing signal.	X	X	X
KT	Kinesthetic tracking of the passively moving contralateral hand.		X	X
KTa	Kinesthetic tracking of the passively moving contralateral hand while a (phase-shifted) auditory signal is presented as distractor.		X	X
UNm	Unimanual coordination with an auditory pacing signal while (phase-shifted) passive movement of the contralateral hand is presented as distractor.			X
UN	Unimanual coordination with an auditory pacing signal.			

Mapping of the five tasks to the three sources of interlimb interaction (IT: integrated timing of feedforward signals; EC: afference-based correction of relative phasing errors; PE: phase entrainment by contralateral afference). The "X" symbols on the right represent the sources of interaction that are assumed to be involved in these tasks.

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Expected influences of movement frequency

As mentioned, the assumption that all three sources are involved in AB may be questioned. Ridderikhoff, Peper et al. (2005) showed that the contribution of error correction in AB was marginal, and much smaller than in KT and KTa. Error correction appeared to act as a secondary control mechanism that becomes manifest when integrated timing alone cannot provide sufficient coordinative stability (Ridderikhoff, Peper et al., 2005; Ridderikhoff et al., 2008). This implies that a decrease in the stabilizing effect of integrated timing may be compensated for by stronger dependence on error corrections. Indeed, the open-loop model proposed by Grossberg et al. (1997) comprises a decrease in the stabilizing effect of integrated timing with increasing frequency, in particular for antiphase coordination. As a working hypothesis, we therefore expected the stabilizing effects of integrated timing (which has been identified as the main contributor to coordinative stability during normal bimanual coordination) to decrease with increasing frequency, especially during antiphase performance.

A reduction in the stabilizing influences of integrated timing would result in greater variability of the relative phasing between the limbs. Hence, the error correction process was anticipated to become more manifest. At the same time, the efficacy of this process was expected to deteriorate with frequency, due to shortening of the time period available to process afferent feedback. For antiphase coordination this effect of frequency was predicted to be stronger than for in-phase coordination, because simultaneous performance of two different movements requires more complicated information processing than performance of two identical movements (Cohen, 1970, 1971; Rosenbaum, 1991).

The strength of phase entrainment has been found to depend on movement amplitude (Ridderikhoff, Peper et al., 2005). Because an increase in frequency typically results in an amplitude drop (Haken et al., 1985; Kay, Kelso, Saltzman, & Schöner, 1987), higher frequencies were expected to induce a decrease in phase entrainment strength. Furthermore, because the effect of movement amplitude on the strength of phase entrainment is comparable for in-phase and antiphase coordination (Ridderikhoff, Peper et al., 2005), no differential effect of movement frequency was expected for the two coordination patterns. Hence, the typically observed amplification of the stability difference between in-phase and antiphase with increasing movement frequency was predicted to stem primarily from changes in the contributions of integrated timing and error correction.

METHODS

Participants were selected on the basis of their critical frequency in task AB and KT, as determined by means of scaled-frequency trials prior to the experiment. The experiment proper involved trials at three fixed frequencies and lasted about 2 hours (including breaks). The experiment was approved by the local ethics committee.

Participants

Based on their critical frequency (see *Preparation and selection*), fourteen participants (11 female, 3 male; mean age = 23.4, standard deviation (*SD*) = 3.34 yr) out of 21 volunteers were invited to participate in the experiment. All participants were right handed (mean laterality quotient = 89.6, *SD* = 8.32; Oldfield, 1971). Participants gave their written informed consent prior to the experiment and were paid a small fee for their services.

Apparatus

Participants sat comfortably in a height-adjustable chair with their elbows slightly flexed and their feet supported. Their forearms were placed on armrests in a neutral position (thumbs up, palms facing inward, fingers extended). Both hands were fixated to two flat manipulanda, allowing flexion and extension movements about the wrist only. The manipulanda could either register wrist movements by means of a potentiometer or control wrist movements by means of a motor (active and passive movements, respectively) – see Ridderikhoff, Peper et al (2005) for a detailed description. The maximum torque of the motor was such that participants were unable to alter the trajectory of the applied movements. A black opaque screen was used to eliminate visual feedback of the hand movements. Auditory pacing stimuli (pitch: 440 Hz, duration: 50 ms) were presented through earmuffs. A moderate level of 'white' background noise eliminated all auditory feedback from the motor.

Surface electromyographs (EMGs) were obtained from M. flexor carpi radialis (FCR) and M. extensor carpi radialis (ECR) of both arms. A bipolar arrangement of disposable electrodes was attached with a center-to-center distance of about 2 cm after cleansing and abrasion of the skin. The electrodes were positioned on the center of the muscle belly on the line from origin to insertion as determined by palpation. EMG signals were sampled at 1000 Hz.

2

Passive-movement trajectories

To allow for a fair comparison between tasks, recorded movements of the dominant hand in task AB were used to generate the passive movements in tasks KT, KTa, and UNm (per individual and per condition), which thus had similar kinematics and variability. Passive movements were based on movements recorded during in-phase (IP) and antiphase (AP) coordination in AB. For each frequency condition the three AP trials with the least cycle duration variability in the dominant-hand movement were selected. Subsequently, three matching IP trials were selected, such that the difference in cycle variability between the IP and AP trials was minimal. After removal of the first three cycles, the dominant hand movements were low-pass filtered (2nd-order bidirectional Butterworth filter; cut-off frequency 18 Hz) and multiplied with a windowing function to generate a smooth increase and decrease in the amplitude of the passive movements in the first and last two cycles, respectively. Passive movement trajectories were further adjusted for tasks KTa and UNm. In KTa and UNm, the dominant hand was moved by the motor while a pacing signal was also presented. Six phase relations between the passive movements and metronome pacing were applied: three phase shifts around IP and three around AP. The phase shifts were: -30°, 0°, and +30° (with 30° corresponding to 1/12th of a movement cycle; the negative phase shift implied a phase advance, the positive shift a phase delay). For UNm, the passive movements were phase shifted using cubic spline interpolation at the start of the trial so that the phase shifts of -30° and +30° were achieved in three cycles. For KTa, these phase shifts were generated by shortening or lengthening the intervals between metronome beeps during the first three cycles. (In a similar manner, passive movements were generated for the scaled-frequency KT trials used to determine the critical frequency; see *Appendix A* for a detailed description.)

Procedure

Preparation and selection
Prior to the experiment participants performed maximum voluntary contractions (MVCs) by generating a maximal isometric flexion or extension torque with either arm for about 3 s (three repetitions for each muscle).

Subsequently, participants executed AB and KT trials in which frequency was scaled from 1.0 Hz to 3.5 Hz in steps of 0.25 Hz. In AB, participants were instructed to rhythmically flex and extend their wrists at a tempo specified by an auditory pacing signal. Peak flexion of both hands had to coincide with the beep for IP, while for AP peak flexion of

the non-dominant hand and peak extension of the dominant hand had to coincide with the beep. In KT, participants were required to coordinate the movements of their non-dominant (active) hand with their passively moving dominant hand[1], either in IP or AP. In both tasks, participants executed six IP and six AP trials (for a detailed description of the procedure, see *Appendix A*).The critical frequencies in AB and KT ($F_{crit,AB}$ and $F_{crit,KT}$) were defined as the last frequency at which the AP coordination pattern was performed in a stable fashion, irrespective of whether it was followed by a transition to IP coordination. A frequency bin was considered stable if the circular standard deviation of the relative phase (CSD_ϕ; see *Kinematics analysis*) was lower than 1 rad (ca. 57.3°). In addition to the stability requirement, the mean relative phase between the hands (Φ; for calculation see *Kinematics analysis*) had to fall within a range of ± 45° around the required relative phase of 180° (or, if a systematic off-set was present, around the value of Φ obtained for the first frequency bin), to ensure that the required pattern was executed. Fcrit was based on the frequency in the final bin of the last series of at least two consecutive bins that were executed correctly and stably. The median values (rounded off to the nearest multiple of 0.25) of the six AB and six KT trials were adopted as $F_{crit,AB}$ and $F_{crit,KT}$, respectively. Participants for the experiment were selected based on two criteria: (1) 2.0 Hz ≤ $F_{crit,AB}$ ≤ 3.0 Hz, thereby limiting the differences in F_{crit} between participants to maximally 1.0 Hz; and (2) $F_{crit,KT}$ ≥ $F_{crit,AB}$ - 1.0 Hz, because lower values of $F_{crit,KT}$ would imply that all frequencies tested in the experiment exceeded the critical value in the KT condition.

Experimental conditions

All five tasks (see Table 2.1) were executed at three different frequencies that were based on $F_{crit,AB}$, as obtained for each individual: $F_{crit,AB}$ (high frequency), $F_{crit,AB}$ - 0.5 Hz (medium frequency), and $F_{crit,AB}$ - 1.0 Hz (low frequency). In AB, participants were instructed to execute IP and AP coordination at the tempo specified by the auditory signal. In KT and KTa, they were required to move their non-dominant hand in IP or AP with their passively moving dominant hand. In UN and UNm, flexion of the non-dominant hand had to coincide with the beep, irrespective of whether the dominant hand was moved passively (in UNm) or not (in UN).

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1   This configuration was opposite to that of Ridderikhoff, Peper et al. (2005) and Ridderikhoff et al. (2007, 2008) in which the non-dominant hand was moved passively. This opposite configuration was chosen in view of the fact that during a transition, phase adaptations are predominantly effectuated by the non-dominant hand (Byblow et al., 1994; de Poel et al., 2007) and because interaction influences from the dominant hand onto the non-dominant hand are stronger than those in reverse direction (de Poel et al., 2007).

2

Because the passive movements were based on performance during AB (see *Passive-movement trajectories*), all participants started with this task. IP and AP trials were presented in separate blocks, in which the three frequency sub-blocks consisting of six repetitions were presented in random order. Thus, in total 2 (Pattern) x 3 (Frequency) x 6 (Repetitions) = 36 AB trials were presented. Trial length was 30 cycles. Prior to each coordination mode block, one practice trial was executed at the medium frequency. The remainder of the experiment consisted of three blocks of trials. Task KT and KTa were grouped with respect to coordination mode, resulting in a block of KT/KTa-IP trials and a block of KT/KTa-AP trials. Participants executed one KT-practice trial at the medium frequency at the start of each block. Subsequently, each condition was repeated three times (i.e., each passive movement trajectory was used once), resulting in 3 (Frequency) x 3 (Repetitions) = 9 KT trials and 3 (Frequency) x 3 (Shift) x 3 (Repetitions) = 27 KTa trials for each block. Trial duration was 27 cycles. The third block of trials consisted of all UN trials (duration: 30 cycles) and UNm trials (duration: 27 cycles). Following one UN-practice trial at the medium frequency, participants executed 3 (Frequency) x 3 (Repetitions) = 9 UN trials and 2 (Pattern) x 3 (Frequency) x 3 (Shift) x 3 (Repetitions) = 54 UNm trials, resulting in 63 trials in total. The order of the three blocks (KT/KTa-IP, KT/KTa-AP, and UN/UNm) was counterbalanced across participants. For each block, the three frequency sub-blocks were presented in random order, while the trials within each sub-block were randomized. Breaks were administered between all blocks, and additional breaks were provided if requested.

Data analysis

Kinematics analysis
The first few and last two cycles of each trial were removed, leaving 20 cycles for analysis. More cycles were removed if: (1) the executed frequency deviated more than 10% from the required frequency; (2) the relative phase between the hands (Φ, see below) increased or decreased progressively over several consecutive cycles, i.e., in case of phase wrapping; (3) the phase relation with the metronome (if present) was not correct (e.g., peak extension instead of peak flexion coinciding with the beep). Analysis of the AB trials was restricted to the trials on which passive movements were based and if cycles were removed from an AB trial, the same section was removed from the corresponding KT, KTa, and UNm trials. Hence, the movements of the dominant hand were identical in the selected parts in the corresponding AB, KT, KTa, and UNm trials. If less than 10 consecutive cycles remained for analysis, a trial was excluded from further

analysis. In total one or more cycles were removed from 138 trials (5.8%). In addition, 195 trials (8.2%) were excluded completely from further analysis, predominantly for the AP conditions (high frequency: 57.7%, medium frequency: 22.9% of the removed trials)[2]. The excluded trials were evenly distributed over AB, KT, KTa, and UNm, whereas considerably fewer trials were removed for UN. Due to removal of these trials, the high frequency and medium frequency could not be analyzed for two participants in tasks AB, KT, KTa, and UNm. These participants were therefore excluded from analysis. In addition, one participant was not able to execute the correct pattern in the high-frequency AP condition in KT. This participant was only excluded from the analyses that included this condition.

The cycles included in the analysis were low-pass filtered (2nd-order bi-directional Butterworth filter; cut-off frequency: 18 Hz). For the tasks in which two hands were involved (AB, KT, KTa, and UNm), the relative phase between the hands was calculated for each cycle as $\Phi_i = 360° (t_{y,i} - t_{x,i})/(t_{x,i+1} - t_{x,i})$, where $t_{y,i}$ and $t_{x,i}$ indicate the time of the *i*th peak flexion (extension) of the non-dominant hand and the dominant hand, respectively (cf. Carson, Goodman, Kelso, & Elliott, 1995). The calculations were executed for flexion and extension separately. For the unimanual tasks (UNm and UN), the relative phase between the metronome beeps and peak flexion of the non-dominant hand was determined for each cycle as $\Psi_i = 360° (t_{y,i} - t_{x,i})/(t_{x,i+1} - t_{x,i})$, where $t_{y,i}$ indicates the time of the *i*th peak flexion of the non-dominant hand and $t_{x,i}$ corresponds to the moment of the *i*th metronome beep. For both Φ and Ψ a positive value implied that the non-dominant hand (*y*) was lagging the reference signal (*x*). Circular statistics (Mardia, 1972) was used to determine the average values of Φ and Ψ, and the corresponding circular standard deviations (CSD_Φ and CSD_Ψ) for each trial. The constant error in Φ was defined as $CE_\Phi = \Phi - \Phi_{required}$ (with $\Phi_{required}$ = 0° for IP and 180° for AP).

An error in relative phasing can be corrected by shortening or lengthening the subsequent half cycle of (one of) the hands, resulting in a negative correlation between the signed error in relative phasing at peak flexion or extension and the duration of the subsequent half cycle[3] (Ridderikhoff et al., 2007). Therefore, the presence of error correction was examined in terms of this error correction correlation (R_{EC}), calculated for each half cycle of the non-dominant hand (i.e., the hand that was moving actively

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2   The remaining number of cycles varied over conditions, which may have influenced the standard deviation. However, because this affected all tasks in the same way, this did not compromise the pairwise comparisons between tasks.

3   Ridderikhoff et al. (2007) showed that whereas the correlation between the signed error and the next full cycle is influenced by between- and within-hand correlations, the correlation between the signed error and the next half cycle is not.

in all tasks). The signed error was defined as the interval between the ith peak flexion (extension) of both hands for IP, and as the interval between the ith peak flexion (extension) of the non-dominant hand and the ith peak extension (flexion) of the dominant hand for AP. Because UNm performance did not entail error correction, the corresponding correlations reflected the influence of phase entrainment and were regarded as baseline values (Ridderikhoff, Peper et al., 2005). Therefore, for all participants the R_{EC} values obtained for each condition in AB, KT, and KTa were corrected by subtracting the corresponding mean values for UNm, as obtained for that participant. For statistical analyses, R_{EC} was transformed to normally distributed values using the Fisher transform. For clarity, the untransformed values are presented in the Results.

EMG analysis

EMG data were first filtered (2nd-order bidirectional Butterworth band-pass filter: 10-400 Hz). The highest root mean square (RMS) value of the three MVC attempts was used for normalization. EMG analyses were performed on the same trials and cycles that were included in the analyses of the kinematics. To visualize the average muscle activity within a cycle, eight bins were defined in relation to the continuous phase of the movement, $\Theta = \arctan[(d\theta/dt)/(2\pi f\theta)]$, where θ and $d\theta/dt$ denote joint angle and joint angular velocity, respectively, and f represents movement frequency. Each bin represented an equal part of the phase evolution of the oscillation. The first bin was centered around $\Theta = 0°$ (i.e., peak extension) and the fifth bin was centered around $\Theta = 180°$ (i.e., peak flexion). For each bin, the normalized RMS values were averaged to visualize the global activation patterns of the muscles.

Coherence analysis was used to examine the degree of coupling in muscle activity (Ridderikhoff, Peper et al., 2005). EMG records were full-wave rectified using the absolute value of the Hilbert transform, and the weighted coherence (C_W, Porges et al., 1980) of the full-wave rectified EMG of homologous muscles was calculated using a frequency bandwidth of 0.2 Hz around the movement frequency. C_W was calculated using Welch's modified periodogram method with a Hamming window of six cycles. C_W was transformed using the Fisher transform, prior to averaging (per participant and per condition). For clarity, the untransformed values are presented in the Results.

Statistical analysis

For AB, KT, KTa, and UNm the effects of coordination pattern and movement frequency on coordinative stability were examined by submitting CSD_ϕ to a 2 (Pattern: IP, AP) x 3 (Frequency: low, medium, high) x 2 (Direction: flexion, extension) repeated-measures analysis of variance (ANOVA; for KTa and UNm, only the trials with a phase shift of 0° were included), for each task separately. Next, the kinematic variables were submitted to pairwise comparisons between two tasks to uncover the contributions of the different sources of interlimb interaction (see *Unraveling interlimb interactions*). First, differences between two tasks in each condition were submitted to a one-sided *t*-test to determine whether they differed significantly from zero. Subsequently, the differences were submitted to a repeated-measures ANOVA with the factors Pattern (IP, AP), Frequency (low, medium, high), Direction (flexion, extension), and, if applicable, Shift (-30°, 0°, +30°). The stabilizing effect of integrated timing was assessed by comparing CSD_ϕ between AB and KT, and between AB and UNm (see *Unraveling interlimb interactions*). The stabilizing influences of error correction were assessed by comparing CSD_ϕ between KTa and UNm. Comparison of CE_ϕ between KTa and KT provided insight into the robustness of the error correction process (indexed by the degree to which the movements were attracted towards the phasing of the metronome). Phase entrainment effects were assessed by comparing Ψ between UN and UNm (indicating the degree to which the movements of the non-dominant hand were attracted to the passive movements of the dominant hand).

C_W was obtained for all tasks that involved movements of both hands and was submitted to a repeated measures ANOVA with the factors Task (AB, KT, KTa, UNm), Pattern (IP, AP), Frequency (low, medium, high), and Muscle (flexor, extensor). R_{EC} was normalized to UNm (see *Kinematics analysis*) so that statistical analysis was confined to tasks AB, KT, and KTa. R_{EC} was analyzed using a repeated-measures ANOVA with the factors Task (AB, KT, KTa), Pattern (IP, AP), Frequency (low, medium, high), and Direction (flexion, extension).

In all ANOVAs, Greenhouse-Geisser adjustment of degrees of freedom was applied if the assumption of sphericity was violated. In the Results, significant effects ($p < .05$) as well as tendencies ($p < .10$) are reported. Effect sizes were based on the partial eta squared (η_p^2, Cohen, 1988). Significant effects were further scrutinized using post-hoc paired-samples *t*-tests. In the Results, values are presented as: between-participants mean [between-participants *SD*].

RESULTS

Although the scaled-frequency trials were performed successfully in the kinesthetic tracking task, F_{crit} in KT (2.19 [0.50] Hz) was significantly lower than in AB (2.69 [0.52] Hz), $t(20) = 4.31$, $p < .001$. The resulting frequencies in the experiment, determined individually for each participant included in the analysis, were on average 1.52, 2.02, and 2.52 Hz for the low, medium, and high frequency, respectively.

Although $F_{crit,KT}$ was significantly lower than the mean high frequency (i.e., $F_{crit,KT}$ for the included participants was on average 2.19 [0.47] Hz), most of the participants were able to execute all three frequencies in KT and KTa. Thus, when frequency remained fixed throughout the trial, the antiphase pattern could be performed at a higher frequency than in the scaled-frequency KT trials. This difference in performance may be the result of destabilizing influences of the frequency increments applied during the latter trials. In addition, in these trials performance may have been negatively affected by fatigue (since those trials were longer), whereas in the trials in which frequency was fixed (i.e., the experiment proper) the intention to perform the antiphase pattern may have further stabilized performance (cf. Lee, Blandin, & Proteau, 1996).

Variability of relative phasing between the hands

Analysis of CSD_Φ revealed that in UNm variability was higher during AP (28.8° [10.1°]) than IP (23.9° [5.17°]), $F(1,11) = 6.93$, $p < .05$, $\eta_p^2 = .39$. In AB, variability also seemed to be higher during AP coordination, but this effect failed to reach significance, $F(1,11) = 4.32$, $p = .06$, $\eta_p^2 = .28$. A main effect of frequency was observed for AB ($F(2,22) = 20.1$, $p < .001$, $\eta_p^2 = .65$), KT ($F(2,20) = 13.9$, $p < .001$, $\eta_p^2 = .58$), KTa ($F(2,22) = 11.8$, $p < .001$, $\eta_p^2 = .52$), and UNm ($F(2,22) = 6.22$, $p < .01$, $\eta_p^2 = .36$). In all four tasks CSD_Φ increased significantly with frequency (see Table 2.2). Post-hoc comparisons showed that for AB, KT, and KTa all frequencies differed significantly from one another, whereas in UNm only the high frequency differed significantly from the other frequency conditions. The Pattern x Frequency interaction in UNm, $F(2,22) = 3.65$, $p < .05$, $\eta_p^2 = .25$, showed that CSD_Φ increased with movement frequency during AP only. As a result, variability in the high-frequency condition was significantly larger for AP than IP, whereas for the other frequencies the coordination patterns showed similar levels of variability. The Pattern x Frequency interaction was also significant for KTa, $F(2,22) = 5.16$, $p < .05$, $\eta_p^2 = .32$, and a tendency for such an interaction was obtained for KT, $F(2,20) = 2.97$, $p = .07$, $\eta_p^2 = .23$.

Table 2.2

Circular standard deviation of the relative phase between the hands

	In-phase			Antiphase		
	Low	Medium	High	Low	Medium	High
AB	10.9 [3.05]	12.2 [2.09]	14.3 [3.01]	11.9 [2.17]	14.1 [3.79]	18.2 [6.17]
KT	19.0 [4.66]	20.2 [4.89]	25.1 [7.95]	17.2 [4.57]	24.6 [7.56]	29.4 [10.0]
KTa	18.7 [5.67]	19.7 [6.67]	22.6 [6.06]	17.5 [2.70]	25.2 [8.18]	26.8 [7.85]
UNm	23.0 [5.29]	23.9 [5.85]	25.3 [4.37]	23.3 [6.38]	26.5 [8.79]	36.1 [15.3]

Circular standard deviation of the relative phase between the hands (CSD$_\Phi$) in all tasks in which two hands were involved, presented as mean [between-participants SD]. In-phase and antiphase refer to the coordination patterns; low, medium, and high refer to the frequency conditions. Values are based on 12 participants in all tasks except KT, in which only 11 participants could be analyzed.

Whereas for AP coordination in KTa CSD_Φ increased over all three frequencies, for IP only the increase in variability from the medium- to the high-frequency condition was significant. Taken together, increasing frequency induced higher values of variability (indicating reduced stability) in all tasks, although for UNm the effect was only observed for AP coordination. For KTa (and KT) the frequency-induced increase in variability was more pronounced for AP than IP.

Furthermore, direction affected CSD_Φ in AB, $F(1,11) = 9.22$, $p < .05$, $\eta_p^2 = .46$, and tended to do so in KTa, $F(1,11) = 4.41$, $p = .06$, $\eta_p^2 = .29$. Post-hoc comparisons showed that CSD_Φ calculated at peak flexion of the non-dominant hand was significantly lower than at peak extension (AB: 13.0° [3.43°] and 14.3° [3.74°]; KTa: 21.2° [6.03°] and 22.3° [6.94°]), for peak flexion and peak extension, respectively). The interaction between pattern and direction in AB, $F(1,11) = 16.7$, $p < .01$, $\eta_p^2 = .60$, and corresponding post-hoc comparisons showed that the difference in CSD_Φ between peak flexion and extension in AB was only present during IP coordination (11.2° [2.04°] and 13.9° [2.90°] for flexion and extension, respectively). In addition, a tendency for the Frequency x Direction interaction for AB, $F(2,22) = 3.12$, $p = .06$, $\eta_p^2 = .22$, and KTa, $F(1.1,12.1) = 3.71$, $p = .08$, $\eta_p^2 = .25$, suggested that the frequency effect might have been stronger for CSD_Φ determined at peak flexion of the non-dominant hand.

Strategic comparisons

Integrated timing
The contributions of the three sources of interaction were assessed by systematic

comparisons between tasks (see *Introduction*). Starting with the contribution of integrated timing to the stability of bimanual coordination, CSD_ϕ in AB was compared with CSD_ϕ in KT. For each participant, the mean values obtained for the KT conditions were subtracted from those obtained for the corresponding conditions in AB (matched for frequency and pattern). One-sided *t*-tests showed that all conditions differed significantly from zero, $t(10) < -3.20$, $p < .01$, implying that variability was significantly higher in KT. This result confirmed the essential contribution of integrated timing to the stability of bimanual coordination in all conditions. The Pattern x Frequency x Direction repeated-measures ANOVA revealed an effect of frequency, $F(2,20) = 3.87$, $p < .05$, $\eta_p^2 = .28$, a trend for the Pattern x Frequency interaction, $F(2,20) = 3.00$, $p = .07$, $\eta_p^2 = .23$, and a significant Pattern x Frequency x Direction interaction, $F(2,20) = 3.89$, $p < .05$, $\eta_p^2 = .28$. Post-hoc comparisons showed that the difference between AB and KT increased with frequency (due to larger increases in CSD_ϕ in KT compared to AB, see Table 2.2). During AP coordination this increase was observed both at peak flexion and peak extension, but during IP it was observed only at peak flexion. In addition, a trend for direction, $F(1,10) = 3.65$, $p = .09$, $\eta_p^2 = .27$, and a significant Pattern x Direction interaction, $F(1,10) = 13.7$, $p < .01$, $\eta_p^2 = .58$, were obtained. Post-hoc comparisons showed that the CSD_ϕ difference was larger for peak flexion than for peak extension during IP coordination. This revealed that the stability difference between the timing of the flexion and extension peaks during IP performance in AB (see *Variability of relative phasing between the hands*) resulted from more pronounced contributions of integrated timing to coordinative stability when timing peak flexion.

Since the results of Ridderikhoff, Peper et al. (2005) suggested that corrections of relative phase errors represent a secondary mechanism that is less prominent when integrated timing alone suffices to stabilize bimanual coordination, the contribution of integrated timing was also evaluated by comparing AB to UNm. This was done by subtracting the values of the UNm conditions (with a zero phase shift) from the matched AB conditions for all participants. One-sided *t*-tests revealed that in all conditions CSD_ϕ was significantly higher in UNm than in AB, $t(11) < -5.04$, $p < .001$. The ANOVA revealed a tendency for the Pattern x Frequency interaction, $F(2,22) = 2.69$, $p = .09$, $\eta_p^2 = .20$, suggesting that in AP the difference between AB and UNm tended to increase with increasing frequency. In addition, a tendency for direction, $F(1,11) = 3.31$, $p = .096$, $\eta_p^2 = .23$, and a significant interaction between pattern and direction, $F(1,11) = 22.7$, $p < .001$, $\eta_p^2 = .67$, were obtained. Similar to the comparison between AB and KT, this interaction showed that in IP the CSD_ϕ difference between AB and UNm was larger for peak flexion than for peak extension. In sum, the comparison between AB and UNm revealed similar

effects of integrated timing as the comparison of AB to KT. Integrated timing led to lower values of variability during IP when calculated at peak flexion, while in AP the contribution of integrated timing tended to be larger at higher frequencies.

Error correction

The stabilizing role of error correction was assessed by comparing CSD_ϕ between KTa and UNm. Only the conditions with a zero phase shift between passive movement and metronome were compared, since the effect of the distractor (i.e., the metronome for KTa and passive movements for UNm) was not relevant for this comparison. For all participants, the values of UNm were subtracted from the matched KTa conditions, and submitted to a one-sided *t*-test. In all conditions CSD_ϕ was significantly larger in UNm, except for IP at the high frequency and AP at the medium frequency (see Table 2.2). The Pattern x Frequency x Direction ANOVA revealed no effects on the difference between UNm and KTa, implying that the stabilizing effect of error correction was not affected by these factors.

The susceptibility of the error-correction process to the distracting metronome was evaluated by comparing CE_ϕ between KT and KTa. For each participant the values of the KT conditions were subtracted from the corresponding KTa conditions (matched for pattern and frequency). One-sided *t*-tests demonstrated significant differences between the matched tasks for the 0° and +30° phase shifts (see Table 2.3). The Pattern x Frequency x Direction x Shift ANOVA on the difference in CE_ϕ yielded an effect of shift, $F(2,20) = 25.4$, $p < .001$, $\eta_p^2 = .71$, and a Frequency x Shift interaction, $F(2.3,23.1) = 4.48$,

Table 2.3
Constant error in the relative phase in KT and KTa

	In-phase			Antiphase		
	Low	Medium	High	Low	Medium	High
KT	-15.2 [5.13]	-7.73 [8.82]	-3.89 [15.6]	13.9 [12.5]	6.61 [26.8]	15.7 [20.8]
KTa (-30°)	-13.3 [8.39]	-6.03 [13.9]	-5.54 [14.8]	11.9 [13.4]	6.82 [26.9]	10.3 [23.0]
KTa (0°)	-6.32 [9.64]**	-1.12 [12.6]	9.19 [20.3]*	11.2 [22.4]	0.66 [24.2]	21.0 [34.0]
KTa (+30°)	-3.80 [10.4]**	3.96 [14.5]**	16.6 [23.5]**	6.23 [14.8]	1.59 [23.4]	47.1 [37.0]**

CE_ϕ in KT and KTa presented as mean [between-participants SD]. The phase shift between the brackets indicates the phase shift of the auditory signal relative to the passive movement (+30°: auditory signal was delayed, -30°: auditory signal was advanced). Negative values of CE_ϕ imply that the active hand was leading the passive hand. Asterisks indicate that the difference between KTa and the matched KT condition was significant (* p < .05, ** p <.01). In-phase and antiphase refer to the coordination patterns; low, medium, and high refer to the frequency conditions. Values are based on 11 participants, the number of participants that could be analyzed in KT.

$p < .05$, $\eta_p^2 = .31$. Post-hoc comparisons showed that the attraction to the distracting metronome was strongest for the high-frequency condition (see Figure 2.1). Whereas for the low and medium frequency only the delayed metronome (+30°) differed significantly from the unshifted metronome (0°), in the high-frequency condition this was also the case for the -30° shift. Moreover, for the +30° phase shift the attraction was significantly stronger in the high-frequency condition compared to the other frequency conditions.
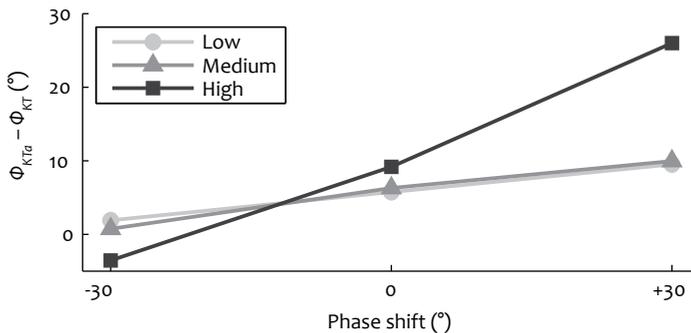

Figure 2.1. Effects of the distracting metronome on kinesthetic tracking in task KTa, presented for the three movement frequencies. The mean relative phase in KTa is presented relative to task KT in which no metronome is present (Φ_{KTa} - Φ_{KT}), as a function of the phase shift between the passive movements and the distracting metronome. A positive shift indicates that the metronome was delayed relative to the passive movements.

Phase entrainment

Phase entrainment results in (unintentional) attraction of the phasing of the active movement towards that of the passive movement. Hence, the entraining influences of the passive movements were evaluated by examining the changes in Ψ in response to the applied phase shifts in UNm. In particular, the +30° shift was predicted to delay the active movements relative to the metronome (reflected by $\Psi > 0$), whereas the opposite effect was expected for the -30° shift. To test this prediction, the mean values obtained for UN performance for each frequency (low: -4.71° [24.2°]; medium: -18.8° [31.1°]; high: -21.6° [27.7°]) were subtracted from the matched UNm conditions for each participant. One-sided t-tests showed that significant differences between the matched tasks existed when the passive movements were advanced relative to the metronome (-30°) at the low frequency in IP and AP (i.e., -36.6° [19.4°] and -28.6° [23.9°], respectively), $t(11) < -3.01$, $p < .05$, and when movements were not shifted (0°) at the low and medium frequency during IP coordination only (i.e., -24.4° [26.5°] and -38.9° [24.3°], respectively), $t(11) < -2.53$, $p < .05$.

The Pattern x Frequency x Direction x Shift ANOVA revealed an effect of shift, $F(2,22)$ = 6.46, $p < .01$, $\eta_p^2 = .37$, and non-significant tendencies for pattern, $F(1,11) = 4.46$, $p = .06$, $\eta_p^2 = .29$, and frequency, $F(2,22) = 3.00$, $p = .07$, $\eta_p^2 = .21$. The effect of shift showed that the passive movements had a significant effect on the phasing of the unimanual movements. The difference between UNm and UN steadily decreased over the phase shifts (-30°: -13.4° [27.1°]; 0°: -8.56° [23.9°]; +30°: 0.64° [30.5°]). Thus, the direction of the effect was in agreement with our expectations. Note, however, that the difference between UNm and UN approached 0° when the passive movements were phase delayed, rather than at the 0° phase shift. This was probably caused by the general tendency to advance the metronome during UN. As a result, the 0° phase shift between the passive movement and the metronome in fact induced a phase advance of the passive movement with respect to the actual movement of the non-dominant hand. The trend of pattern indicated that the difference between UNm and UN was larger in IP, suggesting stronger entrainment during IP coordination. The frequency tendency suggested that participants were attracted more strongly to the passive movements at lower frequencies, resulting in a larger difference between UNm and UN. However, these interpretations were not substantiated by interactions with Shift.

Error correction correlation

The error correction correlation between the signed error and the subsequent half cycle (R_{EC}) was compared for the three tasks in which error correction could be present: AB, KT, and KTa. As motivated in Kinematics analysis, the values obtained for these tasks were normalized with respect to the baseline values obtained for UNm[4]. The average normalized R_{EC} values per task were all significantly different from zero (i.e., -0.08 [0.08] in AB; -0.26 [0.04] in KT; and -0.23 [0.09] in KTa), $t(10) < -3.87$, $p < .01$. The Task x Pattern x Frequency x Direction ANOVA revealed an effect of task, $F(2,20) = 30.7$, $p < .001$, $\eta_p^2 = .75$, a Task x Direction interaction, $F(2,20) = 6.25$, $p < .01$, $\eta_p^2 = .39$, a tendency for a Frequency x Direction interaction, $F(2,20) = 2.76$, $p = .09$, $\eta_p^2 = .22$, a Task x Frequency x Direction

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4   For comparison the non-normalized R_{EC} values were also analyzed, including UNm as an additional level of the factor task. Results revealed similar effects: at the lower frequencies the amount of error correction was significantly smaller in AB than in KT and KTa. At the highest frequency, the amount of error correction (during the flexion half cycle) was larger in AB, with R_{EC} values that did not differ from the corresponding conditions in KT and KTa. This was true during IP and AP. In addition, the amount of error correction was larger in KT and KTa than in UNm in all conditions. In AB the amount of error correction was larger during the flexion than the extension half cycle. As a result, AB differed significantly from UNm in all conditions for the flexion half cycle, but no difference was found between UNm and AB for the extension half cycle.

interaction, $F(4,40) = 3.68$, $p < .05$, $\eta_p^2 = .27$, and a Task x Pattern x Frequency x Direction interaction, $F(4,40) = 2.99$, $p < .05$, $\eta_p^2 = .23$. The effect of task showed that the values in KT and KTa were significantly more negative (indicating stronger error corrections) than that in AB, whereas no difference existed between KT and KTa (cf. Figure 2.2). Post-hoc pairwise comparisons of the four-way interaction revealed that during antiphase coordination in AB, the high-frequency condition resulted in a significant increase in error correction during the flexion half cycle (i.e., error correction during the half cycle following the error at peak extension). This increased level of error correction was statistically similar to the corresponding values in KT and KTa (see Figure 2.2). In addition, this interaction revealed stronger error correction in KT during the extension half cycle (compared to the flexion half cycle) at the low frequency during AP coordination.
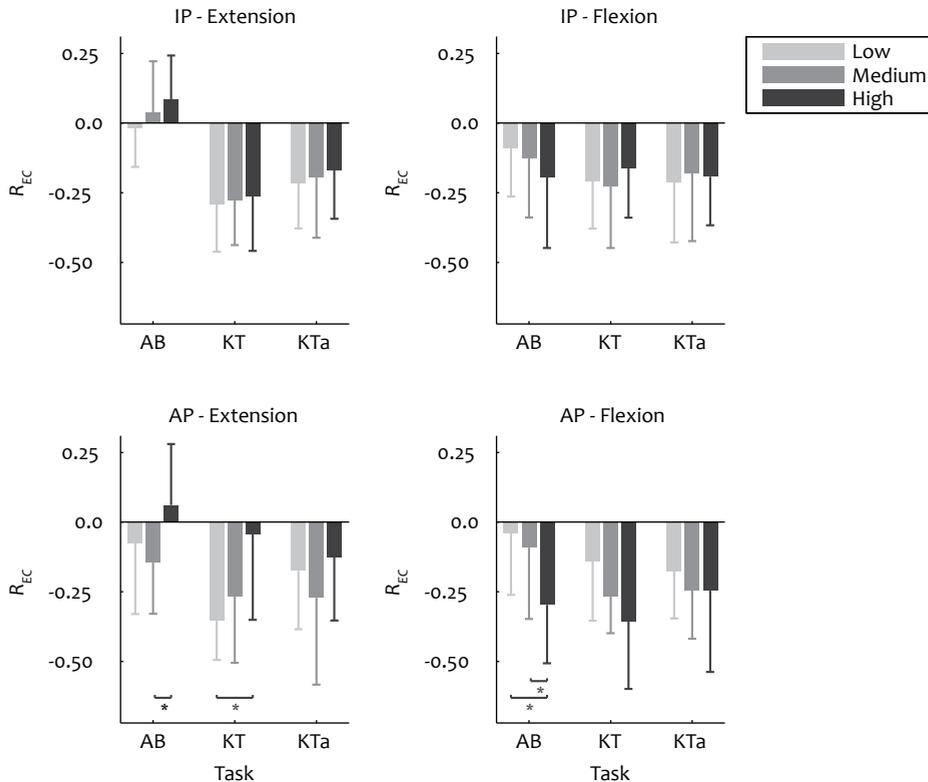
Figure 2.2. Error correction correlation (R_{EC}; normalized to UNm) as obtained for the extension half cycle and the flexion half cycle, presented for AB, KT, and KTa for in-phase (IP) and antiphase (AP) coordination during the low-, medium- and high-frequency conditions. Asterisks indicate significant differences between frequency conditions within a specific task (** p < .01; * p < .05). Error bars indicate the between-participants SD.

EMG: *activation pattern*

The activation patterns were similar to those found by Ridderikhoff, Peper et al. (2005). During kinesthetic tracking the muscles in the passively moving dominant hand were not relaxed, but showed EMG activity similar to that observed during active movements (see Figure 2.3). In the unimanual conditions (UN and UNm), however, no activation of the dominant hand was evident. This indicated that the muscle activity in the passively moving hand during kinesthetic tracking was not merely the effect of its passive movements or the movements of the other hand. When tracking the passive movements of the

Figure 2.3. Average muscle activation patterns (normalized to %MVC) presented for the non-dominant hand (upper panels) and the dominant hand (lower panels) for FCR and ECR for the low-, medium-, and high-frequency conditions. EMG amplitudes were determined for eight phases of the movement cycle, and averaged over participants and coordination pattern.

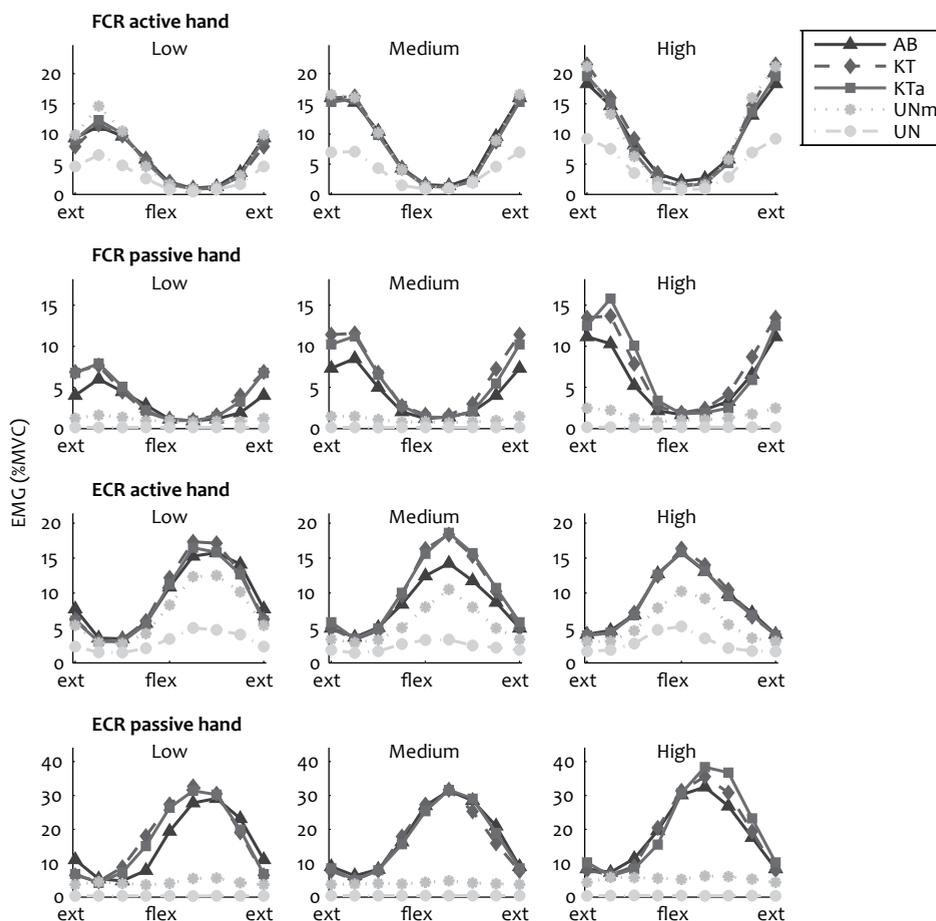dominant hand, participants were 'moving along' by activating the muscles in the non-dominant hand as if they were generating the movements themselves. However, given the strength of the motor, this muscle activation did not have any effect on the actual passive movements. Ridderikhoff, Peper et al. (2005, 2007) argued that this spontaneous muscle activity helps to improve task performance in the tracking task.

EMG: *weighted coherence*

C_w as obtained for the flexion and extension muscles was submitted to a Task x Pattern x Frequency x Muscle ANOVA. Results showed effects of task, $F(1.8,17.8) = 73.9$, $p <$ .001, $\eta_p^2 = .88$, frequency, $F(1.3,12.6) = 7.53$, $p < .05$, $\eta_p^2 = .43$, and a Task x Frequency interaction, $F(6,60) = 2.36$, $p < .05$, $\eta_p^2 = .19$. Post-hoc analysis revealed that all tasks differed significantly from one another, except KT and KTa. C_w (reflecting the strength of coupling between homologous muscles) increased if more interaction sources were involved, with the lowest value in UNm (0.52 [0.11]), larger values in KT and KTa (0.81 [0.08] and 0.81 [0.09]) and the largest value in AB (0.85 [0.04]). In AB the low frequency (0.85 [0.08]) and high frequency (0.83 [0.08]) differed significantly, while frequency had no effect on C_w in the other tasks. Furthermore, a Pattern x Muscle interaction, $F(1,10) =$ 19.0, $p < .01$, $\eta_p^2 = .66$, was obtained, as well as a tendency for the Task x Pattern interaction, $F(3,30) = 2.48$, $p = .08$, $\eta_p^2 = .20$, and significant interactions between task, pattern, and muscle, $F(3,30) = 3.33$, $p < .05$, $\eta_p^2 = .25$, and between muscle and frequency, $F(2,20) = 7.91$, $p < .01$, $\eta_p^2 = .44$. Post-hoc analysis of the Task x Pattern x Muscle interaction revealed that for the flexors C_w was lower in AP than in IP in AB, KT, and KTa. For the extensors, however, C_w was significantly larger in AP than in IP in KT and KTa (see Figure 2.4).
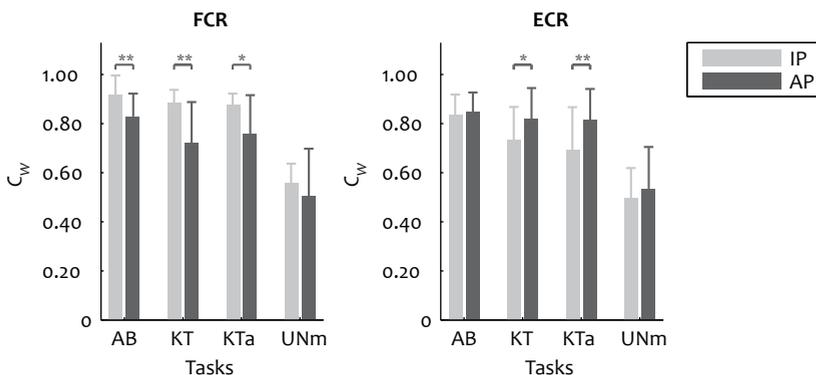

Figure 2.4. Weighted coherence (C_w), as obtained for FCR and ECR muscles, presented for in-phase (IP) and antiphase (AP) performance in the four tasks in which both hands were involved. Asterisks indicate significant differences between in-phase and antiphase within a specific task (** p < .01; * p < .05). Error bars indicate the between-participants SD.

Post-hoc analysis of the Frequency x Muscle interaction showed that, whereas for the flexors C_W was not affected by movement frequency (low: 0.73 [0.06]; medium: 0.77 [0.07]; high: 0.79 [0.07]), for the extensors C_W became smaller with increasing frequency (low: 0.77 [0.10]; medium: 0.73 [0.11]; high: 0.70 [0.10]). As a result, C_W was significantly larger for the flexors than the extensors in the high-frequency condition.

In sum, C_W of the EMG signals was significantly larger when more sources of interlimb interaction were involved. When integrated timing was involved (i.e., in AB), C_W decreased with increasing frequency. Overall, such a decrease in C_W with increasing frequency was observed for the extensors, but not for the flexors. Contrary to the results of Ridderikhoff, Peper et al. (2005), the coherence between the muscles varied over IP and AP coordination: for the flexors C_W was larger during IP than AP (for AB, KT, and KTa), for the extensors the opposite was true (for KT and KTa).

DISCUSSION

Since movement frequency has been identified as a primary control parameter in experiments on phase transitions in bimanual coordination, the goal of this study was to examine how movement frequency affected three sources of interlimb interaction purportedly underlying coordinative stability: (1) integrated timing of feedforward signals, (2) afference-based correction of relative phasing errors, and (3) phase entrainment by contralateral afference. Frequency-induced changes in the contributions of these interaction sources to bimanual stability were estimated based on strategic comparisons of five tasks (AB, KT, KTa, UNm, and UN). Overall, it was shown that the strength of coupling between the hands, as reflected by the weighted coherence of the EMG signals of homologous muscles (C_W), was greater when more interaction sources contributed to coordinative stability (cf. Ridderikhoff, Peper et al., 2005). Moreover, the results revealed an interesting shift in the relative prominence of open-loop and closed-loop control processes, which will be discussed below. However, we first outline the main effects of movement frequency on the three sources of interaction.

Frequency effects on the three sources of interaction

As anticipated, in all tasks the variability of coordination increased with increasing frequency, indicating reduced stability. With our analysis, we examined how movement frequency affected the contribution of each of the three sources of interlimb interaction.

It was expected that the contribution of integrated timing to coordinative stability would decrease with increasing frequency, especially during antiphase coordination (cf. Grossberg et al., 1997). The resulting increase in variability was predicted to result in a more prominent influence of error correction (cf. Ridderikhoff, Peper et al., 2005).

The increase in variability with increasing frequency was lower in AB than KT (and tended to be lower in AB than UNm during antiphase coordination). At first sight, this may be taken to suggest that the relative contribution of integrated timing to coordinative stability increased with increasing movement frequency. However, another picture arises when the error correction correlation results are also taken into account. Analysis of the normalized R_{EC} values revealed that error correction became more prominent during active bimanual antiphase coordination with increasing frequency. This indicated that, as anticipated, integrated timing alone was no longer sufficient to stabilize the antiphase pattern and that error correction was required to correct the resulting relative phasing errors. These corrections were observed during the flexion phase of the movement, and were as prominent as those found in corresponding conditions in KT and KTa. The implications of these results are discussed in more detail in the next section.

The manifestations of error correction during antiphase performance in AB may be the reason why the stability difference between in-phase and antiphase did not increase with frequency. Typically, antiphase is more variable than in-phase coordination (e.g., Kelso et al., 1986; Post, Peper, Daffertshofer, & Beek, 2000; Sternad, Amazeen, & Turvey, 1996) and this difference in stability tends to amplify with increasing frequency (Kelso et al., 1986; Post, Peper, & Beek, 2000). However, although the stability difference between the two coordination patterns was nearly significant for AB, no interaction between movement pattern and frequency was obtained in the present experiment. It is conceivable that, in line with our task instructions, participants counteracted frequency-induced reduction of stability of the antiphase pattern by means of the observed error corrections. Thus, the increased signs of error correction may be associated with intentional intervention aimed at stabilizing the antiphase coordination pattern (cf. Lee et al., 1996).

Error correction was expected to become less effective at higher frequencies as a result of the reduction in time available for feedback processing. The results in this regard were mixed. Both the amount of error correction (as indexed by R_{EC}) and its stabilizing influences (reflected by the comparison of CSD_ϕ between KTa and UNm) remained unaffected by movement frequency. On the other hand, the error-correction process appeared to be less robust at the high frequency, which induced marked attraction to the phase-shifted metronome in KTa.

Finally, phase entrainment strength was predicted to be smaller at higher frequencies, resulting from the drop in amplitude that typically accompanies an increase in movement frequency. This prediction was based on Ridderikhoff, Peper et al. (2005), who demonstrated that reducing movement amplitude by 50% induced a clear reduction in entrainment strength. In the present experiment, movement amplitude was indeed smaller for the higher frequencies (see *Appendix B*). However, no effect of movement frequency on phase entrainment strength was observed, as the shifts in Ψ were immune to the frequency variations. Perhaps the observed reduction in amplitude of about 30% was not sufficient to induce a significant change in entrainment strength, or such a change may have been masked by another frequency-induced effect. The absence of a frequency effect was in accordance with the study by Serrien et al. (2001), which showed that coordination was disrupted by passive movements of a third limb (i.e., a leg), but that disruption was unaffected by a change in frequency.

Open-loop and closed-loop control

As explained in the preceding, the increase in frequency induced a qualitative change in the stabilization process underlying active bimanual performance. Whereas error corrections were hardly noticeable at moderate frequencies, they became clearly manifest (during the flexion movement) when antiphase was performed at the high frequency. Thus, combined contributions of integrated timing and error correction appeared to be required to stabilize the antiphase pattern at these frequencies. This combination of interaction sources was more effective than error correction alone. After all, the observed critical frequencies were considerably higher for active bimanual performance than for kinesthetic tracking (i.e., $F_{crit,AB} > F_{crit,KT}$).

This combination of error correction and integrated timing resembles the situation observed during kinesthetic tracking. Recall that the bilateral EMG activation patterns during kinesthetic tracking were similar to those observed in active bimanual coordination (cf. Figure 2.3, see also Ridderikhoff et al., 2005). Activating muscles in the passive limb has been demonstrated to result in more effective stabilization of the movement pattern; participants who performed kinesthetic tracking while keeping the passively moving hand relaxed showed higher variability in the relative phase between the hands than participants who activated their passively moving hand as if they were moving along (Ridderikhoff et al., 2007). Muscle activation in the passive limb may enhance the error correction process, as active movements lead to differences in kinesthetic afference compared to passive movements. For instance, activation of the limb in KT may have

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enhanced accuracy of the afferent feedback from this arm via the muscle spindles (Murphy & Martin, 1993). In addition, Ridderikhoff et al. (2007) suggested that the observed bilateral muscle activity resulted in enhanced stability because the resulting efference copies generated a bilateral reference for afference-based error correction. This reference signal allows for a prediction of the sensory consequences and may thereby enhance the error correction process. Hence, participants appear to actively incorporate integrated timing into the control process, to enhance their ability to adjust relative phasing errors. The communality between this strategy in kinesthetic tracking and that observed for high-frequency antiphase performance during active bimanual coordination suggests that during the less common tracking task, control processes are exploited that are also available for normal bimanual coordination.

Although the mechanism in both situations appears to be similar, the coordination pattern is significantly less stable during kinesthetic tracking than during active bimanual coordination. This difference may be associated with the fact that during kinesthetic tracking error corrections can only be actuated by one of the hands, while during active bimanual coordination both hands can contribute to the correction process. In addition, the motor control model of Wolpert and Ghahramani (2000) may provide a more specific account of the differences between kinesthetic tracking and active bimanual coordination in this regard. In this model, motor control is described in terms of motor commands and sensory feedback. Both aspects are used in controlling the movement: via a 'dynamics predictor' the efference copy is used to predict the current state of the system, which is further processed via the 'sensory predictor' to predict the sensory feedback. By comparing the actual feedback and the predicted feedback, the estimate of the system's current state is updated, after which a subsequent action (e.g., a correction) can be executed (see Figure 3 in Wolpert & Ghahramani, 2000). For kinesthetic tracking, however, the prediction of the current state (via the 'dynamics predictor') will not fully match the actual state, since the motor commands cannot influence the passive hand trajectory. As a consequence, the comparison of the predicted sensory feedback and the actual sensory feedback will signal a small mismatch that may induce sensory-based corrections that are not particularly useful for stabilizing the coordination pattern. The results of the present experiment indicated that the deteriorating effects of this mismatch between actual and predicted feedback increase with frequency. This was illustrated by the difference in variability between the three frequency conditions and the relatively low critical frequency obtained for kinesthetic tracking. Thus, our results indicated that the combination of integrated timing and error correction is more effective if the reference frame, based on motor commands, matches the movements that are

executed by the hands, as is the case during normal bimanual coordination.

During active bimanual coordination, the combination of error correction and integrated timing was only manifest in the high-frequency condition. This implies that at lower frequencies the stability of active bimanual coordination primarily derives from open-loop processes, which is in accordance with previous findings and suggestions in literature (Baldissera et al., 2006; Grossberg et al., 1997; Spencer, Ivry, Cattaert, & Semjen, 2005). Hence, as long as open-loop control is sufficient to maintain coordinative stability, perception of the relative phase between the hands plays a subordinate role in the control process. Contrary to other suggestions (Bingham et al., 2001; Wilson et al., 2003; Wilson et al., 2005), this implies that the differences in stability in the execution of in-phase and antiphase coordination and the increase in this difference with increasing movement frequency are not primarily due to the limitations in the perception of relative phase and its variability.

At the same time our results are not in line with a purely open-loop account either. According to the neural network model of Grossberg et al. (1997), the transition from antiphase to in-phase coordination with increasing movement frequency can be accounted for solely in terms of open-loop control. However, the observed increased contribution of error corrections reveals that this loss of stability can partly be counteracted by closed-loop processes if necessary. The influences of these feedback-based correction processes only show up when these adjustments are actually needed, that is, when the feedforward control is not sufficiently accurate. The frequency dependence of these contributions is in agreement with the observation that although patients with severe loss of somatosensory feedback showed similar characteristics as control subjects when performing a bimanual coordination task in the absence of visual feedback, healthy controls were able to perform antiphase coordination at significantly higher frequencies than these patients (Spencer et al., 2005).

Taken together, whereas for moderate frequencies bimanual in-phase and antiphase performance derived its stability primarily from open-loop control, at higher frequencies the combination of both open-loop and closed-loop control appeared essential in stabilizing the antiphase pattern. In contrast to the suggestion of Wilson et al. (2005), these results may be taken to suggest that action leads perception rather than vice versa, with integrated timing providing a bilateral reference frame via efference copies (i.e., via the 'sensory predictor'), to which the afferent signals can be compared.

On this account, the loss of stability at a critical frequency results from reduced stabilization of the combination of integrated timing and error correction. Following Grossberg et al. (1997), the relative contribution of integrated timing to coordinative

stability may be expected to deteriorate with increasing frequency. At the same time, we found that the error correction process became less robust at the higher frequency, probably associated with the reduction in time available for signal processing (Cohen, 1970, 1971; Rosenbaum, 1991). Because sensorimotor delays are more or less fixed, afferent information needs to be processed faster in order to subserve effective error corrections at higher frequencies. In a feedforward model, continuous comparisons between predicted and actual states may yield anticipation of future errors, so that feedback can be used with a negligible delay (Desmurget & Grafton, 2000). However, the present results suggest that eventually this is not sufficient for stabilization of the bimanual coordination pattern. Apparently, the predictions used in the feedforward model to overcome the sensorimotor delays are insufficient to compensate the overall loss of stability of the antiphase pattern with increasing frequency.

Timing of flexion and extension

In task AB several results revealed differences between (peak) flexion and extension, which were absent in the other tasks. First, the increasing difference in CSD_{ϕ} between AB and KT with frequency was larger at peak flexion than at peak extension of the actively moving hand, suggesting a more efficient contribution of integrated timing at the moments of peak flexion. For in-phase coordination this increase was significant at peak flexion only, whereas during antiphase it was significant at both reversal points. Furthermore, in AB the increase in the error correction correlation during antiphase performance in the high-frequency condition was only present during the flexion half cycle. In addition, during in-phase coordination the weighted coherence of homologous muscles was larger for the flexors than the extensors. Taken together, these results indicate that active bimanual coordination was directed more towards peak flexion (viz., larger stabilizing effect of integrated timing) and the flexion phase of the movement (viz., more error correction and higher weighted coherence). These results are in line with previous studies showing that anchoring effects are stronger at peak flexion than peak extension (Carson, 1996; Carson & Riek, 1998a; Maslovat, Chua, Lee, & Franks, 2006), and that attentional demands are larger during peak flexion and the flexion phase of the movement than during peak extension and the extension phase of the movement (Ridderikhoff et al., 2008). Note that in the present experiment this attentional focus may have been amplified by the task instructions regarding the coordination with the metronome, in particular during in-phase performance. In this condition participants were instructed to synchronize peak flexion of both hands with the metronome beeps.

Concluding remarks

The present experiment showed that movement frequency had differential effects on the way in which three sources of interlimb interaction (viz., integrated timing of feedforward signals, afference-based error correction of relative phase errors, and phase entrainment by contralateral afference) contributed to coordinative stability. In general, the results showed that the interplay between the sources of interaction changed as a function of movement frequency. Whereas during active bimanual coordination at low frequencies integrated timing sufficed to stabilize the antiphase pattern, increasing manifestations of error correction were present at high frequencies. Thus, increasing movement frequency was found to invoke a shift from (predominantly) open-loop to closed-loop control during bimanual rhythmic performance. This observed shift in control can be understood in terms of a forward model for sensorimotor integration, in which sensory signals are compared to values predicted based on efference copies. Our combined results indicate that the error correction process probably involves a bilateral reference frame, derived from the motor commands sent to the two hands involved in the coordination task.

APPENDIX A. SCALED-FREQUENCY TRIALS: PROCEDURE AND PASSIVE MOVEMENT CALCULATIONS

Participants were selected on the basis of their critical movement frequencies as determined for tasks AB and KT, during scaled-frequency trials. AB trials were administered first, so that the recorded movements could be used to generate the passive movements imposed during KT (see below). Both IP and AP trials were administered (although the analysis was restricted to the AP trials, IP trials were included to avoid a difference in exposure between the coordination patterns, in view of their comparison in the experiment). Frequency was scaled from 1.0 Hz to 3.5 Hz in steps of 0.25 Hz (resulting in 11 bins; trial duration ca. 90 s). The first bin lasted for 20 cycles to enable participants to perform the required coordination pattern in a stable fashion before frequency was increased. The subsequent bins lasted for 15 cycles. IP and AP trials were presented in separate blocks of six trials each. Each block started with one practice trial at 1 Hz (duration 30 s) and one practice trial in which frequency was scaled. If needed, up to five additional practice trials were performed. In view of potential phase transitions participants were told that adhering to the prescribed frequency was more important than performing the required coordination pattern.

For both coordination patterns, passive movements in KT were based on the IP trials in AB. This ensured that the tracking task for both coordination patterns entailed the same level of phase variability in passive movements. Moreover, in this manner the phase transitions that were expected for the AB-AP condition did not intrude in the AP tracking task. For each participant, passive movements were based on the three AB-IP trials for which the difference between the executed and required frequency was minimal. The dominant-hand movements of these trials were low-pass filtered (2nd-order bidirectional Butterworth filter, cut-off frequency 18 Hz). To avoid transient effects at the start of the trial, the first cycle was removed. For the KT-AP trials, the amplitudes and average joint angles of the passive movements were adjusted so that they corresponded to the characteristics of three AB-AP trials that showed the best match between executed and required frequency. Thus, the mean amplitudes and the centers of oscillation in the KT-AP trials corresponded to those in the AB-AP condition, whereas the phase variability was identical to that obtained for AB-IP performance. The trajectories were multiplied with a windowing function to generate a smooth increase and decrease in the amplitude of the passive movements in the first and last two cycles, respectively. The three passive movement trajectories for each coordination pattern were presented twice in random order.

APPENDIX B. PASSIVE MOVEMENT CHARACTERISTICS

Characteristics of the passive movements of the dominant hand were analyzed to delineate potential differences over conditions. Using a 3 (Frequency) x 2 (Pattern) repeated measures ANOVA, movement amplitude, coefficient of variation of cycle duration (CV_{CD}), and average joint angle of the passive movements were analyzed (see Table B.1). During AP CV_{CD} was larger in the high-frequency condition as compared to the low-frequency condition. Movement amplitude decreased significantly over all frequency conditions. Average joint angle differed significantly between IP (-33.7° [16.2°]) and AP (11.7° [22.9°]), i.e., the center of oscillation corresponded to a flexed and slightly extended posture, respectively. For IP all frequency conditions differed significantly from each other (i.e., with a more flexed posture with increasing frequency), whereas for AP the low and medium-frequency condition differed significantly from the high frequency (which showed a more extended posture). In sum, manipulation of movement frequency resulted in significant changes in cycle duration variability, average joint angle, and, as expected (cf. *Introduction*), movement amplitude. However, these characteristics were comparable in all tasks for each condition, since the passive movements were derived from the same dominant-hand trajectories during AB performance.

Table B.1
Passive movement characteristics

	In-phase			Antiphase		
	Low	*Medium*	*High*	*Low*	*Medium*	*High*
Amplitude	28.2 [9.61]	24.6 [10.3]	19.0 [9.10]	29.3 [12.4]	26.6 [13.6]	22.0 [11.9]
CV_{CD}	0.05 [0.02]	0.04 [0.01]	0.04 [0.01]	0.04 [0.08]	0.05 [0.02]	0.06 [0.02]
Joint angle	-26.2 [16.6]	-33.9 [17.2]	-41.2 [14.8]	5.58 [19.4]	8.43 [26.5]	21.0 [22.7]

Characteristics of the passive movements used in KT, KTa, and UNm, presented as mean [between-participants SD]. In-phase and antiphase refer to the coordination patterns; low, medium and high refer to the frequency conditions. CV_{CD} is the coefficient of variation in cycle duration.

3

Phase entrainment strength scales with movement amplitude disparity

The present study examined whether coupling influences from unintended afference-based phase entrainment are affected by movement amplitude as such or by the amplitude relation between the limbs. Entrainment strength was assessed by studying how passive movements of the contralateral hand influenced unimanual coordination with a metronome. Results showed that amplitude as such did not affect entrainment strength, whereas the amplitude relation between the hands did. Larger amplitudes of the passive hand relative to the active hand resulted in stronger entrainment. This dependence on relative amplitude implies that entrainment strength does not only depend on the intensity of afferent signals generated in the entraining limb but also on the susceptibility of the entrained limb to these signals.

3

INTRODUCTION

When moving two limbs simultaneously, the limb movements are affected by one another. As a result, movements that are easily executed in isolation can be difficult to execute due to interference effects stemming from the other limb. This can for instance be observed when drawing two different shapes simultaneously (Franz, Zelaznik, & McCabe, 1991), or when executing rhythmic bimanual coordination patterns other than in-phase and antiphase (Zanone & Kelso, 1992). These interactions do not only result from interference at a planning level (Heuer & Klein, 2006; Ridderikhoff, Peper et al., 2005), but also from entraining influences of kinesthetic afferent signals. The latter influences are illustrated by the finding that moving a hand passively results in unintended attraction of active hand movements to these passive movements (Ridderikhoff et al., 2006; Serrien et al., 2001; Swinnen et al., 1995). In the present study, we further examined the longstanding, but still largely unresolved issue of how movement amplitude affects bimanual stability, in particular via unintentional phase entrainment.

For intended bimanual coordination it has been shown that interlimb coupling can be enhanced by increasing movement amplitude (Buchanan & Ryu, 2006; Kudo, Park, Kay, & Turvey, 2006; Ryu & Buchanan, 2004), although the relation between movement amplitude and interlimb coupling has not been consistently evident (Peper & Beek, 1998a, 1998b; Post, Peper, & Beek, 2000). Furthermore, it has been found that interlimb coupling strength in intended bimanual coordination is influenced by the amplitude relation between the limbs: When moving two limbs with different amplitudes, the limb moving with the larger amplitude influences the limb moving at the smaller amplitude more strongly than vice versa. This has been shown in relation to both interlimb coupling strength (Peper, de Boer, de Poel, & Beek, 2008) and movement planning (Spijkers & Heuer, 1995).

The effects of movement amplitude on unintentional entrainment are less well examined. The influence of the amplitude relation between the limbs on entrainment has only been studied for distracting influences of a third limb on the coordination of two other limbs (Serrien et al., 2001). And although entrainment strength in bimanual coordination seemed to be influenced by the strength of the afferent signals, since a reduced amplitude of passive hand movements induced weaker phase entrainment (Ridderikhoff, Peper et al., 2005), that experiment did not allow for a distinction between effects of amplitude as such vs. the amplitude relation between the limbs. Notably, extended analysis of the data of Ridderikhoff, Peper et al. in the present study showed that a change in amplitude was accompanied by a change in the amplitude relation between the limbs (see *Results*).

The aim of the present experiment therefore was to study how movement amplitude influences unintentional phase entrainment: Is it (predominantly) via the amplitude of the hand movements as such or via the amplitude relation between the hands? To answer this question we extended the analysis of the data of Ridderikhoff, Peper et al. (2005) by examining the amplitude relation between the active and passive hand and compared this to the results of a new experiment. In the present article the experiment of Ridderikhoff, Peper et al. (2005) and the new experiment are referred to as Experiment 1 and 2, respectively, and are described in detail below. In the new experiment the amplitude relation between the hands was set to 1:1 for a small and a large amplitude that were similar to the amplitudes in the first experiment. If phase entrainment strength depends primarily on the amplitude relation between the hands, entrainment strength would be equally strong for both 1:1 amplitude relation conditions, irrespective of the movement amplitudes (small vs. large) of the hands. On the other hand, if movement amplitude as such determines the strength of entrainment, the large amplitude condition would show stronger entrainment effects than the small amplitude condition.

METHODS

Participants

Nine volunteers (aged 18-30 years, seven right handed and two left handed, Oldfield, 1971) participated in Experiment 1 and twelve volunteers (aged 19-29 years, all right handed) participated in Experiment 2. Participants gave their written informed consent and were paid a small fee for their services.

Apparatus

Participants sat in a height-adjustable chair with their elbows slightly flexed and their feet supported (see Figure 3.1). Their forearms were placed on armrests in a neutral position (thumbs up, palms facing inward, fingers extended). Both hands were fixated to two flat manipulanda, allowing wrist flexion and extension only. For one hand, the manipulandum registered the wrist movements using a potentiometer, whereas for the other hand the manipulandum controlled the wrist movements by means of a motor (i.e., for active and passive movements, respectively). In Experiment 1 the dominant hand executed active movements and the non-dominant hand was moved passively,

whereas in Experiment 2 the opposite configuration was used. A screen eliminated visual feedback of the hand movements.

In Experiment 2, in addition a vertically oriented bow with light-emitting diodes (LEDs) was presented to provide amplitude feedback (cf. Figure 3.1; Peper et al., 2008). The LED bow consisted of a slightly curved display with a series of 448 LEDs covering a distance of approximately 94 cm (i.e., a change of 1 LED corresponded to a movement of 3.8° around the wrist). The LED bow was placed 150 cm in front of the participant with its center approximately at eye level. Movement amplitude was prescribed for the actively moving hand: An arrow pointed to the center of the LED bow and two illuminated LEDs specified a tolerance range of ± 10% of the target amplitude around this target amplitude[5].

3

Experiment 1
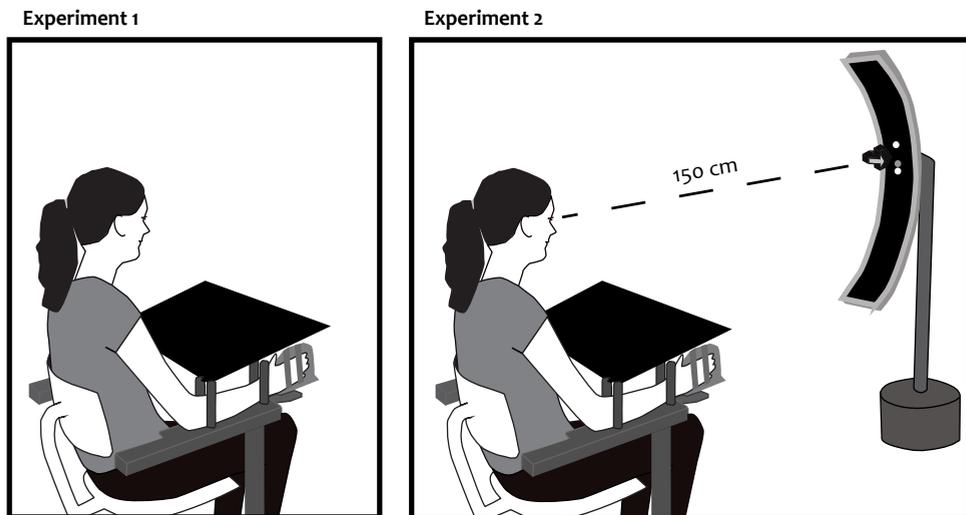
Experiment 2

Figure 3.1. Overview of the experimental setup for Experiment 1 and Experiment 2. Participants executed rhythmic flexion-extension movements about the wrist; a screen eliminated visual feedback of the hand movements. In Experiment 2 a LED-bow was used to prescribe movement amplitude: an arrow pointed to the target amplitude, two illuminated LEDs specified a tolerance range, and a third illuminated LED (here displayed in gray) showed the amplitude the participant was executing.

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5   For the first three participants, the tolerance range was set to ± 3° around the target amplitude, and the amplitude variability (*SD*) was not allowed to exceed 3°. These criteria were broadened for subsequent participants. As kinematics did not differ, data of the first three participants were retained in the analysis.

Task and conditions

Participants executed five different tasks that involved unimanual or bimanual rhythmic flexion-extension movements (cf. Ridderikhoff, Peper et al., 2005). Two of these tasks were analyzed in the present article. In these tasks, participants were required to coordinate the movements of their active hand with a metronome, either in the presence of passive movements of the contralateral hand (task UNm) or without such movements (task UN). Two metronome beeps were presented for each cycle: a high-pitched beep (880 Hz) for one turning point and a low-pitched beep (440 Hz) for the other turning point. Participants were free to choose to which beep they synchronized peak flexion or peak extension, but had to adhere to this choice throughout the experiment. The passive movements were based on recorded movement patterns (cf. Ridderikhoff, Peper et al., 2005), and shifted by -30°, 0°, and +30° relative to the in-phase and antiphase phase relations between the hands. In Experiment 1, individual preferred frequencies were used ranging from 1.2 to 1.6 Hz, while in Experiment 2 movement frequency was set to 1.2 Hz for all participants. In Experiment 1, two different amplitudes of the passive movements were used in task UNm: the amplitude as executed by the participants when performing bimanual coordination (large amplitude condition) and half this amplitude (small amplitude condition). No instructions were given about the amplitude of the active hand. Similar amplitudes were used in Experiment 2 for the passive hand, while in addition this amplitude was prescribed explicitly for the active hand using amplitude feedback. Thus, during Experiment 2 the hands moved at the same amplitude (small or large).

Procedure

In Experiment 1, following one UN practice trial, participants executed 2 (Pattern) x 2 (Amplitude) x 3 (Shift) x 3 (Repetitions) = 36 UNm and 3 UN trials with a trial duration of 35 seconds and 25 seconds, respectively. Trials were randomly divided over two blocks. In Experiment 2, all UNm trials (duration: 23.3 seconds) and UN trials (duration: 25.8 seconds) were randomized in two amplitude blocks. A trial was rerun if the mean amplitude fell outside the tolerance range, if the amplitude variability (*SD*) exceeded 10% of the movement amplitude, or when the wrong pattern was executed. Following one UN practice trial, participants executed 2 (Pattern) x 3 (Shift) x 3 (Repetitions) = 18 UNm and 3 UN trials in each amplitude block, the order of which was counterbalanced across participants.

Analysis

Transients at the beginning of each trial were removed and data were low-pass filtered (2nd-order bi-directional Butterworth filter; cut-off frequency: 15 Hz) prior to analysis. Using a peak-detecting algorithm, movement amplitude was calculated as half the peak-to-peak flexion-extension excursion. The mean movement amplitude was calculated for the active and passive movements. The relative phase between the metronome beeps and peak flexion and extension was determined for each cycle as $\Psi_i = 360° \, (t_{y,i} - t_{x,i}) \, / \, (t_{x,i+1} - t_{x,i})$, where $t_{y,i}$ indicates the time of the ith peak flexion (extension) of the non-dominant hand and $t_{x,i}$ corresponds to the moment of the ith metronome beep specifying peak flexion (extension). Circular statistics (Mardia, 1972) was used to determine the average values of Ψ for each trial.

Statistical analysis

For both experiments, movement amplitude was examined in terms of the relative amplitude between active and passive movements and phase entrainment was examined in terms of the difference in Ψ between UNm and UN ($\Psi_{UNm} - \Psi_{UN}$; indicating the degree to which the active hand was attracted to the passive hand). Both variables were submitted to a repeated-measures analysis of variance (ANOVA) with factors pattern (in-phase, antiphase), amplitude (small, large), and shift (-30°, 0°, +30°). Greenhouse-Geisser adjustment of degrees of freedom was applied if the assumption of sphericity was violated. Effect sizes were based on the partial eta squared (η_p^2, Cohen, 1988). Significant effects were further scrutinized using post-hoc paired-samples t-tests.

RESULTS

In Experiment 1, the amplitude of the passive hand was on average about 20° for the small amplitude and 40° for the large amplitude condition, while the amplitude of the actively moving hand was about 40° in both conditions (see Table 3.1). As a result, the amplitude relation between the two hands differed significantly: For the large amplitude condition the relation of passive and active hand amplitude was about 1:1, whereas for the small amplitude condition it was 1:1.9. In Experiment 2, participants adequately executed the required 20° or 40° amplitudes with the active hand, which resulted in a 1:1 amplitude relation between the active and passive hand for both amplitude conditions (see Table 3.1). The ANOVA confirmed an effect of amplitude in Experiment 1, $F(1,8) = 98.2$, $p < .001$, $\eta_p^2 = .93$, and the absence of this effect in Experiment 2.

Table 3.1

Movement amplitudes of the passive and active limb in small and large amplitude conditions

		Experiment 1			Experiment 2		
		A_{PAS}	A_{ACT}	A_{REL}	A_{PAS}	A_{ACT}	A_{REL}
UNm -30°	S	19.7 [5.83]	36.4 [13.4]	1 : 1.9	19.8 [0.61]	20.4 [0.41]	1 : 1.0
	L	38.1 [10.4]	38.0 [12.7]	1 : 1.0	39.1 [1.41]	40.3 [0.92]	1 : 1.0
UNm 0°	S	19.7 [5.81]	35.7 [12.0]	1 : 1.8	19.8 [0.61]	20.0 [0.50]	1 : 1.0
	L	38.0 [10.4]	38.0 [12.3]	1 : 1.0	39.1 [1.41]	39.6 [1.21]	1 : 1.0
UNm +30°	S	19.7 [5.81]	36.7 [12.7]	1 : 1.9	19.8 [0.61]	20.2 [0.54]	1 : 1.0
	L	38.1 [10.3]	39.6 [13.8]	1 : 1.0	39.1 [1.41]	39.9 [0.83]	1 : 1.0

Movement amplitudes of the passively and actively moving limb (A_{PAS} and A_{ACT}) and the amplitude relation between them (A_{REL} = A_{PAS} : A_{ACT}) as executed in the two experiments for the small (S) and large (L) amplitude, presented for task UNm with phase shifts between the passive movement and the metronome of -30°, 0°, and +30°. Amplitudes are presented as mean [between-participants SD]. Data are averaged over in-phase and antiphase trials.

The entraining influences of the passive movements were evaluated by examining the changes in Ψ in response to the applied phase shifts in UNm (i.e., Ψ_{UNm} - Ψ_{UN}). The ANOVA revealed an effect of shift in experiment 1, $F(2, 16) = 18.8$, $p < .001$, $\eta_p^2 = .70$, and Experiment 2, $F(1.2, 12.7) = 26.5$, $p < .001$, $\eta_p^2 = .71$. All phase shifts differed significantly from each other, revealing attraction of the active hand towards the phase-shifted passive movements (Figure 3.2). Furthermore, a significant interaction between shift and amplitude was only observed in Experiment 1, $F(2, 16) = 3.86$, $p < .05$, $\eta_p^2 = .29$ (cf.

Figure 3.2; Ridderikhoff, Peper et al., 2005), revealing stronger entraining influences for the large amplitude. In Experiment 2, no difference in entrainment strength was observed between the small and large amplitude (Figure 3.2). Results thus showed that entrainment strength was not influenced by amplitude as such (Experiment 2), but by the amplitude relation between the hands (Experiment 1)[6].
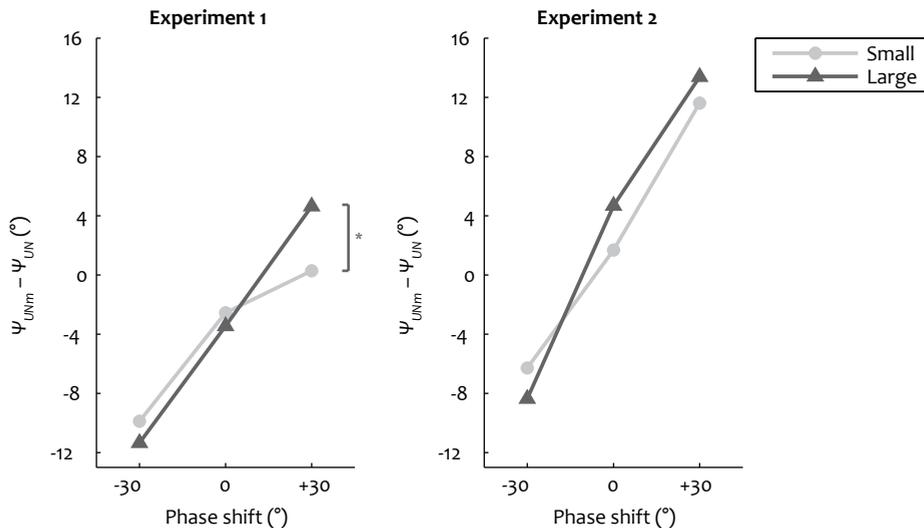
Figure 3.2. Phase entrainment by the passive movements as obtained for the small and large amplitude conditions for Experiment 1 and Experiment 2. The mean relative phase between the active hand movements and the metronome in task UNm is presented relative to UN (Ψ_{UNm} - Ψ_{UN}), for the three phase shifts relative to the metronome as applied to the passive hand movements. Significant differences between amplitudes are indicated with * (p < .05).

Discussion

The aim of the present study was to examine whether the strength of unintended phase entrainment is influenced (predominantly) by movement amplitude as such or by the amplitude relation between the hands. Results showed that phase entrainment

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6   To test for confounding influences of the amplitude feedback on the LED-bow, a control experiment was conducted in which nine new participants were instructed to move their active hand with a small or large amplitude in the absence of LED-bow feedback. After a brief practice session, participants performed the two different amplitudes consistently. Results revealed no change in the amplitude relation between the active and passive hand for the small and large amplitude (i.e., no effect of amplitude, $F(1,8) = 0.51$, $p > .49$), and, as observed in Experiment 2, phase entrainment to the contralateral hand was equally strong for both amplitude conditions (i.e., no interaction between amplitude and shift, $F(2,16) = 0.64$, $p > .54$).

strength was not influenced by amplitude as such, contrary to expectations based on the HKB-model, in which overall interlimb coupling strength scales with amplitude (Haken et al., 1985). Thus, the previously obtained effects of movement amplitude on entrainment strength (Ridderikhoff, Peper et al., 2005) appear to have been mediated by the asymmetry in amplitude between the hands, in accordance with coupling strength effects obtained for intentional bimanual coordination (Peper et al., 2008). The influence of amplitude disparity rather than amplitude as such on entrainment strength may also explain why in a previous study the decrease in amplitude that accompanied increasing frequency did not affect entrainment strength (Chapter 2), because in that study the amplitude relation was about 1:1 in all frequency conditions.

As mentioned in the Methods, the two experiments reported in the present study used a different configuration of passive and active movements. In Experiment 1 the non-dominant hand was being moved by the motor, whereas the dominant hand was moved passively in Experiment 2. Although, in principle, this may have constituted a confounder in the present comparison, this appears to be rather unlikely for two reasons. First, the influence of hand dominance on phase entrainment strength has been studied explicitly for a wide range of phase shifts between the metronome and the passive hand and results showed that attraction to the contralateral hand was not affected by hand dominance (Ridderikhoff et al., 2006). Second, hand dominance is presumed to be related to cortical processes as a result of hemispherical lateralization (e.g., Serrien, Ivry, & Swinnen, 2006), whereas the phase entraining influences of contralateral afferent signals probably involve lower (e.g., spinal) levels of the nervous system (Ridderikhoff, Peper et al., 2005; Ridderikhoff et al., 2006). Therefore, it seems unlikely that this difference between the experiments with respect to hand dominance is related to the current results.

Unintended phase entrainment can be regarded a reflex-like mechanism, which occurs relatively autonomously as a direct consequence of contralateral proprioceptive afferent signals. Increases in movement amplitude are known to activate more afferent fibers and increase afferent firing frequencies (Kandel, Schwartz, & Jessell, 1991), leading to stronger afferent signals. Because increases in amplitude as such did not lead to increased entrainment strength, the present study indicates that entrainment strength is not solely a reflection of this strength of afferent signals from the passively moving limb. On the contrary, because the amplitude relation between the limbs influenced entrainment strength, our results indicate that movement characteristics of both limbs influence entrainment strength. The observed dependence on the active limb's movement amplitude may reflect a change in its susceptibility to external influences. If movement amplitude is relatively small, the limb appears to be more susceptible to

coupling influences stemming from the other limb than when moving at large amplitude. Possibly, this dependence on the amplitude relation is related to the strength of the neural signals involved, with the entraining effects of stronger afferent signals from the contralateral limb being modulated by the strength of the neural efferent signals activating the other limb. How this mechanism may be organized needs to be studied in further experiments.

In intended bimanual coordination, afference-based entrainment to in-phase and antiphase coordination is assumed to be involved, enhancing the attraction to these two coordination patterns (Ridderikhoff, Peper et al., 2005; Ridderikhoff et al., 2006). Hence, the here reported influence of unintentional entrainment strength on the amplitude relation between limbs may explain (in part) the observed amplitude-based asymmetry in coupling between the limbs as observed in previous experiments (Peper et al., 2008; Spijkers & Heuer, 1995). However, the absence of effects of amplitude as such suggests that phase entrainment does not underlie the observed increase in coupling strength between the limbs in intentional bimanual coordination when movement amplitude of both limbs increases (Buchanan & Ryu, 2006; Kudo et al., 2006; Ryu & Buchanan, 2004). Additional research is required to study how the suggested susceptibility to the afferent signals is organized, whether this effect is present to the same extent in intended bimanual coordination, and how the effect varies over a larger range of amplitudes and amplitude relations. In view of the suggested modulating influence of the strength of the neural efferent signals, such experiments should preferably involve electromyographic measurements of relevant muscle groups, in addition to kinematic recordings.

Furthermore, as the present study clearly distinguishes between coupling differences as a result of movement amplitude as such and the amplitude relation between the limbs, this underscores the importance of taking into account or control the amplitude of the individual limbs when studying bimanual coordination processes. As noted previously in the literature (de Poel, Peper, & Beek, 2009), the effect of amplitude disparity may significantly influence bimanual coupling and may obscure experimental findings and interpretations when not accounted for. The demonstrated dependence on the amplitude relation between the hands may also have practical consequences for therapeutic interventions that aim at improvements of an affected limb, for instance following stroke. In bimanual training protocols (e.g., Cauraugh & Summers, 2005; Whitall, McCombe Waller, Silver, & Macko, 2000) it may be advisable to create a large amplitude difference between the hands, to enhance the (presumably beneficial) coupling influences of the less-affected limb (moving at a larger amplitude) onto the affected limb.

4

Learning a new bimanual coordination pattern: Interlimb interactions, attentional focus, and transfer

Since bimanual coordinative stability is governed by interlimb coupling, we examined how learning a new pattern (90°) was reflected in changes in the underlying interlimb interactions. Three interlimb interaction sources were distinguished: integrated timing of feedforward control signals, error corrections based on perceived relative phase, and phase entrainment by contralateral afference. By comparing four tasks that involved these interactions to a different extent, changes in the stabilizing contributions of these coupling sources could be studied. Furthermore, we studied how the learning process and changes in the underlying interactions were influenced by attentional focus (internal vs. external), and we examined retention of the learned pattern and transfer to the mirror-symmetrical pattern (270°). Results showed that stability and accuracy of the new pattern increased significantly with learning, due to improved integrated timing and error correction. Integrated timing improved first, possibly providing a reference frame for the error corrections that subsequently became more effective. Despite some qualitative differences in the learning process, neither performance of the learned pattern nor the underlying interlimb interactions were influenced by attentional focus. Whereas the learned pattern improved directly after practice, transfer followed later, suggesting that a more general representation was formed at a slower rate after practice.

INTRODUCTION

When performing bimanual tasks, the hand movements influence one another and thereby constrain task execution. Movements that can be executed easily in unimanual tasks may deteriorate significantly once coupled to movements of a second limb. For instance, two different shapes are attracted to one another when drawn simultaneously (Franz et al., 1991), a limited number of frequency relations between the hands can be executed when moving the hands rhythmically (Peper, Beek, & van Wieringen, 1995; Summers, Rosenbaum, Burns, & Ford, 1993), and only in-phase (mirror-symmetrical) and antiphase (isodirectional) coordination can be executed stably when moving the hands in a 1:1 frequency relation (Yamanishi et al., 1980; Zanone & Kelso, 1992). Although the use of feedback may reduce or even eliminate these effects (see below), these examples illustrate how the coupling between the limbs may stabilize the execution of certain patterns while simultaneously hampering the performance of other patterns. Because the patterns that can be executed are governed by interlimb coupling, this coupling should change in the course of learning to allow for stable execution of new bimanual patterns. In the present experiment, we examined how the interactions between the hands changed when learning a new bimanual coordination pattern and whether this was affected by the attentional focus (internal or external) that was adopted during the learning period. In addition, we were interested in potential effects on the transfer of learning. To this end, three groups with different foci of attention learned to execute 1:1 frequency coordination with a relative phase between the hands of 90°, a coordination pattern in which the left hand lags the right hand by a quarter of a cycle. To assess transfer, performance of the mirror-symmetrical pattern (a relative phase of 270°) was examined.

Bimanual coupling

To study the coupling between the hands, we used a method for examining three functional sources of interlimb interaction that were deemed to underlie the stability of coordination patterns (Ridderikhoff, Peper et al., 2005). These sources of interlimb interaction were based on empirical results, which indicated the involvement of several neurophysiological processes in the stabilization of bimanual coordination patterns (for more details, see Ridderikhoff, Peper et al., 2005). Whereas these sources were generally studied in isolation, they can be examined in conjunction using the method developed by Ridderikhoff, Peper, et al. (2005). In previous work, this method has been

used to assess the contributions of these interlimb interactions to stability differences associated with the executed coordination pattern (Ridderikhoff, Peper et al., 2005), attention (Ridderikhoff et al., 2008), and movement frequency (Chapter 2). In addition, it has been used to examine changes in bimanual stability associated with development across childhood (Chapter 5). According to this method, three functional sources of interlimb interaction can be dissociated based on the dependence on afferent, sensory information and the intention to execute a specific pattern. First, integrated timing of feedforward control signals (IT) reflects interaction processes related to feedforward timing of the efferent signals that specify the intended bimanual movement pattern, without taking adjustments based on afferent feedback into account. Second, error correction (EC) reflects the intentional correction of perceived relative phasing errors based on kinesthetic afference, in order to stabilize the intended bimanual coordination pattern. Third, phase entrainment by contralateral afference (PE) pertains to the unintentional entraining influences stemming from contralaterally invoked afferences, resulting in unintended attraction towards specific phase relations between the limbs.

The contributions of the three sources of interaction are examined by comparing specific tasks involving unimanual or bimanual rhythmic flexion-extension movements about the wrist (Ridderikhoff, Peper et al., 2005). These tasks differ with regard to the degree in which the three sources of interaction are assumed to be involved (see Table 4.1). First, when executing unimanual coordination with a metronome (task UN), no sources of interaction are present. Second, for unimanual coordination in the presence of passive movements of the contralateral hand (task UNm), PE entrains the active hand towards in-phase or antiphase coordination with the passively moving hand. Third, when tracking a passively moving hand based on kinesthetic afference (task KT), the active hand's movements are not only affected by PE, but also by EC, which stabilizes the intended coordination pattern between the hands. Fourth, when executing active bimanual coordination (task AB), next to PE and EC the bimanual pattern is stabilized by contributions of IT. The sources of interaction are thus assumed to add up in these tasks (cf. Table 4.1): in UN no sources are present, in UNm only PE, in KT the sources PE and EC, while IT, EC, and PE all contribute to stability in AB.

Mastering a new coordination pattern requires adaptations in these interaction sources. In particular, the participant has to acquire the ability to specify the required relative phasing pattern (IT) and the adequate reference frame for correcting deviations from this pattern (EC), such that the required pattern can be actively stabilized.

Table 4.1

Tasks and sources of interlimb interaction

	Task description	Interactions		
		IT	EC	PE
AB	Active bimanual coordination at a tempo specified by a metronome	X	X	X
KT	Kinesthetic tracking of the passively moving contralateral hand		X	X
UNm	Unimanual coordination with a metronome with (phase-shifted) passive movements of the contralateral hand as distractor		X	X
UN	Unimanual coordination with a metronome			

Mapping of the four tasks to the three sources of interlimb interaction: integrated timing of feedforward control signals (IT), error correction based on perceived relative phase (EC), and phase entrainment by contralateral afference (PE). The "X" symbols represent the sources of interlimb interaction that are assumed to be involved in the associated tasks.

Learning and attentional focus

We assessed how the learning process and the associated changes in the underlying sources of interlimb interaction were affected by the adopted focus of attention. As has been shown for a variety of sport tasks, an externally directed focus results in better performance as well as better learning than an internal focus. In other words, focusing on the action goal instead of the movement themselves enhances learning (McNevin, Shea, & Wulf, 2003; Rotem-Lehrer & Laufer, 2007; Wulf, Lauterbach, & Toole, 1999; Wulf & Prinz, 2001) both in terms of retention and transfer performance (Chiviacowsky, Wulf, & Wally, 2010; Rotem-Lehrer & Laufer, 2007), although for novices mixed results have been found (Castaneda & Gray, 2007; Gray, 2004; Perkins-Ceccato, Passmore, & Lee, 2003; Wulf & Prinz, 2001; Wulf & Su, 2007). Moreover, the positive effects of an external focus appear to be larger when the external focus is 'further away' or less closely linked to the movements themselves (McNevin et al., 2003; Porter, Anton, & Wu, 2011; Wulf & Prinz, 2001).

Also in bimanual coordination the use of an external focus of attention in practice has been shown to enhance performance during retention (Kovacs & Shea, 2011). We elaborated on this finding by examining whether the effects of distance of the external focus are also observed in learning a new bimanual coordination pattern, and by studying how the contributions of the underlying sources of interlimb interaction are affected by attentional focus. In accordance to Ronsse et al. (2011), we used auditory feedback or visual Lissajous feedback to induce an external focus of attention, and compared this to learning with an internal focus of attention. An external focus that was still rather closely

related to the hand movements was induced by providing auditory feedback about the turning points of the right and left hand (i.e., participants heard alternating high- and low-pitched tones; following Ronsse et al., 2011), while an external focus further away was induced by using Lissajous feedback (Kovacs, Buchanan, & Shea, 2009; Kovacs & Shea, 2011; Lee, Swinnen, & Verschueren, 1995; Swinnen, Lee, Verschueren, Serrien, & Bogaerds, 1997; Verschueren, Swinnen, Dom, & De Weerdt, 1997). This latter type of feedback entails an integrated representation of the bimanual coordination pattern: the movements of one hand are represented along the x-axis and movements of the other along the y-axis, resulting in a circular motion when the 90° pattern is adequately performed (e.g., Kovacs, Buchanan et al., 2009). However, augmented feedback during learning may create dependence on this extrinsic source of information, deteriorating performance once removed (e.g., Kovacs, Buchanan et al., 2009; Kovacs & Shea, 2011; Maslovat, Brunke, Chua, & Franks, 2009). Recent studies have revealed that this feedback dependence can be decreased in at least two ways: (i) by using a fading schedule, involving increasing periods of time during which participants had to execute the new pattern without Lissajous feedback (Kovacs & Shea, 2011; Winstein & Schmidt, 1990); and (ii) by using a different type of display for the Lissajous feedback (Buchanan & Wang, 2012). We adopted a fading schedule in our experiment, because it could also be applied in the auditory feedback condition, and because it is unclear at present how the results obtained for the adapted Lissajous display translate to learning a 90° pattern at a relatively high frequency.

Retention and transfer

We also assessed retention of the learned 90° pattern and transfer to the mirror-symmetrical 270° pattern. Whereas fast improvements occur during practice of perceptuomotor tasks, additional slower improvements are observed after a subsequent longer period without practice (Brashers-Krug, Shadmehr, & Bizzi, 1996; Karni & Sagi, 1993; Walker, Brakefield, Hobson, & Stickgold, 2003). During this consolidation process the representation of the practiced pattern is stabilized against interferences and further enhanced (Walker & Stickgold, 2005). We examined if further improvement in the learned pattern after a week of retention could be observed for the present task. In addition, it has been shown previously that participants learning the 90° pattern also show enhanced accuracy and stability of the 270° pattern and vice versa (Smethurst & Carson, 2001; Zanone & Kelso, 1997). For this reason, we studied performance of 90° and 270° directly after practice and a week later at retention. By assessing the different

interlimb interactions, we aimed at examining how IT, EC, and PE contributed to the consolidation of the practiced 90° pattern and to transfer to the 270° pattern.

Aims and expectations

In sum, in the present experiment three different aspects of the learning process in bimanual coordination were assessed. First, we examined how learning a new coordination pattern is governed by the changes in the stabilizing contributions of the underlying sources of interlimb interaction (IT, EC, and PE). Improvements in the to-be-learned pattern were expected to rely predominantly on contributions of IT and EC, enabling the participant to generate the required relative phasing pattern and to adequately correct errors in performance. Since previous results have indicated that the generated motor commands (based on IT) may serve as a reference frame for error correction (Chapter 2; Ridderikhoff et al., 2007), we expected changes in IT to precede those in EC.

Based on previous results in the literature (Chiviacowsky et al., 2010; McNevin et al., 2003; Rotem-Lehrer & Laufer, 2007; Wulf et al., 1999; Wulf & Prinz, 2001), we expected that the learning progress would benefit from an external attentional focus, with the strongest effects for the Lissajous group as their focus was further away than in the auditory feedback group. With respect to accompanying changes in the contribution of IT and EC, we expected intuitively that an external focus would result in larger stabilizing contributions of IT in particular, because the external focus was directed to the integrated pattern of the hands. In a similar vein, we tentatively predicted that an internal focus of attention (directed to the hand movements themselves) would result in more enhancement of EC, so that stabilization of the coordination pattern would depend more strongly on error corrections.

Retention and transfer of the learned coordination pattern were assessed by examining performance changes in 90° and 270° directly after learning and a week later. Due to the consolidation process that extends after practice, we expected the learned pattern to improve further at retention. Additional improvements were expected for the transfer to the mirror-symmetrical pattern. We did not have any specific hypotheses with respect to the interlimb interactions in this regard. However, it may be expected that IT is involved in a more abstract representation of the coordination pattern and hence would not differ in its contribution to the two patterns, while EC in the timing of the individual limbs may be better for the pattern that was actually practiced.

Methods

Participants

Thirty-six participants participated in the study and were divided over three groups: an internal group, an external-auditory group, and an external-Lissajous group. The groups were matched on several variables (cf. Table 4.2). Participants gave their informed consent prior to the experiment and received a small fee for their participation. Total duration of the experiment was about 3 hours, divided over three days.

Table 4.2
Group characteristics

	Internal	*External-auditory*	*External-Lissajous*	*p-value*
Gender (F/M)	8 / 4	8 / 4	8 / 4	1.0
Age (year)	22.4 [3.60]	23.3 [5.46]	21.9 [3.80]	.75
Handedness	84.6 [15.4]	76.4 [26.5]	78.5 [21.0]	.63
Frequency (Hz)	1.37 [0.12]	1.36 [0.14]	1.34 [0.11]	.88
Retention day	8.83 [0.72]	8.83 [0.72]	9.00 [0.60]	.79

Group characteristics for the three learning groups. Gender is presented as the number of females/males; all other variables are presented as mean [between-participants SD]. Handedness was measured using the Edinburgh Handedness Inventory; values > 0 indicate that participants were right-handed (Oldfield, 1971). The Kruskal-Wallis Test (Gender) and one-way ANOVAs (all other factors) revealed no significant difference between the groups.

Apparatus

The setup has been described in detail elsewhere (Ridderikhoff, Peper et al., 2005). In short, participants sat in a height-adjustable chair with their elbows slightly flexed and their feet supported. Their forearms were placed on armrests in a neutral position (thumbs up, palms facing inward, fingers extended). Both hands were fixated to two flat manipulanda, allowing wrist flexion and extension only. The manipulandum for the left hand registered the wrist movements using a potentiometer (sampling rate: 1000 Hz), whereas that for the right hand either registered its movements by means of a potentiometer (for active movements) or controlled the wrist movements by means of a motor (for passive movements). A screen was used to eliminate visual feedback of the hand movements. A computer screen was placed about 50 cm in front of the

participants, which was used either to present feedback about performance after each trial (i.e., for all groups) or during the trial (i.e., for the external-Lissajous group) during practice sessions.

Task and conditions

Participants executed four different tasks that involved unimanual or bimanual rhythmic flexion-extension movements (cf. Ridderikhoff, Peper et al., 2005; Table 4.1). In task AB, participants executed rhythmic bimanual coordinated movements in four specified coordination patterns: in-phase (IP), antiphase (AP), 90° coordination (i.e., the pattern that was being learned), or 270° coordination (the transfer pattern). Peak flexion of the hands was specified by means of a pacing signal: participants had to synchronize peak flexion of the right hand to a high-pitched tone (880 Hz) that was presented to the right ear (via headphones), and peak flexion of the left hand to a low-pitched tone (440 Hz) presented to the left ear. In task KT, a motor moved the right hand and participants actively moved their left hand so as to track the passively moved hand in each of the four coordination patterns. No pacing signal was presented. In task UNm, two phase relations between the passive movements and metronome pacing were applied around each of the four coordination patterns: a phase shift of -30° and 0° (with -30° corresponding to a phase advance of the passive movements of 1/12th of a movement cycle). Participants were instructed to ignore these passive movements and to perform rhythmic unimanual flexion-extension movements of the wrist by letting peak flexion of their left hand coincide with the beep presented to the left ear. In task UN, participants performed the same unimanual task as UNm, but without distracting influences of the passive hand.

Procedure

Participants executed bimanual rhythmic coordination in three settings: a preparation part, practice sessions in which the 90° bimanual coordination pattern was practiced, and test sessions that assessed participants' performance of different tasks and patterns. A schematic overview of these sessions is provided in Table 4.3 and the sessions are described in more detail below.

Table 4.3

Experimental design

Session	Tasks	Patterns	Description
Day 1			
Preparation	AB	IP, AP, 90°	Screening of 90°, preferred frequency for AP
Pretest	AB, KT, UNm, UN	IP, AP, 90°, 270°	Test all coordination patterns
Practice	AB	90°	Practice 90° with specific focus of attention and feedback after each trial
Test90-1	AB, KT, UNm, UN	90°	Test 90° pattern
Day 2			
Test90-2	AB, KT, UNm, UN	90°	Test 90° pattern
Practice	AB	90°	Practice 90° with specific focus of attention and feedback after each trial
Post-test	AB, KT, UNm, UN	IP, AP, 90°, 270°	Test all coordination patterns
Day 3			
Retention	AB, KT, UNm, UN	IP, AP, 90°, 270°	Test all coordination patterns

Schematic overview of the practice and testing sessions. Abbreviations: AB = active bimanual coordination, KT = kinesthetic tracking; UNm = unimanual coordination with a metronome with a motor as distractor; UN = unimanual coordination with a metronome; IP = in-phase coordination; AP = antiphase coordination. Day 1 and 2 were two consecutive days; Day 3 was a week later (6-8 days after Day 2).

Preparation

In the preparation session, first one IP and AP trial were executed at 1 Hz to familiarize participants with the use of the pacing signal. Subsequently, we tested whether participants were already able to execute the 90° pattern. One participant was able to execute this pattern prior to learning, and was therefore replaced by a new participant. Subsequently, the preferred frequency for AP was assessed. For this purpose, movement frequency was increased in steps of 0.2 Hz, and decreased again in steps of 0.1 Hz once a participant had indicated that the previous frequency was more convenient. The preferred frequency was used for all conditions in the experiment, to allow for a fair comparison of different tasks, patterns, and learning groups.

Motor trajectories for the passive movements were based on characteristics of the last trial at the preferred frequency of the participant. To this end, sinusoidal trajectories were calculated around a mean joint angle of 10° in flexion (i.e., the comfortable neutral position; cf. Roerdink, Ophoff, Peper, & Beek, 2008). To prevent the trajectories from being perceived as predictable, the periods and amplitudes of the cycles were randomly varied to obtain a moderate level of variability: $SD_{frequency} = (0.3/1.4) \times$ preferred frequency

and $SD_{amplitude}$ = (5/35) x mean amplitude (i.e., in accordance with Ridderikhoff et al., 2007). The trajectories were phase shifted using cubic spline interpolation at the start of the trial so that the phase shift of -30° for task UNm was achieved in three cycles. The trajectories were multiplied with a windowing function to generate a smooth increase and decrease in the amplitude of the passive movements in the first and last two cycles. The passive movements were calculated for the different movement patterns and were used in the entire experiment.

Practice

For learning the 90° pattern, participants executed on two consecutive days 45 trials, with a small break between the first 25 and last 20 trials at each day. Each trial lasted 30 seconds. A pacing signal specified movement frequency and the required coordination pattern in the first 10 seconds. In the last 20 seconds, participants were instructed to continue performing the 90° pattern without the pacing signal. After each trial, feedback about the error and variability was presented in a graph on the computer screen. Feedback was presented for the last three trials to allow for a comparison across trials. Participants were instructed to reduce the variability and error as much as possible.

According to the group they were assigned to, participants received different instructions and feedback during the last 20 seconds of continuation without pacing. Participants in the internal group were instructed to continue with the pattern as prescribed by the metronome: to alternate the moments of peak flexion of the hands as specified by the pacing signal. The external-auditory group received auditory feedback during the trial indicating the moments of peak flexion of each hand (cf. Ronsse et al., 2011), with flexion of the right hand generating a high-pitched tone and flexion of the left hand generating a low-pitched tone. Participants were instructed to reproduce the auditory signal as presented during the first 10 seconds of the trial; if they succeeded in doing so, the 90° pattern was executed correctly. Participants in the external-Lissajous group received visual feedback: the bimanual movement pattern was presented in a graph plotting the left hand movements (y-axis) against the right hand movements (x-axis). Participants were instructed to produce a circular movement in counterclockwise direction, corresponding to the 90° pattern (Kovacs, Buchanan et al., 2009). Feedback during the trial for the two external-focus groups was presented in a fading schedule, to reduce the dependence on this externally provided feedback (Kovacs & Shea, 2011). During a block of trials, feedback was gradually decreased every 1/5th of the total number of trials: for 25 trials feedback was presented in trial 1-5 for 20 seconds, trial 6-10 for 15 seconds, trial 11-15 for 10 seconds, trial 16-20 for 5 seconds, and trial 20-25 for 0

seconds. Participants in the external-focus groups thus received concurrent feedback in a fading schedule during the practice trials, whereas all training groups received terminal feedback about task performance after each practice trial.

Testing conditions: pre-test, post-test, retention and Test90-1, Test90-2

In the pre-, post-, and retention tests, participants executed task AB, KT, UNm, and UN for four different coordination patterns: IP, AP, 90°, and 270°. Throughout these trials the required coordination pattern was specified by means of metronome beeps. In each test participants executed four coordination-pattern blocks in AB and KT with two repetitions, resulting in 8 AB and 8 KT trials in total. All UNm and UN trials were presented randomly in an additional block, consisting of 4 (Pattern) x 2 (Phase shift) x 2 (Repetitions) = 16 UNm trials and 2 UN trials. The blocks were presented randomly across participants and tests. In the pre-test each block started with one practice trial. Trial duration was equal to 25 cycles for all tasks and patterns. The retention test was executed a week after the post-test (i.e., after 6-8 days), again including 8 AB, 8 KT, 16 UNm, and 2 UN trials. In addition, this test included two extra trials of 90° for task AB, in which participants followed the pacing signal for 10 seconds and continued 20 seconds without. However, because comparison of the obtained performance for these two trials with that in the practice session did not produce additional insights, performance in the absence of a pacing signal in the retention test is not further addressed in the Results.

In the two tests in between the two practice days (Test90-1 and Test90-2, see Table 4.3), only the 90° pattern was executed for the four different tasks, resulting in a block of 2 AB trials, a block of 2 KT trials, and a block of 2 (Phase shift) x 2 (Repetitions) = 4 UNm trials and 2 UN trials. The order of blocks was randomized across participants and tests. Again, trial duration was set to 25 cycles.

Data analysis

The first and last three cycles of each trial were removed, leaving 20 cycles for analysis. More cycles were removed if (1) the phase relation between the hands increased or decreased progressively over several consecutive cycles (i.e., phase wrapping); (2) the phase relation with the pacing signal differed from the intended pattern (i.e., executing peak extension instead of peak flexion at the beep). If less than 10 consecutive cycles remained for analysis, a trial was excluded from further analysis. In total, one or more additional cycles were removed from 552 trials (12.6%), and 324 trials (7.38%) were excluded completely from further analysis. The cycles included in the analysis were low-

pass filtered (2nd-order bidirectional Butterworth filter, cut-off frequency: 18 Hz). For the tasks in which two hands were involved (AB, KT, and UNm), the relative phase between the hands was calculated for each cycle as $\Phi_i = 360° (t_{y,i} - t_{x,i}) / (t_{x,i+1} - t_{x,i})$, where $t_{y,i}$ and $t_{x,i}$ indicate the time of the ith peak flexion (extension) of the left hand and the right hand, respectively (cf. Carson et al., 1995). For the unimanual tasks (UNm and UN), the relative phase between the metronome and peak flexion of the left hand was determined for each cycle as $\Psi_i = 360° (t_{y,i} - t_{x,i}) / (t_{x,i+1} - t_{x,i})$, where $t_{y,i}$ indicates the time of the ith peak flexion of the left hand and $t_{x,i}$ corresponds to the moment of the ith metronome beep. For both Φ and Ψ a positive value implied that the left hand (y) was lagging the reference signal (x). Circular statistics (Mardia, 1972) was used to determine the average value of Ψ, and for Φ the circular standard deviation (CSD_Φ) and the absolute error (i.e., $AE_\Phi = | \Phi - \Phi_{required} |$ with $\Phi_{required}$ being 0°, 90°, 180°, or 270°).

An error in Φ can be corrected by shortening or lengthening the subsequent half cycle of (one of) the hands, resulting in a negative correlation between the signed error in relative phasing at peak flexion or extension and the duration of the subsequent half cycle (Ridderikhoff et al., 2007). The signed error was defined as the interval between the ith peak flexion (extension) of both hands for IP, and as the interval between the ith peak flexion (extension) of the left hand and the ith peak extension (flexion) of the right hand for AP, 90°, and 270° coordination (because preliminary analyses had pointed out that all participants corrected for errors in the 90° and 270° patterns as if these patterns were executed in an alternating fashion similar to AP coordination). The presence of error correction was thus examined in terms of this error correction correlation (R_{EC}), by correlating the signed error at each turning point to the duration of the subsequent half cycle of the hand that predominantly effectuated error correction.[7] Because UNm performance did not involve error correction, the obtained correlation values reflected the influence of PE and were regarded as baseline values (Chapter 2; Ridderikhoff, Peper et al., 2005). Therefore, for all participants the R_{EC} values obtained for each condition in AB and KT were corrected by subtracting the corresponding mean values for UNm, as obtained for that participant. R_{EC} values close to zero thus indicated that error correction did not exceed baseline level, while more negative values revealed a larger amount of error correction. For statistical analyses, R_{EC} was transformed into normally distributed

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7 Statistical analysis revealed that in all tests, participants (predominantly) effectuated error corrections in task AB with the right (dominant) hand for the IP, AP, and 270° patterns, while the left hand corrected for errors for the 90° pattern in AB and in all patterns in task KT (i.e., the only hand that was moving actively). This difference between 90° and 270° in AB is probably due to the hand configuration: the hand that shortly followed the other corrected predominantly for errors (e.g., for 90° the left followed the right hand by a quarter of a cycle).

values using the Fisher transform. For clarity, the untransformed values are presented in the Results.

Statistical analysis

Statistical analysis comprised three parts in which several test variables were compared: (a) pre-test scores to examine baseline contributions of the three sources of interaction to stabilization of the four coordination patterns and to assess groups differences; (b) learning effects for all five tests that involved 90° (pre-test, Test90-1, Test90-2, post-test, retention); and (c) learning effects for the three tests in which all four patterns were executed (pre-test, post-test, retention). Furthermore, the acquisition phase was evaluated by comparing performance of the first and last 20 trials.

To assess the effects of integrated timing and error correction on bimanual performance, tasks AB and KT were compared regarding AE_ϕ, CSD_ϕ, and R_{EC}. In contrast to previous experiments in which the difference between two tasks was submitted to statistical analysis (e.g., Ridderikhoff, Peper et al., 2005), tasks AB and KT were now compared directly to allow for head-on interpretations regarding changes in the course of learning that were due to integrated timing (task AB) and error correction (task KT). The corresponding repeated-measures analyses of variances (ANOVAs) involved between-participants factor Group (internal, external-auditory, external-Lissajous), within-participant factors Task (AB, KT), and (a) for pre-test performance factor Pattern (IP, AP, 90°, 270°); (b) factor Test (pre-test, Test90-1, Test90-2, post-test, retention) for the five tests that included 90°; and (c) for the three tests factors Pattern (IP, AP, 90°, 270°) and Test (pre-test, post-test, retention). Phase entrainment was assessed by comparing Ψ between UN and UNm. The ANOVAs involved between-participants factor Group (internal, external-auditory, external-Lissajous), within-participant factors Shift (-30°, 0°), and the factors Pattern and Test as described above. Acquisition of the 90° pattern was assessed by comparing AE_ϕ and CSD_ϕ in the first and last block of 20 trials during practice, using an ANOVA with between-participants factor Group and within-participants factor Block (first, last).

In all ANOVAs, Greenhouse-Geisser adjustment of degrees of freedom was applied if the assumption of sphericity was violated. Effect sizes were based on the partial eta squared (η_p^2, Cohen, 1988). Significant effects ($p < .05$) were further scrutinized using post-hoc paired-samples t-tests. In the Results, values are presented as mean [between-participants *SD*].

RESULTS

Pre-test performance

Pre-test variability and accuracy of the relative phase (CSD_ϕ and AE_ϕ) and R_{EC} were submitted to a Task x Pattern x Group ANOVA. Statistical analysis revealed for CSD_ϕ an effect of Task, $F(1,33) = 50.9$, $p < .001$, $\eta_p^2 = .61$, and Pattern, $F(1.9,61.1) = 50.5$, $p < .001$, $\eta_p^2 = .61$, and for AE_ϕ an effect of Task, $F(1,33) = 10.4$, $p < .01$, $\eta_p^2 = .24$, Pattern, $F(2.0,66.1) = 72.9$, $p < .001$, $\eta_p^2 = .69$, and a Task x Pattern interaction, $F(1.8,60.4) = 4.1$, $p < .05$, $\eta_p^2 = .11$. No group differences were observed between the three groups. Post-hoc analysis showed that both CSD_ϕ and AE_ϕ were smaller in task AB (CSD_ϕ: 15.5° [5.34°]; AE_ϕ: 34.6° [13.4°]) than in KT (CSD_ϕ: 22.5° [6.18°]; AE_ϕ: 44.0° [12.4°]), revealing the stabilizing contribution of integrated timing. Furthermore, CSD_ϕ differed between all coordination patterns (IP: 11.5° [3.25°], AP: 13.2° [3.71°], 90°: 23.5° [7.72°], 270°: 27.8° [12.1°]). Performance of IP and AP was more accurate (viz. lower AE_ϕ) than 90° and 270° in task AB (IP: 10.2° [2.54°], AP: 11.2° [5.81°], 90°: 54.5° [26.9°], 270°: 62.7° [31.7°]) and in task KT (IP: 23.8° [11.5°], AP: 26.4° [9.6°], 90°: 50.3° [27.7°], 270°: 75.7° [38.8°]). Additionally, in task KT the 90° pattern was executed more accurately than 270°. This may have been associated with the configuration of the hands in the two patterns: for 90° the active hand followed the passive hand by a quarter of a cycle, whereas the active hand needed to be in advance of the passive movement for the 270° pattern. Only for IP and AP task AB was more accurate than task KT.

Analysis of R_{EC} revealed an effect of Task, $F(1,33) = 17.2$, $p < .001$, $\eta_p^2 = .35$, Pattern, $F(3,99) = 13.8$, $p < .001$, $\eta_p^2 = .30$, and a Task x Pattern interaction, $F(3,99) = 4.1$, $p < .01$, $\eta_p^2 = .10$. Post-hoc analysis showed that the amount of error correction was larger during IP and AP than during 90° and 270°. In addition, more error correction was observed in AB than KT for IP (AB: -.32 [.25], KT: -.16 [.15]) and AP (AB: -.35 [.25], KT: -.13 [.13]), whereas there was no difference between the tasks for 90° (AB: -.07 [.20], KT: -.08 [.18]) and 270° (AB: -.11 [.19], KT: -.05 [.16]).

Taken together, the results of CSD_ϕ, AE_ϕ, and R_{EC} showed that performance of the two patterns that are intrinsically stable (IP and AP) was superior to that of the to-be-learned patterns at pre-test, and that these two patterns were stabilized by integrated timing and error correction. In addition, error correction was most useful for IP and AP, and especially when integrated timing also contributed to stability of the bimanual coordination pattern (i.e., task AB vs. task KT).

The Pattern x Group ANOVA on Ψ revealed no significant effects at pre-test, showing no group effect and indicating no systematic attraction towards the two intrinsically

stable patterns (IP and AP) or repulsion from the two patterns unstable prior to learning (90° and 270°).

Practice

During practice, participants improved their performance of the 90° pattern. As can be observed in Figure 4.1, for participants in all three groups CSD_ϕ changed only slightly over practice, whereas participants considerably decreased AE_ϕ of the 90° pattern. Learning was examined by comparing the first and last blocks of 20 trials using a Block x Group ANOVA. Results revealed an effect of Block for CSD_ϕ, $F(1,33) = 13.0$, $p < .001$, $\eta_p^2 = .28$, and AE_ϕ, $F(1,33) = 67.3$, $p < .001$, $\eta_p^2 = .67$, and a Block x Group interaction for AE_ϕ, $F(2,33) = 5.17$, $p < .05$, $\eta_p^2 = .24$. The effect of Block revealed that for all groups variability and error of relative phase decreased significantly over the learning period (cf. Figure 4.1). Post-hoc analysis of the Block x Group interaction for AE_ϕ showed that although the groups did not differ at the start or end of practice, the decrease in error was largest for the external-Lissajous group as compared to the internal and external-auditory group. Comparison of the additional tests in the following section provided further information on how contributions of the three sources of interlimb interaction changed and whether this differed for the three learning groups.
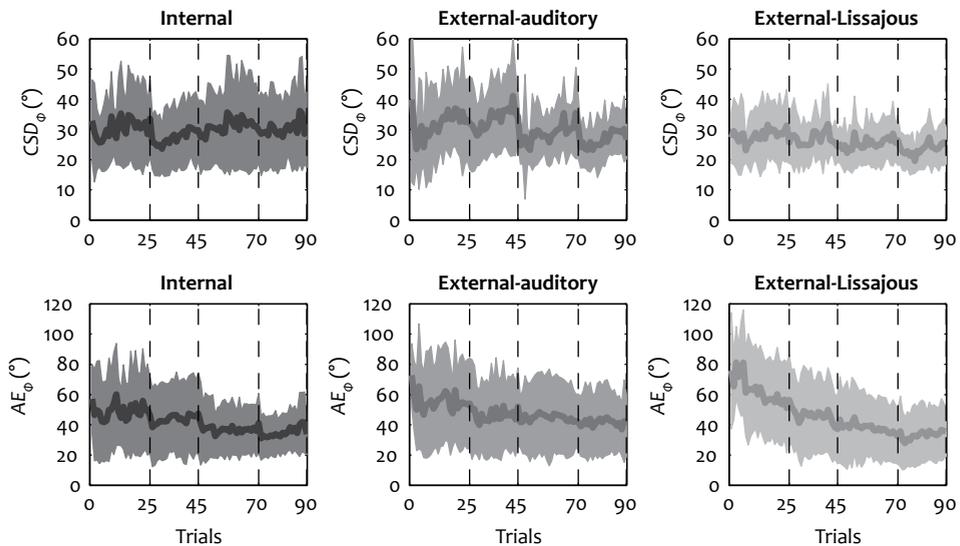

Figure 4.1. The learning curves of the three groups (Internal, External-auditory, External-Lissajous) regarding CSD_ϕ and AE_ϕ. Performance is presented for all learning trials (i.e., 45 learning trials on 2 consecutive days) with the vertical dashed lines indicating the breaks between practice trials. The shaded area around the mean represents between-participants SD.

Test performance

Testing 90°

Performance of the 90° pattern was assessed for five tests, including the two tests that were executed in between the two learning sessions, using Test x Task x Group ANOVAs on CSD_Φ, AE_Φ, and R_{EC}. Analysis revealed an effect of Test for CSD_Φ, $F(4,132) = 7.9$, $p < .001$, $\eta_p^2 = .19$, and AE_Φ, $F(4,132) = 11.4$, $p < .001$, $\eta_p^2 = .26$. Post-hoc analysis showed that CSD_Φ decreased significantly after the two practice sessions, i.e., performance was more variable at pre-test (23.5° [7.72°]), Test90-1 (22.5° [9.31°]), and Test90-2 (22.3° [8.28°]), as compared to post-test (17.9° [4.57°]) and retention (17.9° [6.19°]). AE_Φ decreased significantly from pre-test (52.4° [23.2°]) to the tests following practice (Test90-1: 44.9° [21.0°], Test90-2: 41.7° [21.6°], post-test: 36.4° [17.9°], retention: 33.8° [19.5°]), with Test90-1 also differing from post-test and retention, and Test90-2 from retention. Thus, participants improved gradually the accuracy of the learned pattern during learning, while variability improved only after the two learning sessions.

Analysis of R_{EC} revealed a Test x Task interaction, $F(4,132) = 3.0$, $p < .05$, $\eta_p^2 = .08$. Post-hoc analysis showed that only at pre-test the amount of error correction did not differ between task AB (-.07 [.20]) and task KT (-.08 [.18]), while in tests following practice the amount of error correction was significantly larger in AB than in KT, as a result of an increase in the amount of error correction in AB after practice (Test90-1: -.14 [.18], Test90-2: -.16 [.16], post-test: -.13 [.16], retention: -.16 [.18]). In KT no such difference with the pre-test was observed (Test90-1: -.02 [.22], Test90-2: -.09 [.20], post-test: -.09 [.16], retention: -.09 [.19]), although the amount of error correction was significantly smaller at Test90-1 than at post-test.

Taken together, these results revealed improved performance of the learned 90° after the first and second practice session. Furthermore, the amount of error correction was more effective after learning when integrated timing also contributed to stability of the 90° coordination pattern (i.e., task AB vs. task KT).

The Test x Group ANOVA on Ψ did not reveal any changes regarding the strength of PE.

Testing all patterns

To assess changes in performance of all coordination patterns (IP, AP, 90°, 270°), CSD_Φ, AE_Φ, and R_{EC} were submitted to Test x Task x Pattern x Group ANOVAs. For CSD_Φ the results showed an effect of Test, $F(2,66) = 4.9$, $p < .05$, $\eta_p^2 = .13$, and a Test x Pattern interaction, $F(2.9,94.4) = 4.5$, $p < .01$, $\eta_p^2 = .12$, and for AE_Φ an effect of Test, $F(2,66) = 22.8$,

$p < .001$, $\eta_p^2 = .41$, a Test x Task interaction, $F(1.5,49.2) = 3.8$, $p < .05$, $\eta_p^2 = .10$, and a Test x Pattern interaction, $F(2.8,91.8) = 10.5$, $p < .001$, $\eta_p^2 = .24$. Post-hoc analysis showed that CSD_ϕ and AE_ϕ decreased significantly from pre- to post-test for the practiced 90° pattern, and decreased from post-test to retention for the 270° (transfer) pattern (cf. Figure 4.2). Also small differences were observed for AE_ϕ during IP and AP, showing larger errors at the post-test, which probably reflected the effect of practice of the 90° pattern (i.e., the post-test was executed directly after the second practice session). The Test x Task interaction revealed that for task AB the accuracy improved over all tests (pre-test: 34.6° [13.4°], post-test: 27.1° [11.9°], retention: 22.6° [11.1°]), whereas for task KT accuracy improved only from post-test to retention (pre-test: 44.0° [12.4°], post-test: 43.8° [15.1°], retention: 36.6° [13.2°]).

Analysis of R_{EC} showed a Test x Task interaction, $F(2,66) = 5.3$, $p < .01$, $\eta_p^2 = .14$, revealing that for task AB the amount of error correction increased from post-test (-.18 [.11]) to retention (-.23 [.09]); both tests did not differ from pre-test (-.21 [.12]). For task KT no significant differences were observed between tests (pre-test: -.10 [.08], post-test: -.11 [.09], retention: -.08 [.09]).

Taken together, these results showed how performance of the learned 90° pattern improved significantly after practice, while the transfer pattern showed a delayed improvement at retention. Furthermore, first the integrated timing contribution improved (i.e., at the post-test), while the error correction part improved later:
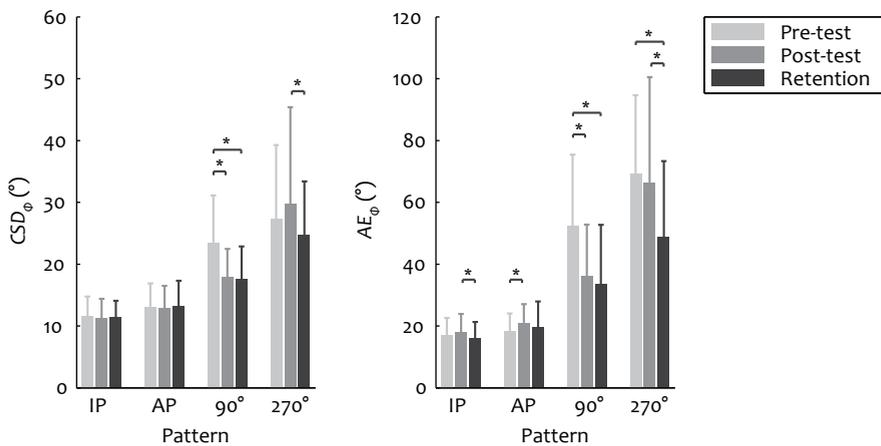

*Figure 4.2. Variability (CSD$_\phi$) and accuracy (AE$_\phi$) of the bimanual coordination pattern at pre-test, post-test and retention for the four different patterns: IP, AP, 90°, and 270°. Error bars represent between-participants SD. Significant differences between tests are indicated with * (p < .05).*

performance in task KT as well as the amount of error correction in AB only improved from post-test to retention.

Submitting Ψ to the Test x Pattern x Group ANOVA did not reveal any changes regarding the strength of PE.

Discussion

The aim of the present study was threefold: to determine how different sources of interlimb interaction change when learning a new bimanual coordination pattern, to examine the influence of attentional focus (including the distance of an external focus) on learning and the underlying interlimb interactions, and to assess how retention and transfer of learning are organized in this regard. For this purpose, participants learned a 90° relative phase between the hands and the changes in the stabilizing contributions of integrated timing, error correction, and phase entrainment were studied for in-phase, antiphase, 90°, and 270° (i.e., the transfer pattern). The influence of attentional focus was assessed by comparing learning in a group with an internal focus of attention, a group with an external focus closely related to the hand movements (auditory feedback), and a group with an external focus further away (Lissajous feedback).

Three main findings were obtained in the study. First, performance improved due to the combined stabilizing contributions of integrated timing and error correction; phase entrainment did not change during learning. Second, although some differences between groups were observed during practice, the absence of differences in the tests suggested that learning in this task was not significantly affected by attentional focus. Third, all groups improved bimanual stability and accuracy of the 90° and 270° patterns with learning, but the practiced 90° pattern improved directly after learning whereas the transfer to the 270° pattern improved a week later at retention. These findings are discussed more into detail below.

Learning and interlimb interactions

By assessing the stabilizing contributions of integrated timing, error correction, and phase entrainment, we examined how learning a new coordination pattern was governed by changes in these interlimb interactions. As expected, the improvements of 90° and 270° resulted from improved stabilizing contributions of integrated timing of feedforward control signals, i.e., the specification of the bimanual pattern, as well as from enhanced

error correction based on the perceived relative phase. Phase entrainment to the contralateral hand did not change during learning, as the attraction to or repulsion from the different coordination patterns did not change over the tests.[8] Improved accuracy and stability of 90° and 270° thus only resulted from the contributions of integrated timing and error correction. Two results exposed an interesting interplay between these two sources of interlimb interaction. First, overall accuracy of active bimanual 90° coordination (task AB) improved directly after learning at the post-test, whereas 90° kinesthetic tracking of the passively moving hand (task KT) improved not until retention. In addition, the amount of error correction for the learned 90° pattern only improved for the active bimanual coordination task (i.e., when integrated timing was present). Together, these results indicate that participants were only able to adequately correct for errors in the required relative phase after they were able to generate the required integrated timing signal, representing the intended pattern.

These results support previously obtained results indicating that the presence of a bimanual reference signal allows for more effective error corrections (Chapter 2; Ridderikhoff et al., 2007). When an integrated pattern of control signals specifying the required coordination pattern is sent to the hands, a copy of the motor commands (i.e., an efference copy) may be used to predict sensory consequences of those efferent signals. Given the nature of the task, this bimanual reference may be expected to involve the coding of the desired movement in terms of the required relative timing of the limbs. Although this timing template may also involve spatial components, these seem to be of subordinate importance in the bimanual coordination task examined. As such, planning of the desired timing template may be used to generate expected sensory consequences, to which subsequently the actual sensory consequences can be compared (Desmurget & Grafton, 2000; Wolpert & Ghahramani, 2000). This result and theoretical interpretation may be contrasted with indications that learning to perform a new coordination pattern depends primarily on improving one's perceptual abilities to discriminate the required pattern (Wilson, Snapp-Childs, & Bingham, 2010) and the observation that performance of the correct pattern without issuing the required patterning of motor commands suffices to acquire a new coordination pattern (Atchy-Dalama, Peper, Zanone, & Beek, 2005). Hence, it seems that the reference frame underlying error corrections can be established in various ways. In the current context, participants simply practiced the required pattern, thereby improving their ability to generate the required phase relation in a feedforward manner (viz. AB improved prior

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8   Contrary to previous studies (Chapter 2; Ridderikhoff, Peper et al., 2005; Ridderikhoff et al., 2006) no entrainment towards in-phase or antiphase coordination was observed for any of the UNm tests.

to KT), which subsequently may have served as reference for error correction processes. However, whereas improved perceptual ability to discriminate the pattern (cf., Wilson et al., 2010) and the establishment of an afference-based reference frame (Atchy-Dalama et al., 2005) both may benefit error correction in bimanual coordination, a learning process that involves actual execution of the required pattern additionally enhances stability of the new pattern, as has been shown previously (Beets et al., 2012; Feijen, Hodges, & Beek, 2010). The present results indicate that this may result from additional stabilizing influences stemming from the integrated timing level.

Learning and attentional focus

Superior learning was expected for an external focus of attention, in particular for the external focus less closely related to the hand movements as induced using Lissajous feedback. Although the external-Lissajous group showed larger improvements during practice, no significant effects of attentional focus or the distance of the external focus were observed on the tests. The initial difference in the absolute error of the relative phase (cf. Figure 4.1) probably reflected the part in which participants in the external-focus groups needed to discover how the transformation of their movements to the feedback was organized, in order to obtain the correct auditory pattern or visual Lissajous figure. The external-Lissajous group seemed to take longer to decrease these errors than the external-auditory group, possibly because feedback was less closely related to the hand movements. Although Lissajous feedback has been shown to be a useful method to execute difficult coordination patterns (Kovacs, Buchanan et al., 2009; Kovacs, Buchanan, & Shea, 2010a), in the present experiment it may have been more difficult to utilize initially due to the presence of a pacing signal (cf., Kovacs & Shea, 2011). The lack of differences between the groups at the tests following practice indicated that attentional focus did not significantly affect the learning process or the associated changes in the contributions of integrated timing, error correction, and phase entrainment. Many studies have shown enhanced learning performance for an external focus of attention as compared to an internal focus of attention (Chiviacowsky et al., 2010; McNevin et al., 2003; Rotem-Lehrer & Laufer, 2007; Wulf et al., 1999; Wulf & Prinz, 2001), although mixed results have been obtained for novices (Castaneda & Gray, 2007; Gray, 2004; Perkins-Ceccato et al., 2003; Wulf & Su, 2007). As all participants in the current study were novices, this might explain why we did not observe performance differences between the groups. In addition, the effectiveness of an external focus may have been influenced by individual preferences, since an internal focus has been shown

to be detrimental for individuals who prefer an external focus, but not for those who prefer an internal focus of attention (Weiss, Reber, & Owen, 2008). Possibly, participants preferred an internal focus of attention in the present experiment, thereby minimizing the difference between the different attentional foci groups (Weiss et al., 2008). In addition, it is conceivable that the fading schedule applied to the feedback presentation encouraged a shift from an external to an internal focus, to cope with the withdrawal of the feedback. Perhaps this concern may be circumvented in future experiments by using the adapted Lissajous display proposed by Buchanan and Wang (2012), but such a solution is not readily available for the presentation of auditory feedback.

Moreover, also task characteristics may have influenced the effect of attentional focus in the present experiment. On the one hand, the presence of a pacing signal to prescribe the movement pattern and movement frequency may have restricted the induced external focus of attention, by initially inducing a tendency to an internal focus in all groups and by making the use of the Lissajous feedback more difficult (Kovacs & Shea, 2011). On the other hand, it may have been difficult to establish an external focus, given that the current bimanual coordination task did not have a direct impact in the environment. Whereas beneficial effects of an external focus have been established for tasks such as baseball batting, golf pitching, or the long jump (Castaneda & Gray, 2007; Perkins-Ceccato et al., 2003; Porter et al., 2011; Wulf & Su, 2007), it may have been more difficult to detach the attentional focus from the actual hand movements in the present 90° coordination task. This may suggest that an external focus of attention is more useful if a task has a discernible effect in the environment, i.e., if movement effects can be separated easily from the movements that are executed. Indeed, Wulf and colleagues (e.g., Wulf & Prinz, 2001) have argued that learning is not enhanced by the absence of an internal focus of attention, but by the ability to capture motor control in the perceptual effects. If a motor task does not result in clear perceptual effects in the environments, it is difficult to focus on its external effects. This interpretation is in line with recent results regarding the lack of benefits from an external focus in learning gymnastic routines, which also did not involve direct effects in the environment (Lawrence, Gottwald, Hardy, & Khan, 2011). However, because additional factors may have contributed to the absence of an effect of attentional focus in the present study and in the study of Lawrence et al., further research is needed to determine whether indeed the impact on the environment mediates the effectiveness of an external focus of attention.

Retention and transfer

To examine retention and transfer, we compared performance of the practiced 90° pattern and the 270° transfer pattern. Enhanced performance was expected at retention due to the process of consolidation (Brashers-Krug et al., 1996; Karni & Sagi, 1993; Walker et al., 2003; Walker & Stickgold, 2005) and improved performance of the 270° pattern was expected due to transfer effects (Smethurst & Carson, 2001; Zanone & Kelso, 1997). With respect to the underlying interlimb interactions, no specific hypotheses were formulated, although it was suggested that integrated timing may contribute equally to the practiced and transfer pattern because it forms a more abstract representation, whereas error correction was expected to contribute more to the practiced pattern than the transfer pattern. The results, however, showed that integrated timing and error correction contributed equally to improvements of the 90° and 270° coordination patterns.

Interestingly, whereas accuracy and stability of the 90° pattern improved directly after learning at the post-test and did not improve further afterwards, the 270° pattern only improved at retention. Although transfer has also been observed directly following learning (Zanone & Kelso, 1997), earlier results also revealed improved performance for 270° from post-test to retention, whereas the practiced 90° did not improve any further (Maslovat, Chua, Lee, & Franks, 2004). This suggests that in these settings participants first learned the pattern as practiced, and that a more abstract representation of the coordination pattern, involving the same temporal structure but inversed timing of the two hands, was formed in a later stadium following practice. However, the absence of further enhancement of the 90° pattern at retention does not match the expected consolidation effects that have been observed previously for various perceptuomotor tasks (Brashers-Krug et al., 1996; Walker et al., 2003; Walker & Stickgold, 2005). This may have resulted from our training schedule, which involved practicing at two separate days. Indeed performance was already enhanced over nighttime between Day 1 and Day 2 (i.e., compare accuracy at Test90-1 and Test90-2).

The improved performance of the 270° pattern at retention may suggest that the consolidation process after Day 2 included a process of generalization of the practiced pattern to a more abstract representation. Research on sequential movement tasks has indicated that learning may involve fast development of a spatial representation allowing generalization to another effector, and slower development of a motor representation that allows generalization to the mirror-symmetrical pattern (Hikosaka et al., 1999; Kovacs, Han, & Shea, 2009; Panzer, Krueger, Muehlbauer, Kovacs, & Shea,

2009). However, because these transfer effects were obtained after a retention period of 24 hours and were not compared to a post-test, it is unclear how these generalizations are influenced by consolidation. Only a few studies have tested if generalization of some kind indeed occurs during the time period after practice in which consolidation takes place (Buchanan, 2004; Cohen, Pascual-Leone, Press, & Robertson, 2005; Fischer, Hallschmid, Elsner, & Born, 2002; Witt, Margraf, Bieber, Born, & Deuschl, 2010). In two of these experiments consolidation was shown to result in generalization of the perceptual goal. For a finger sequence task, improvements were observed after sleep for execution of the same spatial sequence by different fingers, but not for the execution of the mirror-symmetric sequence by different fingers (Cohen et al., 2005; Witt et al., 2010). Fischer et al. (2002) showed consolidation effects for a practiced finger tapping sequence, but not for the mirror-symmetric transfer sequence. Furthermore, Buchanan (2004) showed consolidation of transfer for intersegmental coordination of the arm. Together, these experiments suggest that participants learn the perceptual representation of the to-be-learned-task task (cf., Atchy-Dalama et al., 2005; Feijen et al., 2010), which allows the acquired performance to be generalized to another effector. However, generalization to the mirror-symmetrical pattern (i.e., involving the same muscles of the contralateral hand) appears not to take place during consolidation (Cohen et al., 2005; Fischer et al., 2002; Witt et al., 2010).

The transfer observed in our experiment (and in Maslovat et al., 2004) however, did not involve generalization of the pattern to another effector but to its mirror-symmetrical counterpart. Perhaps task characteristics have influenced the differential results in this regard. In the finger tapping experiments more elements contributed to the task (i.e., four fingers) and the spatial organization was more important (i.e., in a reaction time task), whereas our task involved two hands that were coupled in a temporal pattern. This may have influenced the way the task could be generalized to the mirror-symmetrical pattern. Clearly, more research is needed to examine the consolidation effects in this regard, and to determine whether and how this process may involve generalization besides stabilization and improvement of the practiced pattern (Walker & Stickgold, 2005).

Summary and conclusions

In sum, the present experiment showed that learning a new bimanual coordination task influenced the underlying contributions of interlimb interaction. Whereas the contribution of phase entrainment did not change significantly during learning, the contribution of

integrated timing and error correction improved significantly, thereby enhancing the stability and accuracy of the learned pattern. Furthermore, results showed that the combination of integrated timing and error correction was most useful to enhance performance: integrated timing appears to form a bimanual representation of the required coordination pattern, which can be used as a reference for the error corrections based on kinesthetic afference. In addition, attentional focus was found not to affect learning in this bimanual coordination task. Perhaps this unexpected result indicated that effectiveness of an external focus of attention during learning is a function of the degree of influence that the to-be learned task inflicts in the environment. Finally, the observed delayed improvement of the transfer pattern may indicate that consolidation does not only regard the learned pattern but may also influence generalization of the practiced pattern to a more abstract representation. As only a few studies have studied this process, more research is needed to understand whether and how generalization occurs in motor learning.

4

5

Development of temporal and spatial bimanual coordination during childhood

Developmental changes in bimanual coordination were examined in four age groups: 6/7, 10/11, 14/15 years, and young adults. Temporal coupling was assessed through the stabilizing contributions of interlimb interactions related to planning, error correction, and reflexes during rhythmic wrist movements, by comparing various unimanual and bimanual tasks involving passive and active movements. Spatial coupling was assessed via bimanual line-circle drawing. With increasing age, temporal stability improved. Relative contributions of planning and reflex interactions to the achieved stability did not change, whereas error correction improved. In-phase and antiphase coordination developed at similar rates; implications of this result were discussed in terms of mirror-activity inhibition. Overall spatial drawing performance (circularity, variability, smoothness) improved with age, and spatial interference was smaller in adults than children. Whereas temporal coupling increased from 6/7 years to adulthood, spatial coupling changed mainly after 14/15 years. This difference in the development of temporal and spatial coupling corresponds to the anterior-posterior direction of corpus callosum myelination as reported in the literature.

INTRODUCTION

Bimanual coordination is required in many daily life activities, such as cooking, writing, and getting dressed. In order to successfully coordinate bimanual movements, information needs to be exchanged between the cerebral hemispheres. The primary structure for interhemispheric communication is the corpus callosum (CC), which allows interhemispheric integration of motor, sensory, and cognitive processes (Muetzel et al., 2008; Wolff, Kotwica, & Obregon, 1998). The myelin sheath around the CC fibers enables rapid and synchronized information transfer. During development across childhood this myelin sheath matures, increasing the rate of interhemispheric communication (Deoni et al., 2011; Giedd et al., 2009). To examine the effects of these developmental changes on bimanual coordination, we examined bimanually coordinated movements across different age groups. Although developmental changes in other brain structures and networks may contribute to improved motor control and bimanual coordination as well, our predictions regarding the changes in interlimb coordination were based on pertinent literature regarding CC functioning in relation to bimanual temporal and spatial coordination.

Corpus callosum

Myelination of the CC not only leads to rapid and synchronized information transfer, but it may also enhance interhemispheric inhibition of mirror movements (Daffertshofer et al., 2005; Hubers, Orekhov, & Ziemann, 2008). Mirror movements – unintended movements of the limb that is not active during intended unilateral movements of the contralateral limb – are often observed in young children. Communication via the CC may result in mirror activity (e.g., interference effects disappear in callosotomy patients, see below), but mirror movements are also suppressed via interhemispheric inhibition across the CC (Hubers et al., 2008; Mayston, Harrison, & Stephens, 1999). During development the occurrence of mirror movements decreases in frequency and intensity; around the age of 10 a sharp decline has been observed, possibly as a result of CC myelination (Cincotta & Ziemann, 2008; Cohen, Taft, Mahadeviah, & Birch, 1967; Hubers et al., 2008). Since in everyday tasks the two hands often have to execute different movements simultaneously, increased mirror movement inhibition with age will lead to improved bimanual coordination and hence improved task execution.

Studies with callosotomy patients – i.e., patients in whom (part of) the CC has been dissected – have highlighted the importance of the CC in bimanual coordination. These

patients made fewer errors than control participants in spatially incompatible drawing tasks, indicating that the tendency to execute the same movements during bimanual coordination was suppressed as a result of their callosotomy. In other words, spatial coupling of the hands appears to be organized via the CC (Eliassen, Baynes, & Gazzaniga, 2000; Franz, 1997; Franz, Eliassen, Ivry, & Gazzaniga, 1996), particularly via its posterior part (Eliassen, Baynes, & Gazzaniga, 1999). The anterior part of the CC has been shown to be involved in temporal coupling (Eliassen et al., 1999; Ouimet et al., 2010), albeit in a task-dependent manner (Ivry & Hazeltine, 1999; Kennerley, Diedrichsen, Hazeltine, Semjen, & Ivry, 2002; Tuller & Kelso, 1989). Specific parts of the CC thus appear to be involved in different coupling processes in bimanual coordination: the posterior part primarily in spatial coupling and the anterior part primarily in temporal coupling.

Based on in vitro studies, it has been suggested that CC myelination during development is completed around the age of 10 or 11 (cf., see discussion in Fagard, Morioka, & Wolff, 1985). However, more recent magnetic resonance imaging (MRI) studies revealed that myelination is not completed until the early twenties (Giedd et al., 1996; Rajapakse et al., 1996; Thompson et al., 2000). In a longitudinal study, (Thompson et al., 2000) showed that specific parts of the CC differ in growth rates: the anterior parts grow fastest between the age of 3 to 6, while the largest posterior growth was observed between the age of 6 to 15. Because callosotomy studies indicated that these parts of the CC are differentially involved in the spatial and temporal aspects of bimanual coordination, the question arises how these aspects of bimanual coordination are mediated by CC myelination during childhood. In this study we therefore examined how temporal and spatial coupling of the limbs change across childhood.

Temporal bimanual coupling

Temporal coupling between the limbs has been investigated in a variety of tasks and across various ages. Performance has been found to improve with age in children in bimanual tapping (Muetzel et al., 2008; Wolff et al., 1998), bimanual circle drawing (Robertson, 2001), bimanual reaction tasks (Fagard, Hardy-Leger, Kervella, & Marks, 2001), and clapping (Fitzpatrick et al., 1996). CC myelination was demonstrated to contribute positively to alternate tapping performance (Muetzel et al., 2008).

A task that is often used to examine temporal interlimb coupling is isofrequency bimanual coordination, usually by studying the relative phase between the hands (Φ) and its variability (Haken et al., 1985; Kelso, 1984; Schöner et al., 1986). As a result of interlimb interactions, only two coordination patterns can usually be executed stably

without learning: in-phase (IP) and antiphase (AP) coordination (Zanone & Kelso, 1992). IP coordination ($\Phi = 0°$) refers to mirror-symmetric movements or the simultaneous activation of homologous muscles, whereas AP coordination ($\Phi = 180°$) refers to parallel movements or the simultaneous activation of non-homologous muscles. AP is less stable than IP coordination, and when frequency increases to a critical value, an involuntary switch from AP to IP may occur (Haken et al., 1985; Schöner et al., 1986). The coupling between the limbs and these differences between IP and AP coordination are the result of interlimb interactions. When studying bimanual coordination across different age groups, the question arises how these interactions contribute to developmental changes in bimanual coordination. But what are these interlimb interactions and how may they evolve during development?

Recently, specific forms of interlimb interaction that underlie the stability of coordination patterns have been investigated in relation to the coordination pattern performed (Ridderikhoff, Peper et al., 2005), movement frequency (Chapter 2), and the associated attentional costs (Ridderikhoff et al., 2008). In particular, three forms of interlimb interactions can be dissociated based on the dependence on afferent, sensory information and the intention to execute a specific pattern (see Table 5.1).

Table 5.1
Sources of interlimb interaction underlying bimanual coordination.

Interlimb interaction		*Afference-dependence*	*Bimanual intentionality*
Planning	Generation of an integrated control signal for both limbs, specifying the bimanual pattern	No	Yes
Correction	Correction of relative phase errors based on kinesthetic afference, stabilizing the bimanual pattern	Yes	Yes
Reflex	Phase entrainment by contralateral afference	Yes	No

First, movement planning reflects interaction processes related to feedforward timing of the efferent signals that specify the bimanual coordination pattern, without taking adjustments based on afferent feedback into account. Second, error correction pertains to the correction of perceived relative phasing errors based on kinesthetic afference, to stabilize the intended bimanual coordination pattern. Third, reflex interactions refer to the unintentional attraction to specific phase relations between the limbs. This is a relatively automatic or reflex-like mechanism based on kinesthetic signals. Whereas error correction concerns the intentional use of kinesthetic feedback to correct

for relative phase errors in the intended pattern, reflex interactions result in unintended attraction toward IP and AP coordination with the movements of the contralateral limb (Ridderikhoff et al., 2006; Serrien et al., 2001).

Planning, correction, and reflex interactions can be assessed by comparing specific tasks in which the interactions are present to a different extent, as demonstrated by Ridderikhoff, Peper et al. (2005). As we were testing children in the present study, we used a limited number of tasks and conditions (see Ridderikhoff et al., 2008 for a detailed description). All four tasks involved unimanual or bimanual rhythmic flexion-extension movements about the wrist. The tasks differed with regard to the degree in which the three sources of interaction are assumed to be involved (cf. Table 5.2): (1) in task UN (unimanual coordination with the metronome) no interlimb interactions are present; (2) in task UNm (task UN while a motor moves the contralateral hand) reflex interactions entrain the active hand to the passively moving hand; (3) in task KT (kinesthetic tracking) correction interactions furthermore stabilize the coordination pattern based on kinesthetic signals; (4) in task AB (active bimanual coordination) planning interactions further stabilize the coordination pattern. Systematic pairwise comparisons of two tasks can be used to single out the contributions of each of the sources of interlimb interaction (cf. Table 5.2): reflex interactions can be studied by comparing UNm and UN, correction interactions by comparing KT and UNm, and planning interactions by comparing AB and KT. Previous results showed that this method yields a useful dissociation between the contributions of the interlimb interactions in question to the stability of bimanual coordination, but that the sources do not add up linearly (as suggested in Table 5.2).

Table 5.2
Tasks and sources of interlimb interaction

Task		Planning	Correction	Reflex
AB	Active bimanual coordination at a tempo specified by an auditory signal.	X	X	X
KT	Kinesthetic tracking of the passively moving contralateral hand.		X	X
UNm	Unimanual coordination with an auditory pacing signal while (phase-shifted) passive movements of the contraleral hand are presented as distractor.			X
UN	Unimanual coordination with an auditory pacing signal.			

Mapping of the four tasks to the three sources of interlimb interaction. The "X" symbols represent the sources of interlimb interaction that are assumed to be involved in the associated tasks.

In particular, error correction appeared to be hardly involved in AB, because the planning interactions provided sufficient stability. Therefore, planning interactions were also examined by comparing AB to UNm (Chapter 2; Ridderikhoff, Peper et al., 2005).

Spatial bimanual coupling

The effects of development across childhood on spatial coupling in bimanual coordination have seldom been studied. Spatial coupling between two hands can be assessed in bimanual incompatible drawing (i.e., incompatible orientations or shapes), to determine how the hands affect each other. Spatial incompatible drawing has only been examined in adults (Eliassen et al., 1999; Franz et al., 1996; Franz et al., 1991; Swinnen, Dounskaia, Levin, & Duysens, 2001) and in children with a disorder (Volman, 2005). Bimanual drawing has been studied across age groups (Lantero & Ringenbach, 2007; Robertson, 2001), but these studies did not involve incompatible drawing.

In the present experiment, we therefore assessed the developmental effects on spatial coupling by asking various age groups to draw two different shapes simultaneously. We used line-circle drawing, as this task is also feasible to perform by young children (Volman, 2005). For these line-circle drawings, unimanual drawings and bimanual drawings of the same shape served as control conditions. In this way, the development of spatial drawing of two different shapes (i.e., bimanual line-circle drawing) was contrasted to changes with age in unimanual drawing with the left and right hand (i.e., unimanual line and unimanual circle drawing) and to changes in bimanual drawing of the same shape (i.e., bimanual line-line and circle-circle drawing).

Aims and hypotheses

The leading research question of the experiment was: How do spatial and temporal coupling of the hands develop across childhood? Children between 6 to 15 years of age were tested in the experiment. This age span was chosen in view of CC growth rates (Thompson et al., 2000) and the ability of young children to attend to the task and pace their movements with a metronome (Fitzpatrick et al., 1996). Notably, the tasks used in the present experiment were neither purely temporal nor purely spatial, as the 'spatial' drawing tasks also involved timing of the hands and the 'temporal' bimanual patterns involved spatial aspects like amplitude and direction. However, these tasks emphasized one particular aspect and were therefore used to examine either temporal or spatial coupling between the limbs.

With respect to the suggested anterior-posterior direction of myelination (Giedd et al., 1996; Thompson et al., 2000), the largest changes in temporal coupling were expected in the younger age groups compared to the older, whereas the opposite was expected for spatial coupling. Both IP and AP coordination were predicted to improve across development, but the largest improvements were expected to occur for AP, due to CC myelination and associated inhibition of mirror movements (Hubers et al., 2008; Mayston et al., 1999). This differential improvement of IP and AP was predicted for planning and correction interactions only, because these interlimb interactions are assumed to involve interhemispheric communication and both interactions contribute to the differential stability of IP and AP coordination (Chapter 2; Ridderikhoff, Peper et al., 2005). Potential age-related changes in reflex interactions were expected to be equally strong for IP and AP (Ridderikhoff et al., 2006). Regarding spatial coupling, performance in the drawing task was expected to increase in all conditions because children typically become more skilled in drawing with age. In addition, due to CC myelination and associated inhibition of mirror activity, the attraction of each hand to the contralateral hand was expected to weaken with age. As a result, the distortions that were predicted to deteriorate performance when drawing two different shapes (relative to the control conditions) were expected to become smaller with age.

METHODS

Participants

Four age groups were examined: 6/7 years, 10/11 years, 14/15 years, and young adults (mean age 26.2 years, standard deviation (*SD*) 1.70 years). In each group 10 participants were tested (5 female, 5 male). All participants were right-handed as determined on a shortened version of the Edinburgh handedness scale (Oldfield, 1971; in view of the youngest age group two questions were removed: dealing cards and striking a match). Informed consent was provided prior to the experiment by the parents of the children and by the adults. Children received a small present after participating in the experiment.

Apparatus

To assess the temporal coupling between the hands and underlying interlimb interactions, a setup was used that has been described in detail elsewhere (Ridderikhoff, Peper et al.,

2005). In short, participants sat in a height-adjustable chair with their elbows slightly flexed and their feet supported. Their forearms were placed on armrests in a neutral position (thumbs up, palms facing inward, fingers extended). Both hands were fixated to two flat manipulanda, allowing wrist flexion and extension only. The manipulandum for the left hand registered the wrist movements using a potentiometer, whereas that for the right hand either registered its movements (potentiometer) or controlled the wrist movements by means of a motor (i.e., for active and passive movements, respectively). A screen was used to eliminate visual feedback of the hand movements.

For spatial drawing, participants sat in a height-adjustable chair behind a table with a drawing tablet (Intuos A4 serial tablet, sample frequency 100 Hz, spatial accuracy 0.25 mm) on which they could make drawings with one or two cordless pens (Intuos standard pens). Templates that specified the shape(s) were placed on the tablet underneath a transparent cover. Participants were instructed to trace the presented shapes while looking at their hands. The vertically-oriented lines were 9 cm long and the circles had a diameter of 9 cm; line thickness of both shapes was 1.1 mm. The center-to-center distance between two shapes was 14.8 cm.

For both the temporal and spatial tasks, auditory pacing stimuli (pitch: 440 Hz, duration: 50 ms) were presented through speakers positioned close to the participant.

Procedure

The order of the temporal and spatial coordination parts was quasi-counterbalanced across participants (i.e., over each age-gender subgroup).

Temporal coordination

Participants executed four different tasks that involved unimanual or bimanual rhythmic flexion-extension movements about the wrist. Starting with UN, participants performed unimanual rhythmic flexion-extension movements of their left wrist at the tempo specified by the auditory signal. Participants were instructed to let peak flexion coincide with the beep. Next, participants executed bimanual coordinated movements (task AB) of the wrist in IP or AP coordination. During IP peak flexion of both hands had to coincide with the beep, while for AP peak flexion of the left hand and peak extension of the right hand had to coincide with the beep.

In tasks UNm and KT the right hand was moved by the motor. The motor trajectories were based on sinusoidal trajectories, with an amplitude of 25° (peak-to-peak 50°) around a wrist position of 10° in flexion (i.e., approximately the neutral position). To

prevent the trajectories from being perceived as predictable, the period lengths and the amplitudes of the cycles were randomly varied to obtain a moderate level of variability: $SD_{frequency}$ = 0.02 Hz and $SD_{amplitude}$ = 3.6° (i.e., in accordance with Ridderikhoff et al., 2007). In UNm, four phase relations between the passive movements and metronome pacing were applied: a phase shift of -30° and 0° around IP and AP (with 30° corresponding to 1/12th of a movement cycle and the negative phase shift implying a phase advance of the passive movements). The passive movements were phase shifted using cubic spline interpolation at the start of the trial so that the phase shift of -30° was achieved in three cycles. The trajectories were multiplied with a windowing function to generate a smooth increase and decrease in the amplitude of the passive movements in the first and last two cycles respectively. In task UNm, participants were instructed to ignore these passive movements and to let peak flexion of their active (left) hand coincide with the beep (i.e., as in task UN). In task KT participants were instructed to move their active hand so as to track their passively moving hand, either in IP or AP (again defined in terms of the phase relation at the turning points of the movements). In this task, no pacing signal was present.

Each condition was repeated twice. Thus, in total, 2 UN trials, 2 (Pattern) x 2 (Repetitions) = 4 AB trials, 2 (Pattern) x 2 (Shift) x 2 (Repetitions) = 8 UNm trials, and 2 (Pattern) x 2 (Repetitions) = 4 KT trials were executed. Trials were grouped in several blocks which were ordered according to instruction and difficulty: UN, AB-IP, AB-AP, UNm, KT-IP, and KT-AP. Prior to each block a single practice trial was presented. In all conditions frequency was set to 1.1 Hz and trial length was 21 cycles.

Spatial coordination

Participants executed five conditions, which were ordered according to difficulty to facilitate their performance by the children: (1) Unimanual circle drawing with the right hand; (2) Unimanual line drawing with the left hand; (3) Bimanual-same, circle: bimanual circle drawing; (4) Bimanual-same, line: bimanual line drawing; and (5) Bimanual-different: drawing a line with the left hand and a circle with the right hand. Each condition was repeated twice. For circle drawing, movement direction was specified: the right hand drew the circles in counterclockwise direction and the left hand in clockwise direction (i.e., bimanual circle drawing was mirror symmetrical). Movement frequency was set to 1.0 Hz and trial duration was 20 seconds. A pacing signal prescribed movement frequency: participants were instructed to complete one circle and/or line (up and down) for each beep. Participants were free to choose which point of the line or circle to synchronize with the beep.

Data analysis

Temporal coordination

The first and last three cycles of each trial were removed, leaving 15 cycles for analysis. More cycles were removed if (1) Φ increased or decreased progressively over several consecutive cycles (i.e., phase wrapping); (2) the phase relation with the pacing signal or between the hands was not correct (i.e., in case of a switch to the other pattern). The cycles included in the analysis were low-pass filtered (2nd-order bidirectional Butterworth filter, cut-off frequency 18 Hz). For the tasks in which two hands were involved (AB, KT, and UNm), the relative phase between the hands was calculated for each cycle as $\Phi_i = 360° (t_{y,i} - t_{x,i}) / (t_{x,i+1} - t_{x,i})$, where $t_{y,i}$ and $t_{x,i}$ indicate the time of the *i*th peak flexion (extension) of the left hand and the right hand, respectively (cf. Carson et al., 1995). For the unimanual tasks (UNm and UN), the relative phase between the metronome and peak flexion of the left hand was determined for each cycle as $\Psi_i = 360° (t_{y,i} - t_{x,i}) / (t_{x,i+1} - t_{x,i})$, where $t_{y,i}$ indicates the time of the ith peak flexion of the left hand and $t_{x,i}$ corresponds to the moment of the ith metronome beep. For both Φ and Ψ a positive value implied that the left hand (*y*) was lagging the reference signal (*x*). Circular statistics (Mardia, 1972) was used to determine the average values of Φ and Ψ, and the corresponding circular standard deviations (CSD_Φ and CSD_Ψ). To assess accuracy, the absolute error in Φ was calculated as $AE_\Phi = | \Phi - \Phi_{required} |$ with $\Phi_{required}$ equal to 0° and 180° for IP and AP, respectively.

An error in relative phasing can be corrected by shortening or lengthening the subsequent half cycle of (one of) the hands, resulting in a negative correlation between the signed error in relative phasing at peak flexion or extension and the duration of the subsequent half cycle (Ridderikhoff et al., 2007). Therefore, the presence of error correction was examined in terms of this error correction correlation (R_{EC}), calculated for each half cycle of the left hand (i.e., the hand that was actively moving in all tasks)[9]. Because UNm performance did not involve error correction, the obtained correlation values reflected the influence of reflex interactions and were regarded as baseline values (Ridderikhoff, Peper et al., 2005). Therefore, for all participants the R_{EC} values obtained for each condition in AB and KT were corrected by subtracting the corresponding mean values for UNm, as obtained for that participant. In addition, the correlation between

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9   Ridderikhoff et al. (2007) showed that whereas the correlation between the signed error and the next full cycle is influenced by between- and within-hand correlations, the correlation between the signed error and the next half cycle is not. Furthermore, analysis showed that errors in the current experiment were mainly corrected during the first half cycle and hardly in the subsequent half cycles.

the duration of simultaneously performed cycles (R_{CD}) was calculated as an index of the strength of interlimb interactions, with higher values of R_{CD} reflecting stronger coupling (Ridderikhoff, Peper et al., 2005). For statistical analyses, R_{EC} and R_{CD} were transformed into normally distributed values using the Fisher transform. For clarity, the untransformed values are presented in the Results.

Spatial coordination

The first two cycles were removed from the analysis and additional cycles were removed if the pattern was not executed in the correct direction. The cycles included in the analysis were low-pass filtered (2nd-order directional Butterworth filter, cut-off frequency 10 Hz). The velocity profile of movements in the Y dimension (anterior-posterior) was used to calculate movement amplitudes. Amplitudes were calculated as $X_{amp} = |X_{t,a} - X_{t,b}|$ and $Y_{amp} = |Y_{t,c} - Y_{t,d}|$, where t,a and t,b indicate the time of peak positive and peak negative velocity, and t,c and t,d indicate the time of zero crossing in the velocity profile in positive and negative direction (Franz et al., 1991). The index of circularity was defined as X_{amp}/Y_{amp}, yielding 1 for drawing a perfect circle and 0 for drawing a perfect vertical line. For each trial, the index of circularity was averaged over the included cycles, and the corresponding standard deviation was taken as a spatial variability measure. Drawing performance was also assessed in terms of smoothness of the shapes drawn, which was operationalized as the number of velocity peaks in the tangential velocity signal per cycle that exceeded a velocity threshold of 2.0 cm/s: $|v_{max} - v_{min}| > 2.0$ cm/s. This threshold value was chosen based on the study of (Volman, Wijnroks, & Vermeer, 2002), taking into account the frequency of the drawing movements. For each trial, the mean number of peaks was calculated over the included cycles.

Statistical analysis

The repeated-measures analyses of variances (ANOVAs) for the temporal tasks involved between-participants factor Age (6/7 years, 10/11 years, 14/15 years, adults) and within-participant factors Task (AB, KT, and UNm; unless specified otherwise), Pattern (IP, AP), Shift (-30°, 0°), and Direction (flexion, extension) for the temporal tasks. Direction was taken as a factor because effects have been reported to concentrate around the moment of pacing (Fink, Foo, Jirsa, & Kelso, 2000). First, Ψ and CSD_ψ were examined separately for UN and UNm (with a 0°-phase shift) using ANOVAs with factor Age, and, for UNm, Pattern. Second, AE_ϕ and CSD_ϕ as obtained for AB, KT, and UNm (with a 0°-phase shift)

were examined using an ANOVA with factors Age, Task, Pattern, and Direction. Next, strategic comparisons between two tasks were performed to uncover how the different sources of interlimb interaction contributed to coordinative stability (see *Introduction*). The difference between two tasks in each condition was submitted to an ANOVA with factors Age, Pattern, Direction, and, if applicable, Shift. The stabilizing effect of planning interactions was assessed by comparing CSD_Φ between AB and KT, and between AB and UNm (see *Introduction*). The stabilizing influences of error correction were assessed by comparing CSD_Φ between KT and UNm. Entraining effects of reflex interactions were assessed by comparing Ψ between UN and UNm. Furthermore, R_{EC} and R_{CD} were analyzed using an ANOVA with factors Age, Pattern, Direction, and Task. For R_{EC} tasks AB and KT were examined; for R_{CD} tasks AB, KT, and UNm.

For the spatial tasks, Age was included as between-participants factor and Condition (unimanual, bimanual-same, bimanual-different) as within-participant factor. The corresponding ANOVAs were conducted for line and circle drawing separately, examining the index of circularity, its variability, and the smoothness of drawing.

In all ANOVAs, Greenhouse-Geisser adjustment of degrees of freedom was applied if the assumption of sphericity was violated. Effect sizes were based on the partial eta squared (η_p^2, Cohen, 1988). Significant effects ($p < .05$) were further scrutinized using post-hoc paired-samples *t*-tests. All significant effects obtained in the ANOVAs are presented in Table 5.3. In the Results section only results involving factor Age are discussed, to focus on changes as a result of development. Values are presented as mean [between-participants *SD*].

RESULTS

Temporal coordination

Several cycles were removed from the analysis, due to incorrect task performance (see *Data analysis*). In particular the 6/7-year olds had difficulties to meet the task requirements regarding the coordination between the hands and synchronization with the pacing signal. Considerably more cycles were removed for this group (519) than for the older groups (on average 89.5 per group).

Table 5.3

Results ANOVAs

Variable	Effect	F-value	p	η_p^2	Comparison level
CSD_ψ UN	Age	$F_{3,36} = 24.3$	.001	.53	see text
CSD_ψ UNm	Pattern	$F_{1,36} = 7.3$	.05	.16	IP (25.0°) < AP (31.4°)
	Age	$F_{3,36} = 7.9$	.001	.35	see text
AE_ϕ	Direction	$F_{1,36} = 6.8$	.05	.16	flexion (24.6°) < extension (26.0°)
	Task	$F_{2,72} = 42.1$	.001	.54	AB (10.3°) < KT (34.7°) & UNm (20.1°)
	Pattern	$F_{1,36} = 9.7$	.01	.21	IP (22.7°) < AP (27.9°)
	Age	$F_{3,36} = 3.9$	.05	.25	see text
	Task x Direction	$F_{2,72} = 4.9$	.05	.12	AB flexion (8.26°) < extension (12.4°), KT n.s. (35.5° and 33.9°), UNm n.s. (30.0° and 31.7°)
	Task x Age	$F_{6,72} = 4.8$	.001	.28	see text
CSD_ϕ	Direction	$F_{1,36} = 6.8$	.05	.16	flexion (20.3°) < extension (21.5°)
	Task	$F_{1.5,52.6} = 45.2$	.001	.56	AB (15.7°) < KT (18.9°) < UNm (28.1°)
	Pattern	$F_{1,36} = 11.0$	.01	.23	IP (18.9°) < AP (22.9°)
	Age	$F_{3,36} = 18.9$	.001	.61	see text
$\Psi_{UNm} - \Psi_{UN}$	Shift	$F_{1,36} = 5.9$	.05	.14	-30° (-15.2°) < 0° (-5.94°)
	Pattern	$F_{1,36} = 4.8$	.05	.12	IP (-17.6°) < AP (-3.44°)
R_{EC}	Task	$F_{1,36} = 19.5$	.001	.35	AB (-.02) > KT (-.13)
	Age	$F_{3,36} = 3.1$	.05	.21	see text
	Direction x Task x Pattern	$F_{1,36} = 4.1$	.05	.10	AB = KT for flexion AP (-.05 and -.03), AB > KT for flexion IP (-.07 vs. -.19), extension IP (.05 vs. -.13), and AP (-.01 vs. -.15)
R_{CD}	Direction	$F_{1,36} = 15.1$	.001	.30	flexion (.24) > extension (.19)
	Task	$F_{2,72} = 104$	.001	.74	AB (.49) > KT (.11) & UNm (.06)
	Age	$F_{3,36} = 3.2$	.05	.21	see text
	Task x Direction	$F_{1.6,58.7} = 4.2$	.05	.11	AB flexion (.54) > extension (.44), KT n.s. (.13 and .09), UNm n.s. (.06 and .05)
	Task x Direction x Age	$F_{4.9,58.7} = 2.6$	.05	.18	see text
	Task x Pattern	$F_{2,72} = 7.9$	.001	.18	IP: AB (.53) > KT (.16) > UNm (-.02) AP: AB (.45) > KT (.06) & UNm (.13)
CI circle	Condition	$F_{2,72} = 99.5$	.001	.73	uni (0.94) & bi-same (0.94) < bi-diff (0.78)
	Condition x Age	$F_{6,72} = 2.6$	.05	.18	see text
CI line	Condition	$F_{1.2,41.5} = 144$	.001	.80	uni (0.04) & bi-same (0.05) < bi-diff (0.10)
	Age	$F_{3,36} = 17.8$	.001	.60	see text
SD_{CI} circle	Condition	$F_{1.2,41.6} = 13.0$	.001	.27	uni (0.09) & bi-same (0.10) < bi-diff (0.13)
	Age	$F_{3,36} = 23.4$	.001	.66	see text
SD_{CI} line	Condition	$F_{1.4,51.4} = 162$	.001	.82	uni (0.03) & bi-same (0.03) < bi-diff (0.07)
	Condition x Age	$F_{4.3,51.4} = 4.7$	.01	.31	see text
	Age	$F_{3,36} = 43.8$	.001	.79	see text

Abbreviations: Variables: CSD_ψ: circular standard deviation of the relative phase between the hand and metronome; AE_ϕ: absolute error of the relative phase between the hands; CSD_ϕ: circular standard deviation of the relative phase between the hands; Ψ: relative phase between the hand and the metronome; R_{EC}: error correction correlation; R_{CD}: cycle duration correlation; CI = circularity index; SD_{CI} = standard deviation of the circularity index; Comparison levels: AB = active bimanual coordination; KT = kinesthetic tracking; UNm = unimanual coordination with a metronome with a motor as distractor; UN = unimanual coordination with a metronome; IP = in-phase coordination; AP = antiphase coordination; uni = unimanual drawing; bi-same = bimanual, drawing of the same shapes; bi-diff = bimanual drawing of different shapes; n.s. = not significant

Accuracy and variability of unimanual and bimanual performance

The relative phase between the actively moving (left) hand and the metronome in tasks UN (6.71° [29.4°]) and UNm (-0.77° [35.0°]) was not affected by Age: all age groups were equally accurate in timing their movements in accordance with the metronome. Variability in the relative phase between hand and metronome, however, decreased with age in task UN (cf. Table 5.3). The 6/7-year olds (47.7° [11.7°]) were significantly more variable in coordinating their movements than the three older age groups while the adults (15.5° [4.10°]) were less variable than the three younger age groups (10/11: 24.5° [10.5°]; 14/15: 21.9° [7.21°]). In UNm, variability also decreased with age: the 6/7-year olds (39.6° [12.6°]) were significantly more variable than the 14/15-year olds (23.2° [6.01°]) and the adults (18.9° [3.51°]), and the 10/11-year olds (31.2° [14.7°]) were more variable than the adults as well. Unimanual coordination with the metronome was thus adequately executed in all age groups, and the variability of these movements decreased with age.

The absolute error of the relative phase between the hands (AE_ϕ) decreased with age: the 6/7-year olds were less accurate than the 14/15-year olds and the adults, and the 10/11-year olds were less accurate than the adults (see Tables 5.3 and 5.4). In addition, differences between age groups varied over tasks: for AB the 6/7-year olds were less accurate than all older age groups and for UNm both the 6/7- and 10/11-year olds were less accurate than the 14/15-year olds and the adults. In task KT, AE_ϕ did not differ significantly over the age groups (see Table 5.4).

Table 5.4
Absolute error of the relative phase between the hands

Age	AB	KT	UNm
6/7	16.8 [4.56]	30.4 [17.9]	46.4 [21.3]
10/11	8.84 [3.44]	35.5 [19.0]	39.5 [15.8]
14/15	7.59 [3.22]	36.3 [13.9]	21.6 [15.5]
adults	8.01 [3.49]	36.5 [12.2]	15.8 [10.2]

The absolute error in the relative phase between the hands (AE_ϕ) for the four age groups in all tasks in which two hands were involved (AB, KT, and UNm), presented as mean [between-participants SD] in degrees.

Table 5.5
Circular standard deviation of the relative phase between the hands

Age	AB	KT	UNm
6/7	24.1 [5.32]	28.7 [10.3]	39.4 [10.3]
10/11	16.2 [4.72]	18.9 [6.00]	31.6 [16.3]
14/15	13.0 [2.84]	16.1 [3.21]	22.7 [5.06]
adults	9.67 [1.58]	11.8 [4.96]	18.7 [3.41]

The circular standard deviation of the relative phase between the hands (CSD_Φ) for the four age groups in all tasks in which two hands were involved (AB, KT, and UNm), presented as mean [between-participants SD] in degrees.

In all three bimanual tasks variability of relative phase decreased with age: CSD_Φ differed significantly between all groups, except for the 10/11- and 14/15-year olds. In addition, CSD_Φ varied over tasks, being smallest in AB, larger in KT, and largest in UNm (see Table 5.5). As this effect did not interact with Age (cf. Table 5.3), the enhanced stability (revealed by lower CSD_Φ) in task KT relative to UNm indicates that all age groups were able to intentionally use afferent information to stabilize the pattern by correcting for relative phase errors. In addition, the high stability obtained for AB performance indicates that participants in all age groups increased stability by actively planning the bimanual coordination pattern. Because overall performance improved with age, the strategic comparisons between the tasks (cf. Table 5.2) were conducted to examine how each of the three interlimb interactions contributed to these improvements, and whether the outcome of these comparisons differed over the four age groups. This is discussed in the next section.

Strategic comparisons

Planning. To determine how the stability of the coordination pattern was affected by the planning process, AB and KT were compared with respect to CSD_Φ (cf. Table 5.2). Because error correction has been found to be minimally involved in task AB when planning by itself can engender sufficient coordinative stability (Chapter 2; Ridderikhoff, Peper et al., 2005), the stabilizing effect of movement planning was assessed by comparing AB to UNm as well. Values of the KT and UNm conditions (with a 0°-phase shift) were subtracted from the matched AB conditions for all participants and tested in two separate ANOVAs. The negative differences in the comparisons of AB and KT (-3.16° [7.86°]) and AB and UNm (-12.4° [13.7°]) reflected the stabilizing influence of planning interactions. The absence of a main effect of age in the two comparisons revealed that the relative contribution of planning to the stabilization of the coordination pattern did not change during development for the tested age groups (cf. Table 5.3).

Correction. The stabilizing effect of interactions aimed at error correction was assessed by comparing CSD_Φ between KT and UNm. For all participants, the values of UNm with a 0°-phase shift were subtracted from the matched KT conditions. The negative difference between KT and UNm (-9.21° [15.0°]) revealed the stabilizing effect of error correction. Similar as to planning interactions, the absence of an effect of age showed that the relative stabilizing contributions of error correction did not change during development over the ages examined (cf. Table 5.3).

Reflex. Reflex interactions between the limbs result in (unintentional) attraction of the phasing of the active movement towards IP or AP coordination with the passive movement. Hence, the entraining influences of the passive movements were evaluated by examining the changes in Ψ in response to the applied phase shifts. The effect of shift showed that -30° and 0° differed significantly from each other (-15.2° [36.1°] and -5.9° [35.9°], respectively), showing attraction to the passively moving limb. This effect did not differ between age groups (cf. Table 5.3).

Correlations

The error correction correlation (R_{EC}) was examined for tasks AB and KT, i.e., the two tasks in which error correction could be present (cf. Table 5.3). As mentioned, the values in these tasks were corrected with respect to the baseline values obtained for UNm. The effect of age showed that the 6/7-year olds exhibited less error correction (.01 [.14]) than the adults (-.11 [.09]). The degree of error correction obtained for the 10/11-year olds (-.10 [.13]) and the 14/15-year olds (-.06 [.12]) was statistically equivalent to that of the adults. Thus, although the relative stabilizing contributions of error correction did not change with age (cf., comparison CSD_Φ between KT and UNm), the degree of error correction increased after the age of 6/7.

Analysis of the cycle duration correlation (R_{CD}) showed that coupling strength increased with age (cf. Table 5.3): R_{CD} was significantly larger for the 14/15-year olds (.25 [.07]) and the adults (.26 [.05]) than the 6/7-year olds (.17 [.08]). The 10/11-year olds (.19 [.11]) did not differ from the other groups. Post-hoc analyses of the interaction between task, direction, and age showed additional age differences (see Figure 5.1). Whereas for the younger ages only AB differed from KT and UNm (i.e., for the 6/7- and 10/11-year olds during flexion and extension, for the 14/15-year olds during extension only), all three tasks differed from each other for the older ages (i.e., for the 14/15-year olds during flexion, for the adults during flexion and extension). Thus for all ages, interlimb coupling was stronger in AB than in KT and UNm, and for the older ages this coupling was also stronger in KT than in UNm. This latter difference showed that the correction

interactions (viz. comparison between KT and UNm, cf. Table 5.2) contributed more to interlimb coupling after the age of 10/11 (during flexion and extension) and the age of 14/15 (during extension).
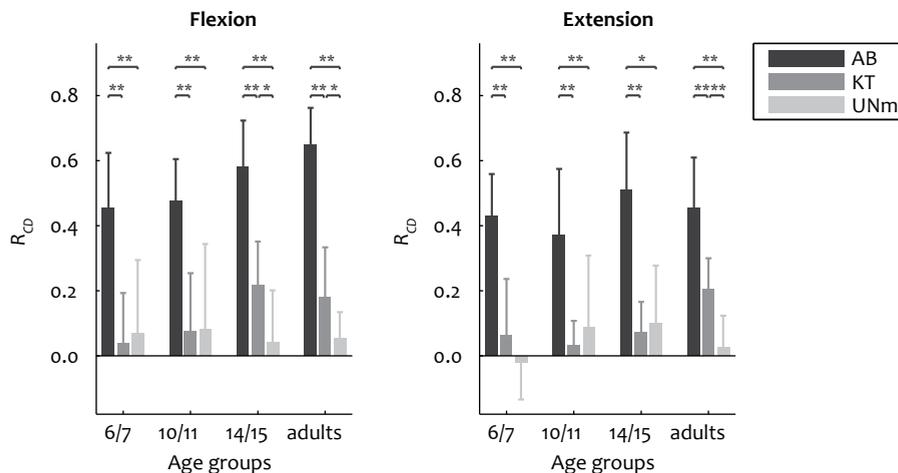

Figure 5.1. Cycle duration correlation (R_{CD}) presented for the four age groups for AB, KT, and UNm, calculated separately for cycles from peak flexion to peak flexion and from peak extension to peak extension. Error bars represent between-participants SD. Significant differences between tasks are indicated (* p < .05, ** p < .01).

Spatial coordination: drawing different shapes

Mean circularity index

With increasing age, overall performance of circle drawing did not change (cf. Table 5.3), whereas line drawing improved: performance of the 14/15-year olds (0.05 [0.01]) and the adults (0.05 [0.01]) was better than that of the 10/11-year olds (0.07 [0.01]), which in turn was better than performance of the 6/7-year olds (0.09 [0.03]).

Drawing two different shapes deteriorated performance of both circle and line drawing, showing that the two hands influenced each other (as reflected by the effect of condition, cf. Table 5.3). For line drawing this effect did not differ over the age groups: the circularity index of line drawing in unimanual drawing (0.04 [0.02]) was better than bimanual-same drawing (0.05 [0.02]) and both were superior to that in bimanual-different drawing (0.10 [0.04]). For circle drawing an age-related difference was obtained when the two different shapes were drawn simultaneously. In all age groups bimanual-different drawing was performed worse than bimanual-same and unimanual drawing, but the size of deterioration differed between age groups: the decrease in circularity

in bimanual-different drawing compared to bimanual-same drawing was larger for the 6/7-, 10/11-, and 14/15-year olds than for the adults, In addition, compared to unimanual drawing, the decrease in circularity was larger for the 14/15-year olds than for the adults (cf. Figure 5.2).
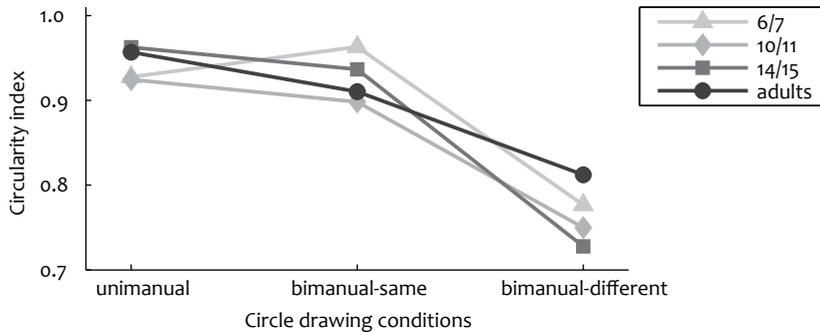

Figure 5.2. Mean circularity index of circle drawing with the right hand, presented for the four age groups, for unimanual drawing, bimanual-same drawing, and bimanual-different drawing.

Variability of the circularity index

Variability in circularity of circle drawing decreased with age: the 6/7-year olds (0.17 [0.05]) were more variable in drawing circles than the older groups, and the 10/11-year olds (0.11 [0.02]) and the 14/15-year olds (0.09 [0.02]) were more variable than the adults (0.06 [0.01]). For line drawing, variability in general decreased with age (cf. Figure 5.3), indicating that drawing consistency improved gradually with age for the different conditions. For all age groups unimanual and bimanual-same drawing was less variable than bimanual-different drawing, but for the three drawing conditions the age groups differed significantly from one another (unimanual: 6/7 and 10/11 > 14/15 > adults; bimanual-same: 6/7 > 10/11 > 14/15 and adults; bimanual-different: 6/7 > 10/11 and 14/15 > adults).

Smoothness

The drawing movements became smoother with age (viz. the number of velocity peaks decreased with age). Both circles and lines were drawn smoother by the adults than the children, whereas the children age groups did not differ from one another (circle drawing: 6/7 year: 6.27 [0.57], 10/11 year: 6.26 [0.85], 14/15 year: 6.19 [1.25], adults: 4.59 [0.43]; line drawing: 6/7 year: 5.04 [0.55], 10/11 year: 5.16 [0.68], 14/15 year: 4.61 [0.69], adults: 4.11 [0.17]).
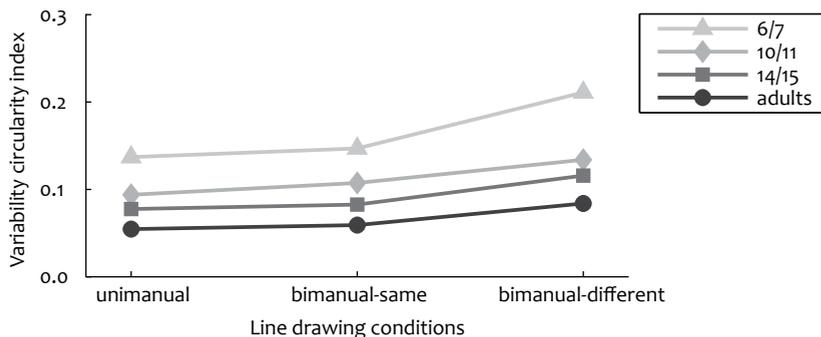
Figure 5.3. Variability of circularity index of line drawing with the left hand, presented for the four age groups, for unimanual drawing, bimanual-same drawing, and bimanual-different drawing.

Discussion

The aim of the present study was to examine how spatial and temporal coupling of the hands change as a function of development. Temporal bimanual coupling improved with age, as evidenced by the accuracy and variability of the relative phase between the hands. Because improvements in temporal bimanual coordination as a function of development have been shown in previous studies (Fagard et al., 2001; Fitzpatrick et al., 1996; Muetzel et al., 2008; Wolff et al., 1998), we focused on unraveling these improvements in terms of three interlimb interactions governing bimanual stability: planning, correction, and reflex interactions. This is discussed in the next section. Regarding the spatial task, overall drawing performance improved with age, in line with previous drawing experiments (Lantero & Ringenbach, 2007; Robertson, 2001). Because simultaneously drawing two different shapes has provided vital information regarding spatial coupling (e.g., Franz et al., 1996; Franz et al., 1991; Swinnen et al., 2001), we examined this task in the four age groups; this is discussed in the second part of the discussion.

Although the development of bimanual coordination may involve a multitude of changes in brain networks and functioning, we were particularly interested in the match between our results and the myelination of the CC. After all, the CC plays an essential role in interhemispheric communication, and thus is likely to contribute substantially to the interlimb interactions that we examined. The results are therefore discussed further in relation to myelination of the CC and mirror activity and in relation to the direction of CC myelination as reported in the literature.

Temporal coupling and planning, correction, and reflex interactions

For all age groups differences were observed between the four tasks, revealing the stabilizing contribution of the three sources of interlimb interaction to the bimanual coordination pattern. To recall, three sources of interaction between the limbs were examined, related to (1) movement planning of the bimanual coordination pattern, (2) correction of observed errors in the relative phase, and (3) reflexes inducing entrainment to the contralateral hand. These interactions were examined by pairwise comparison of two tasks that differed in one source of interaction only (cf. *Introduction*).

Results showed that all three sources of interaction contributed to the stability of the coordination pattern: planning and error interactions reduced the relative phase variability and reflex interactions enhanced stability by entraining the actively moving hand towards in-phase and antiphase coordination. However, the relative contributions of the three interlimb interactions did not differ over the examined age groups, suggesting that from the age of 6 to adulthood the degree to which the achieved coordinative stability depended on the three sources of interaction did not change. Already at the age of 6 stabilizing properties of all interactions contributed to the stability of in-phase and antiphase coordination.

The absence of age effects in the pairwise comparisons may have resulted from insufficient sensitivity to unravel developmental changes in these interactions. In particular, the differences in relative phase variability in task UNm across the four age groups (cf. Table 5.5) may have hampered these comparisons. With increasing age, participants showed significantly less variability of the relative phase between the hands in UNm, which may have resulted from overall improvement in the timing their movements as reflected by the reduced variability with age in task UN. As a result the older age groups had less opportunity (relative to younger ages) to improve stability in the tasks involving more sources of interlimb interaction (KT and AB). Hence, a potential increase in stabilizing effort due to planning and correction interactions at older ages may have been masked.

Despite the absence of age-related effects in the abovementioned comparisons, results regarding cycle duration correlation (R_{CD}) showed that interlimb coupling strength increased with age. Furthermore, both R_{CD} and the error correction correlation (R_{EC}) indicated that error correction improved significantly over the examined ages. The amount of error correction was significantly smaller for the 6/7-year olds than for adults. In addition, analysis of R_{CD} indicated that error correction interactions also improved after the age of 10/11 and 14/15, resulting in stronger coupling for the older groups when

performing task KT (involving error correction) than when performing task UNm (not involving error correction).

Taken together, these results indicate that over the age span of 6 years to young adulthood, coordinative stability improved with age. However, the degree to which the achieved stability resulted from planning and reflex interactions did not change significantly with age. That is, although performance was less stable in the younger children, the degree to which this stability depended on entrainment to the contralateral hand and on active planning of the bimanual coordination pattern was comparable to that in the older children and adults. In contrast, although its effect was not visible at the level of relative phase variability, the use of kinesthetic feedback to correct errors in relative phasing improved significantly from the age of 6 to young adulthood.

Spatial coupling in bimanual line-circle drawing

With increasing age, participants drew more consistently (i.e., less variably) and smoother (i.e., with less velocity changes). Overall circularity of circle drawing did not improve with age, whereas it did for line drawing. These results correspond to bimanual drawing performance observed in previous experiments with children aged 4-8 years and adults (Lantero & Ringenbach, 2007; Ringenbach & Amazeen, 2005).

Spatial coupling between the hands was assessed by comparing performance in the bimanual-different condition to the unimanual and bimanual-same conditions. Drawing the circle and line together resulted in attraction of both hands to each other (i.e., resulting in vertically-oriented oval-shaped circles and lines), yielding deteriorated performance relative to unimanual and bimanual-same drawing (Franz et al., 1996; Franz et al., 1991; Volman, 2005). In all age groups performance decreased when drawing the line and circle simultaneously. The decrease in circularity of circles was smaller for adults than for children, revealing that adults were better in executing two different spatial tasks with both hands. For line drawing the effect of bimanual-different drawing did not differ over the age groups.

In sum, previously observed age-related improvements in unimanual and bimanual circle drawing were also observed in the present experiment. Furthermore, spatial coupling between the hands was stronger for children aged 6-15 than for adults. No difference was observed between the children groups. This suggests that after the age of 15, the spatial coupling between the hands decreased such that adults are better in executing different movements with the two hands simultaneously.

Myelination of the corpus callosum and temporal coupling

With respect to the temporal coupling tasks, improvements across the age span of 6-15 year were expected to be more pronounced for antiphase than in-phase coordination as a result of enhanced interhemispheric inhibition of mirror activity due to increased myelination of the CC (Cincotta & Ziemann, 2008; Cohen et al., 1967; Hubers et al., 2008). However, the results did not reveal any differences in developmental improvement rates of the two coordination patterns. In all age groups in-phase was performed more accurately and less variably than antiphase, and the increases in stability and accuracy across development occurred in parallel for in-phase and antiphase coordination.

Although this parallel development of in-phase and antiphase coordination from the age of 6 to young adulthood was not expected, it was in line with the results of at least two previous studies (Fagard & Pezé, 1997; Wolff et al., 1998), whereas another experiment did reveal larger developmental effects for the AP pattern (Marion, Kilian, Naramor, & Brown, 2003). Unfortunately, however, most studies examined only one bimanual coordination pattern, and thus did not provide information in this regard (Lantero & Ringenbach, 2007; Muetzel et al., 2008; Pellegrini, Andrade, & Teixeira, 2004; Robertson, 2001).

The current results suggest that the stability difference between in-phase and antiphase coordination is present at young ages and improvements of these two coordination patterns develop in parallel. Therefore, although myelination of CC has been shown to enhance bimanual coordination (Muetzel et al., 2008), these improvements appear not to result from enhanced inhibition of mirror activity. After all, improved suppression of the mirror symmetric coupling between the limbs would only benefit antiphase coordination. This topic may be further scrutinized by examining younger children and by increasing movement frequency, since in-phase-antiphase stability differences are more pronounced at higher frequencies (Haken et al., 1985; Schöner et al., 1986). Moreover, it would be useful to assess mirror activity (during unimanual performance) as well, using fine-grained analysis of electromyographic activity (cf. Ridderikhoff, Daffertshofer, Peper, & Beek, 2005). The current results, however, suggest that, for the examined age span, the observed general improvements in bimanual coordination stem primarily from other developmental changes.

Direction of myelination and spatial and temporal coupling

Previous studies examining CC myelination using magnetic resonance imaging have

suggested that the CC myelinates across childhood in an anterior-posterior direction, with largest myelination rates of the anterior CC between the ages of 3 to 6 and largest myelination rates of the posterior CC between the ages of 6 to 15 (Giedd et al., 1996; Thompson et al., 2000). Since callosotomy studies showed predominant involvement of the anterior CC in temporal coupling and the posterior CC in spatial coupling (Eliassen et al., 1999; Ouimet et al., 2010), temporal coupling may be expected to change more in early development, whereas developmental changes in spatial coupling would be more prominent at later ages.

The present study revealed that development across the examined ages resulted in less spatial interference between the two hands after the age of 14/15. Adults differed from children, but no differences were observed between the children age groups, whereas spatial performance measures not directly related to spatial coupling (viz., smoothness and variability of circularity) improved significantly over all age groups. This corresponds to the general expectation that improvement in spatial coupling (viz. decreased interference) would manifest itself relatively late in development. Temporal coupling on the other hand (indexed by relative phase accuracy and variability) changed over all age groups, indicating that these improvements indeed set in at younger ages.

Although our behavioral data showed a general correspondence to the previously reported direction of myelination of CC, they did not exactly fit the identified moments of peak myelination rates. As such, CC myelination appears not to be related to changes in spatial and temporal coordination in a 1:1 fashion. Developmental improvements in temporal and spatial coordination appear to become manifest somewhat after the moment of peak myelination rate of the corresponding CC parts, suggesting that increased myelination of CC fibers may be a prerequisite for further developmental improvement. Furthermore, although largest myelination rates were found between 3 to 6 years in anterior CC fibers and between 6 to 15 years in posterior fibers, myelination of these fibers continues at lower rates until the early twenties (Giedd et al., 1996; Thompson et al., 2000). Therefore, it remains to be established whether the observed improvements in temporal and spatial coordination are dependent on these ongoing myelination processes, or whether they are primarily due to the development of specific control processes following peak myelination rates.

Although myelination of the CC plays a significant role in the development of bimanual temporal and spatial coordination, this does not exclude the importance of other brain areas and connections: bimanual movements are not controlled by one specific area in the brain, but rather by a distributed network of different brain sites (Debaere et al., 2001; Swinnen, 2002). Thus, even if myelination results in enhanced temporal and spatial

coupling between the hands, this does not rule out the contributions of other brain areas and connections. On the contrary, it is highly plausible that increased temporal and spatial coordination is engendered by changes in pertinent neural networks.

Concluding remarks

Based on the results in the present experiment, three conclusions can be drawn. First, for the temporal task, coordinative stability improved with age. Although stability increased over the age groups, the achieved stability resulted from similar relative contributions of planning and reflex interactions in all age groups. Correction interactions on the contrary improved with age, showing enhanced use of kinesthetic feedback. Second, at our low movement frequency we did not find indications of differential improvements as a function of age for the in-phase and antiphase coordination patterns. Hence, although myelination of the CC contributes to improved bimanual coordination (Muetzel et al., 2008), the current results did not provide evidence that this was due to enhanced inhibition of mirror activity. Third, the results correspond to the suggested anterior-posterior direction of CC myelination with temporal coupling improving at relatively young ages and spatial coupling improving more markedly at older ages. However, although CC myelination probably plays a significant role in the development of bimanual temporal and spatial coupling, presumably various other areas are involved as well (Debaere et al., 2001; Swinnen, 2002).

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Epilogue

The results presented in this thesis indicated that integrated timing of feedforward control signals and correction of relative phase errors were the primary interlimb interaction sources that contributed to stability changes induced by movement frequency, acquisition of a new coordination pattern, and development across childhood. The third source of interaction, phase entrainment, was found to be affected only by the amplitude relation between the hands. In this Epilogue, these results are discussed in relation to the traditional division between the higher-order level of planning and the lower-order level of execution in motor control, and in relation to the intention to perform a particular bimanual coordination pattern. Comparable changes in the contributions of the specific interaction sources were observed for short and long time scales. Both at a short time scale (frequency manipulation) and at a longer time scale (learning) a tight relation between integrated timing and error correction was observed. These findings are interpreted as an indication of a form of predictive control that appeared to be employed in particular during difficult coordination tasks. Furthermore, the theoretical assumptions regarding interlimb interactions underlying the methodology used in the present thesis are discussed and suggestions for application of this methodology in future research are made.

Summary of the main findings

Considering that bimanual coordination is governed by coupling between the hands, the present thesis was set up to gain further insight into how changes in bimanual coordination can be understood in terms of changes in the underlying sources of interlimb interaction. For this purpose, changes in bimanual coordination at various time scales were studied in terms of three functionally defined interlimb interactions: integrated timing of feedforward control signals, error correction based on kinesthetic afference, and phase entrainment by contralateral afference.

At a short time scale, *movement frequency* was found to induce a change in the relative contributions of the sources of interlimb interaction. Chapter 2 showed that at low frequencies integrated timing was predominantly involved in stabilizing bimanual coordination, whereas at higher frequencies a shift towards a more prominent role of error correction was observed for the more difficult antiphase pattern. These results revealed a shift from predominantly open-loop to closed-loop control with increasing frequency. Bilateral muscle activation during kinesthetic tracking and improved error correction during active bimanual coordination indicated that error corrections were more effective when a reference frame was present that was based on bilateral control signals. Perhaps this bimanual reference frame allowed for sensory predictions to which the actual kinesthetic afference could be compared. Because active bimanual performance was superior to kinesthetic tracking performance, it was concluded that the combination of integrated timing and error correction was most effective when the predicted sensory consequences matched the actual sensory consequences of the executed movements (as was the case during active bimanual coordination).

In Chapter 3 the effect of *movement amplitude* was studied in relation to phase entrainment. Based on two experiments the effect of a change in amplitude as such was compared to the effect of a change in the amplitude relation between the hands. The results of this study indicated that phase entrainment to the passively moving contralateral hand was not influenced by a change in amplitude as such, but only by a change in the amplitude relation between the hands. Stronger entrainment was observed when the hands were moving with equal amplitudes, compared to the situation in which the amplitude of the passive (entraining) hand was smaller than that of the active hand.

At a longer time scale, Chapter 4 assessed changes in interlimb interaction that accompany *learning* of a new bimanual coordination pattern. For this purpose, participants learned to execute a relative phase of 90° between the hands, with an internal or external attentional focus. As expected, performance of the practiced 90° pattern improved via

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changes in the contributions of integrated timing and error correction, whereas no changes were observed in phase entrainment. The changes in the stabilizing interlimb interactions appeared to be independent of the adopted attentional focus. The mirror-symmetrical transfer pattern ($\Phi = 270°$) was found to improve later than the practiced 90° pattern, suggesting that generalization to an abstract representation took place at a lower rate than improvement of the practiced pattern itself. Furthermore, in accordance with Chapter 2, results showed that corrections of relative phase errors were most effective when integrated timing of the bimanual pattern served as a reference frame for the new coordination pattern.

Regarding the effects of *development*, Chapter 5 examined changes in bimanual performance and underlying interlimb interactions for four age groups ranging from 6/7 years to young adulthood. In addition, spatial coupling of the hands was studied across development using a bimanual line-circle drawing task. Results showed that although performance of the temporal coordination task improved over all age groups (thanks to an overall increase in coupling strength, as reflected by increased cycle duration correlation), the relative contributions of the three interlimb interactions to this performance hardly changed. Only the (absolute) amount of error correction (as indexed by the error correction correlation) was found to increase with development, suggesting enhanced use of kinesthetic afference with increasing age. Furthermore, the results revealed parallel improvement of in-phase and antiphase coordination over the studied age groups, thereby suggesting that the differential stability of the two patterns had evolved before the age of 6/7 years. Spatial coupling of the hands was found to improve after the age of 14/15 years: less deterioration of task performance was observed for adults than children when drawing two different shapes simultaneously. These results were consistent with the anterior-posterior direction of myelination of the corpus callosum reported in the literature, with early improvements in temporal coupling (mediated by the anterior corpus callosum) and later improvements in spatial coupling of the hands (more closely related to the posterior corpus callosum).

CHANGES IN INTERLIMB INTERACTIONS AT VARIOUS TIME SCALES

For the different interaction sources examined in the previous chapters, the main changes observed in bimanual coordination were related to integrated timing and error correction. These two interaction sources have been found to be involved predominantly in the differential stability of in-phase and antiphase coordination

(Chapter 2; Ridderikhoff, Peper et al., 2005), in changes related to movement frequency (Chapter 2), and in stabilizing the new 90° coordination pattern (Chapter 4). Across childhood the error correction correlation indicated that amount of error correction also improved from the age of 6/7 years to young adulthood, although no changes were observed in the relative contributions of the three sources of interaction to bimanual performance (cf. Chapter 5). Bimanual coordination differences induced by the examined factors were hardly engendered by phase entrainment: movement frequency did not affect phase entrainment at a short time scale and also at a longer time scale entrainment strength was not influenced by changes due to learning and development. Only the amplitude relation between the hands was found to affect phase entrainment strength.

As mentioned in Chapter 1, the distinction between the three sources of interlimb interaction relies on two different aspects: intentionality to perform a specific bimanual coordination pattern and afference-dependence (cf. Table 1.1). The observed main contributions of integrated timing and error correction probably reflect the distinction between intentional and unintentional stabilizing contributions, as integrated timing and error correction are directed at stabilizing a specified coordination pattern, whereas phase entrainment reflects unintentional attraction to in-phase and antiphase coordination. Note that the intentional specification of the bimanual pattern might be accompanied by unintentional effects resulting from neural cross-talk via ipsilateral and callosal pathways (cf. General introduction; Cattaert et al., 1999; Kagerer et al., 2003; Swinnen, 2002). These effects may be addressed separately by measuring EMG activity of both limbs during unimanual movements to assess mirror activity (Ridderikhoff, Daffertshofer et al., 2005; Vardy, Daffertshofer, Ridderikhoff, & Beek, 2007). Despite these potential unwanted influences, the differential contributions of the sources of interlimb interaction seem to relate predominantly to the distinction in terms of intentionality to perform a specific coordination pattern, for short and long time scales alike. Also the interplay between integrated timing and error correction, which will be discussed in more detail later, was observed for factors relating to shorter as well as longer time scales.

Hierarchical levels of interlimb coupling

The distinction between the sources of interlimb interaction that govern coordinative stability and the influence of intentionality to perform a specific coordination pattern may relate to a more traditional division between the higher-order level of motor

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planning and the lower-order level of motor execution (e.g., Allen & Tsukahara, 1974), which has also been suggested to apply to coupling between limb movements in bimanual coordination tasks (Spijkers & Heuer, 1995). The influence of these distinct levels has been linked explicitly to assimilation of movement direction and movement amplitude in bimanual tasks in which the hands have to move in different directions or with different amplitudes (Cardoso de Oliveira & Barthelemy, 2005; Franz, 1997; Heuer & Klein, 2006; Spijkers & Heuer, 1995; Swinnen et al., 2001; Weigelt & Cardoso de Oliveira, 2003). The higher-order level of planning has been related to interference arising from moving the hands in different directions (Cardoso de Oliveira & Barthelemy, 2005; Franz, 1997; Swinnen et al., 2001) and moving with different amplitudes (Heuer, Spijkers, Kleinsorge, & van der Loo, 1998; Spijkers & Heuer, 1995; Weigelt & Cardoso de Oliveira, 2003), whereas the lower-order level of execution has been related only to amplitude interference (Spijkers & Heuer, 1995; Swinnen et al., 2001; Weigelt & Cardoso de Oliveira, 2003). Although the controlled variables and instructions in these tasks are different from those examined in the present thesis, relating these levels of motor control to the different sources of interlimb coupling studied in the present thesis may provide further insight into bimanual motor control.

Intuitively, one may suggest that integrated timing of feedforward control signals relates to the planning level and that phase entrainment by contralateral afference relates to the execution level. Error correction in this regard may be situated in between these levels, because this interaction source depends on movement-elicited afference but also is intentional in stabilizing a specific coordination pattern. As such, the distinction between only a planning level and an execution level may be insufficient to account for the role of error correction in the control of bimanual movements. In this regard, some experiments only included fast ballistic movements, such that corrections of the bimanual movement could not take place during movements execution (Cardoso de Oliveira & Barthelemy, 2005; Weigelt & Cardoso de Oliveira, 2003), whereas in other experiments error correction could take place but was not mentioned (e.g., Franz, 1997; Spijkers & Heuer, 1995). Perhaps, corrective movements were regarded implicitly as a feature of the higher-order level of adjusting motor plans and as such were incorporated in the planning level. However, none of the studies address this issue explicitly.

Interference resulting from movement direction can be related to the interaction sources contributing to the differential stability of in-phase and antiphase coordination. In these patterns the hands either move mirror symmetrically (in-phase) or in opposite directions relative to the body midline (antiphase), while the turning points of both hands are coupled in time. Differential stability of in-phase and antiphase coordination and

increases in this differential stability with movement frequency were found to originate from integrated timing of feedforward control signals as well as error correction based on perceived errors (Chapter 2; Ridderikhoff, Peper et al., 2005). In-phase and antiphase was not differentially stable for phase entrainment (Chapter 2; Ridderikhoff, Peper et al., 2005; Ridderikhoff et al., 2006), which agrees with the literature in which directional interference was not observed for the execution level (Franz, 1997; Swinnen et al., 2001).

The fact that phase entrainment only leads to attraction towards in-phase and antiphase and not to other patterns (Ridderikhoff et al., 2006) may seem to suggest that directional interference is also present at the execution level. However, there is a caveat in interpreting this result in this regard. Because the turning points of the hands are not timed simultaneously in patterns other than in-phase and antiphase coordination, the influence of the involved timing differences form a confounder and preclude conclusions regarding the influence of directional differences in this regard. Therefore, the influence of phase entrainment in repulsion from other patterns than in-phase and antiphase cannot be taken as an indication of directional interference at the execution level. Results in the present thesis indicated that directional coupling as observed for planning (Cardoso de Oliveira & Barthelemy, 2005; Franz, 1997; Swinnen et al., 2001) results from planning interactions (generating integrated feedforward signals) and the use of kinesthetic afference to correct for observed errors. This would imply that directional coupling in bimanual tasks not only results from feedforward planning-related interactions between the hands, but more generally from processes that are directly associated with the intention to perform specific bimanual patterns.

Furthermore, amplitude interference as a result of moving with different amplitudes during bimanual reaching and drawing has been related to the planning and execution level (Cardoso de Oliveira & Barthelemy, 2005; Heuer et al., 1998; Spijkers & Heuer, 1995; Swinnen et al., 2001; Weigelt & Cardoso de Oliveira, 2003). In these tasks, amplitudes have been found to influence each other such that the smaller amplitude is attracted towards the larger amplitude and vice versa. For bimanual rhythmic performance, moving with different amplitudes has been demonstrated to result in amplitude assimilation as well as a decrease in coordinative stability (de Poel et al., 2009; Peper et al., 2008). However, because we are dealing here with different aspects of interlimb coupling, it is difficult to establish a direct link between the two conceptual frameworks. Whereas amplitude assimilation reflects the effects of amplitude coupling, the stability of coordination depends on temporal coupling, which was the main focus of this thesis. The effects of an amplitude difference on coordinative stability (de Poel et al., 2009; Peper et al., 2008) may be mediated by associated variations in phase entrainment strength (Chapter

3). However, it remains to be established whether amplitude coupling as observed in previous studies for both the execution and the planning level is related to stability characteristics as observed in bimanual temporal coupling and to the associated sources of interaction.

Taken together, relating the effects that were observed for integrated timing, error correction, and phase entrainment to the conventional motor control dichotomy of the higher-order level of planning and the lower-order level of execution was not straightforward. On the one hand, amplitude coupling, which has been found to be associated with planning as well as execution, cannot be compared directly to the different interlimb interaction sources that stabilize bimanual coordination, because these sources pertain to different types of interlimb interference. The amplitude effects observed for phase entrainment (cf. Chapter 3) revealed that coordinative stability was affected at the execution level, but more research is required to determine how amplitude assimilation effects may relate to coordinative stability characteristics. On the other hand, directional interference as observed for the higher-order level of planning may indeed be related to interlimb interactions due to integrated timing, which was found to contribute predominantly to differential stability of in-phase and antiphase coordination. However, this would imply that directional interference also involves aspects associated with error correction, because this source of interaction also contributed to the differential stability of in-phase and antiphase coordination. As mentioned above, error correction interactions do not fit easily into a scheme that is limited to only a planning and an execution level, given the involved intentional use of feedback to enhance bimanual coordination. Hence, an additional level (or process) in this division would have to be incorporated, linking execution and planning so that errors can be sensed and subsequently corrected.

Furthermore, the higher-order level of planning traditionally precedes the lower-order execution level, whereas the distinction between the different sources of interlimb interaction in the present thesis is less sequential, allowing simultaneous influences and even interdependencies between these different coupling processes. Although our results also show that error corrections are more effective when preceded by integrated timing, this interplay is less strong than the time-dependency of planning and execution levels. The results also suggest that this interplay does not always occur, allowing for more flexibility depending on task characteristics. Therefore, the distinction between the three sources of interlimb interaction seems more adequate in capturing the coupling characteristics, in particular given the observed interplay between integrated timing and error correction. Interference between assimilation effects for amplitude and direction

(Heuer, 2006; Swinnen et al., 2001) has demonstrated that different types of coupling may interact. This was further emphasized by an experiment in which independent brain networks were found for direction and amplitude interference, but which also revealed brain areas that were involved in both processes (Wenderoth, Debaere, Sunaert, & Swinnen, 2005). The results of the present thesis indicate that also different levels of motor control may be interrelated, such that these levels can interact and influence each other. Determining the neural networks associated with the various interlimb interactions would greatly advance to our understanding of how these interactions and their interdependencies are organized.

INTERPLAY BETWEEN INTERLIMB INTERACTIONS

For stability differences in bimanual coordination related to coordination pattern, movement frequency, and learning a new coordination pattern, stabilizing contributions of integrated timing and error correction were found to depend on one another: error correction of perceived relative phase errors was more effective when integrated timing also contributed to coordinative stability. In addition, changes in integrated timing preceded changes in error correction when a new coordination pattern was learned. Thus, both at a short and long time scale integrated timing seemed a prerequisite for effective error corrections. This result speaks to a tight coupling between perception and action in motor control and suggests that in the examined coordination task action guides perception: the specification of an integrated pattern of bimanual control signals helps the performer to adequately use relative phase perception to correct for errors.

It was shown previously that activating both hands based on an integrated timing pattern significantly enhanced correction of relative phasing errors when tracking the contralateral passive hand, even though activation of the passively moving hand could not alter the movement trajectories in any way (Ridderikhoff et al., 2007). Such a bilateral activation pattern was also observed in Chapter 2 in the measured electromyographic (EMG) signals, showing similar bimanual activations during kinesthetic tracking and active bimanual coordination. As mentioned in the previous chapters in which the movement frequency (Chapter 2) and learning (Chapter 4) results were discussed, the integrated timing of bilateral control signals was likely used as a reference frame to enhance effective error correction. When an integrated pattern of control signals specifying the required coordination pattern is sent to the hands, a copy of the motor commands (or efference copy) may be used to predict sensory consequences of those

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efferent signals. Subsequently, the actual sensory feedback can be compared to the predicted sensory consequences after which corrections can be executed to enhance performance (Desmurget & Grafton, 2000; Miall & Wolpert, 1996; Wolpert & Ghahramani, 2000). The use of efference copies to generate a prediction of the sensory consequences thus allows error corrections to be based not only on movement afference from the two hands, but also on the difference between predicted and actual sensory consequences. Via these continuous comparisons between predicted and actual states, anticipation of future errors can occur so that feedback can be used with a negligible delay (Desmurget & Grafton, 2000; Miall & Wolpert, 1996). Despite the slight discrepancies between predicted and actual sensory signals during the kinesthetic tracking task (cf. Chapter 2), this mechanism thus allows for more predictive motor control.

Although the use of predictions to enhance error correction by comparing sensory predictions with actual sensory feedback has been suggested as a model of motor control (Desmurget & Grafton, 2000; Wolpert & Ghahramani, 2000), there are only a few empirical results showing directly that sensory predictions are indeed used for adequate and rapid error correction. This type of control has been found to account for characteristics of reaching and pointing movement trajectories that could not be explained by alternative models (Beaubaton & Hay, 1986; Wolpert, Ghahramani, & Jordan, 1995), but also the negligible delay in visuomotor tracking tasks and grip force adjustments when moving weights at various speeds supported the reliance on anticipatory feedforward control (Flanagan & Wing, 1993; Vercher & Gauthier, 1992; Vercher et al., 1996). The involvement of sensory predictions has also been shown more directly. For instance, expected sensory consequences of one's actions were taken into account when lifting objects, in order to quickly correct for unexpected perturbations (Ohki, Edin, & Johansson, 2002) and were found to enhance grasping performance under visual feedback conditions (Ietswaart, Carey, & Della Sala, 2006). Our results support and extend this evidence, by indicating that the combined use of efference copies (via integrated timing of the control signals to the hands) and kinesthetic feedback (via error corrections based on afferent information) was especially useful in more difficult bimanual coordination conditions. Whereas relatively easy instances of bimanual coordination appeared to be governed primarily by the feedforward specification of the bimanual control signals, the combined use of integrated timing and error correction was observed in conditions in which such merely open-loop control was not sufficient to maintain bimanual coordinative stability: kinesthetic tracking of a passively moving hand (Chapter 2), antiphase coordination at high movement frequencies (Chapter 2), and during executing a new coordination pattern (Chapter 4).

Based on the present results, we can only speculate how this form of predictive control was influenced by development across childhood (Chapter 5). The correlation measures showed how the amount of error correction increased with development during active bimanual coordination and kinesthetic tracking. Because the use of predictive control has been observed in both tasks (cf. Chapters 2 and 4), this may also have stabilized bimanual coordination in this experiment. However, because no EMG signals were recorded, we cannot be certain about the use of this form of control during kinesthetic tracking. In this regard, the increased amount of error correction may also be taken to suggest that the use of afferent information improved with development (i.e., without a relation to integrated timing). Furthermore, because the task was executed at a low frequency and was therefore relatively easy, open-loop control may have been predominantly involved in the stabilization of bimanual coordination as well. Therefore no conclusions can be drawn regarding the change of this form of control during development across childhood.

On the other hand, based on the literature, it may be expected that aging in the elderly affects the use of predictive control to correct for errors. The results of a study focusing on the effect of aging on bimanual coordination performance (Wishart et al., 2000), seem to suggest that elderly participants have more difficulties in combining integrated timing and error correction to stabilize difficult coordination patterns. In this study, aging effects were not observed for in-phase coordination across a range of frequencies and for antiphase coordination at low frequencies, but accuracy and stability significantly decreased with aging for antiphase coordination at higher frequencies. It was concluded that aging effects were not observed for tasks that relied on automatic processing, whereas tasks that required more effortful processing were influenced significantly by aging (Wishart et al., 2000). Because aging selectively affected the more difficult patterns, these results may suggest that the combination of integrated timing and error correction could no longer sufficiently stabilize bimanual coordination. Further research is needed to determine if this alleged effect of aging also influences other complex bimanual tasks in daily life and whether it may affect the ability to learn and improve (new) bimanual coordination patterns in the elderly.

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Methodological considerations

In the present thesis, the contributions of the interlimb interactions related to integrated timing, error correction, and phase entrainment were examined by comparing a

set of tasks in which these interlimb interactions were involved to a different extent (cf. Ridderikhoff, Peper et al., 2005). The use of this methodology gave insight into the contributions of the different interaction processes to bimanual performance, but also introduced some methodological questions and concerns. As the reader may have noted, the methods used in the previous chapters differed on a number of characteristics. Taking into account the time needed to complete the full experiment (i.e., keeping the participants focused) and considering the research questions of interest, a shortened version of the protocol (cf. Ridderikhoff et al., 2008) was used to assess changes associated with development and learning. Using this version, only four of the original five tasks were included to assess the three interlimb interactions of interest; task KTa (kinesthetic tracking in the presence of a distracting auditory signal) was not executed. Although this task could reveal information regarding the robustness of error correction (cf. Chapter 2), the execution of the four different tasks combined with the error correction correlation measure provided adequate information regarding the error correction process. Furthermore, no EMG was measured in these studies. Although EMG proved informative by revealing a bilateral activation pattern during kinesthetic tracking and confirmed the strength of interlimb coupling between the hands (cf. Chapter 2), eliminating EMG measurements considerably reduced the time required to test children on spatial and temporal coupling and enabled us to schedule multiple practice and test sessions to study learning. Furthermore, our main interest in the different interlimb interactions was warranted by the pairwise comparisons and different correlation measures. Finally, the passive movements used as a distractor during unimanual task performance and during kinesthetic tracking were based on the actual movements during active bimanual coordination in Chapters 2 and 3, whereas in Chapters 4 and 5 largely sinusoidal trajectories (with imposed variability) were used – again to save time to invest in other aspects of the experiment. As the mean joint angle, amplitude, and frequency were based on the participant's performance, the use of these sinusoidal trajectories proved useful in the comparisons of the different tasks. Taken together, changing these specific aspects of the methodology enabled us to assess the stabilizing contributions of the interlimb interactions at various time scales and, moreover, provided additional time to incorporate relevant conditions in the experiments.

Tasks and pairwise comparisons

The sources of interlimb interaction were studied using a design composed of different tasks that involved passive and active hand movements. The sources of interlimb

interaction were supposed to be involved to different degrees in these tasks (e.g., Table 2.1). To recall, during unimanual coordination with a pacing signal (task UN) no sources of interlimb interaction are assumed to be present. For unimanual coordination in the presence of phase-shifted passive movements of the contralateral hand (task UNm), phase entrainment results in attraction towards in-phase and antiphase coordination. Furthermore, when tracking a passively moving hand based on kinesthetic afference, either with or without an auditory distracting signal (task KTa and KT, respectively), bimanual coordination is also stabilized by error correction. Finally, during active bimanual coordination (task AB), performance is also enhanced by integrated timing. The sources of interaction are thus assumed to add up in these tasks: in UN no interactions are present, task UNm involves phase entrainment, KT and KTa involve phase entrainment and error correction, and task AB encompasses all three sources of interlimb interaction. Via systematic comparisons of two tasks that differ with respect to one of these interlimb interactions, the contributions of that coupling source were examined.

Results indicated that this method allowed dissociation between the contributions of the interlimb interactions to the stability of bimanual coordination, but that the comparison of tasks to assess these contributions may also be hampered in several ways. First and foremost, the sources of interlimb interaction are not as additive as assumed. The amount of error correction was found to depend on the sufficiency of feedforward control to stabilize bimanual coordination and was therefore minimally involved in task AB (Ridderikhoff, Peper et al., 2005). For this reason, this source of interlimb interaction may be studied by combining comparisons of task AB with task KT and of task AB with task UNm (cf. Chapter 2). Furthermore, results showed how integrated timing and error correction appear to be interrelated in stabilizing bimanual coordination (cf. Chapters 2 and 4). In addition, the comparison between task AB and KT may be influenced by the presence of a pacing signal in task AB. The use of a metronome enabled us to control movement frequency in the different tasks and allowed for prescribing a fixed frequency during all trials, which was important to make fair comparisons over tasks and conditions. However, this introduced the disadvantage that the pacing signal may have induced anchoring effects, such that the paced flexion and extension turning points were especially stabilized in AB (Carson, 1996; Fink et al., 2000; Maslovat et al., 2006). Since in task KT a more continuous signal was tracked, these anchoring effects were less likely to occur in this task (cf. Chapter 2). Thus, although auditory pacing allows for comparisons of tasks that are executed at the same frequency, anchoring effects may influence the way in which these tasks are stabilized and hence may influence the comparison of tasks AB and KT. Finally, as suggested in Chapter 5, performance of task UNm may

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influence the comparison of task KT and UNm. When for a given group or condition low variability values are obtained for UNm there may be less room for improvement in task KT. As such, differences in 'baseline' values of variability in task UNm may influence the observed stabilizing effect of error correction.

These shortcomings reveal how the method applied in this thesis is evidently (but also inevitably) based on a simplified account of the biological reality (e.g., the interlimb interactions do not add up as assumed and performance may be influenced by additional factors). Despite this simplification, the method used served to identify (changes in) the relative contributions of the different interlimb interaction sources that underlie bimanual coordinative stability, thereby revealing interesting interrelations between sources of interlimb coupling. As such, the method used represents a first step in assessing different levels of functional interlimb interactions underlying bimanual coordination and their interrelations. Note that to date, this method is the only method taking into account various sources of interlimb interaction simultaneously. As mentioned in Chapter 1, these sources of interlimb interaction have been suggested in the literature to account for observed bimanual coordination characteristics (e.g., Baldissera et al., 1991; Cattaert et al., 1999; Grossberg et al., 1997; Helmuth & Ivry, 1996; Stinear & Byblow, 2001; Swinnen et al., 1995; Wilson et al., 2003), but the contribution of each of these interactions has typically been studied in isolation.

When interpreting the results in the present thesis, the simplifying assumptions underlying the pairwise comparisons of tasks in the used methodology have to be kept in mind. Labeling the outcomes as integrated timing, error correction, or phase entrainment was necessarily based on the associated logic. Unfortunately, these interpretations cannot be readily verified based on the results of other studies. However, they were backed up with some additional measures in the experiments presented in this thesis. First, the weighted coherence of EMG signals of the limbs showed that interlimb coupling strength increased when more interlimb interactions were involved that stabilized bimanual coordination (cf. Chapter 2). Also the cycle duration correlation revealed increased interlimb coupling strength when more sources of interlimb interaction contributed to bimanual coordination (cf. Chapters 2 and 5), indicating that the contributions of the interlimb interactions added up (although not necessarily linearly). Furthermore, since error correction was found to act as a secondary mechanism that stabilized bimanual performance especially when integrated timing could not sufficiently stabilize bimanual coordination (cf. Chapters 2 and 4), the error correction correlation turned out to be useful in assessing the extent to which the correction process was involved in the different tasks (cf. Chapters 2, 4, and 5).

Taken together, our methodology was based on a simplified model, aimed at making a first dissociation between the stabilizing contribution of different sources of interlimb interaction and their interrelations. Hence, as is the case for any model-based research, our interpretations followed from the assumptions underlying the protocol. To alleviate the dependence on those assumptions, additional indices of coupling strength and error corrections were included in the analyses. Given the coherence of the obtained results, we were confident that our interpretations indeed represent relevant features of the interlimb coupling during rhythmic bimanual coordination that could only be delineated using a method that addresses various sources of interaction simultaneously (such as the differential contributions of intentional and unintentional processes and the interplay between feedforward control and error correction).

Future directions

There search reported in the present thesis revealed how changes in bimanual coordination at various time scales are engendered by contributions of various sources of interlimb coupling, thereby also generating new leads for future research.

Interlimb interactions and neural networks

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The observed changes in various movement characteristics at various time scales could be expressed successfully in terms of the three functionally defined interlimb interactions. As a next step it seems useful to examine how specific neurophysiological pathways and neural networks mediate these functionally defined sources of interlimb coupling. By doing so, the involvement of distinct brain areas may be related to the different sources of interlimb interaction. Whereas bimanual coordination tasks in general have been studied in relation to the brain areas involved (for a review, see Swinnen, 2002), the distinction between the various sources of coupling may provide a basis for guiding research towards the different functional aspects involved in stabilizing bimanual coordination. Neural networks may be studied in relation to the three types of interlimb interaction separately, but also with respect to interrelations between these coupling sources. Since integrated timing and error correction appear to be interdependent in stabilizing difficult bimanual coordination patterns but seem to act independently in stabilizing easier coordination patterns, possibly combined as well as distinct brain networks are involved in these processes (cf. Wenderoth et al., 2005). Furthermore,

as phase entrainment seems to be influenced by a limb's susceptibility to external influences and not to the contralateral afferent signal strength per se, this source of interlimb interaction may involve higher-order modulation of spinal processes (Zehr et al., 2004; Zehr, Collins, Frigon, & Hoogenboom, 2003).

To date, especially cortical and subcortical brain areas have been studied extensively with respect to specific bimanual coordination tasks, using functional magnetic resonance imaging (fMRI) techniques. In these studies, a distinct bilateral network of cortical and subcortical areas has generally been observed, including the supplementary motor area (SMA), primary motor cortex (M1), primary sensory cortex (S1), premotor areas (PM), cingulate motor area (CMA), the cerebellum, basal ganglia, and thalamus (Debaere et al., 2001; Debaere, Wenderoth, Sunaert, Van Hecke, & Swinnen, 2004; Puttemans, Wenderoth, & Swinnen, 2005; Remy, Wenderoth, Lipkens, & Swinnen, 2008; Swinnen, 2002). Whereas previously in the literature the role of the SMA was suggested to contribute predominantly to bimanual coordinative stability, these studies revealed how a much broader network of brain areas is involved in rhythmic bimanual coordination (Debaere et al., 2001; Swinnen, 2002). By assessing the contributions of the different sources of interlimb interaction, it may be feasible to relate certain brain areas to more specific aspects of motor control. For instance, it has been shown that in the abstract representation of bimanual control patterns various brain areas are involved, including the SMA, PM, cerebellum, basal ganglia, and thalamus, but also the parietal cortex (Swinnen et al., 2010). Because brain areas involved in the abstract representation are very similar to those more generally observed to be involved in bimanual control (see above), we may expect that this network may be associated with the integrated timing of feedforward control. Furthermore, a significant role has been suggested for the cerebellum. On the one hand, the cerebellum appears to play an essential role in the timing of bimanual movements (Helmuth & Ivry, 1996; Ivry, Keele, & Diener, 1988), which possibly relates the cerebellum to the contribution of integrated timing. On the other hand, the cerebellum has been shown to be involved in feedforward predictive control in eye-hand coupling (Miall, Reckess, & Imamizu, 2001) and bimanual coordination (Debaere et al., 2004; Puttemans et al., 2005). Moreover, in bimanual coordination also the parietal cortex (Debaere et al., 2004) and the basal ganglia (Puttemans et al., 2005) were supposedly involved in predictive control. These areas have been suggested to contribute to the monitoring of afferent information during bimanual tasks and its comparison to predicted sensory feedback to enhance performance (Puttemans et al., 2005; Swinnen, 2002). The cerebellum, parietal cortex, and basal ganglia may therefore be involved in integrated timing of feedforward control signals as well as error correction

based on kinesthetic afference.

In sum, a broadly distributed neural network is involved in controlling bimanual coordination. Specific areas appear to be related to the representation of a more abstract integrated pattern and in the use of predictive feedforward control to facilitate error corrections. Also when learning a new bimanual coordination pattern, large differences have been observed in either increased or decreased activation of distinct brain areas for the pre-existing coordination patterns as well as the to-be-learned patterns (Debaere et al., 2004; Puttemans et al., 2005; Remy et al., 2008; Swinnen, 2002). Future studies are needed to determine whether and how the functional sources of interlimb interaction examined in this thesis are associated with specific brain areas and neural networks.

Action-perception coupling in daily life

An important finding in the present thesis concerns the relation between action and perception, as the results revealed how feedforward control of bimanual patterns may provide a reference frame for effective corrections of observed errors. This finding was observed in stabilizing rhythmic bimanual coordination for more difficult patterns, in which errors were corrected based on kinesthetic feedback from the hands. But how do these results relate to more complex tasks in daily life? In these tasks not only additional sources of sensory information can be used to observe and correct errors, but also the action representation of the required movement goal and hence motor control may be organized differently.

In everyday life, visual information provides an important additional source of information in achieving our task goals. Interestingly, similar characteristics have been observed when judging relative phase variability based on visual and kinesthetic information (Wilson et al., 2003). Although these judgments have been suggested to underlie motor performance, it is unclear how these tasks using verbal judgments of coordinative stability exactly relate to tasks involving the use of sensory feedback when executing motor actions, because these actions themselves may influence perception of coordinative stability and because the control process may depend on other (unconscious) use of afferent signals. Furthermore, combining visual and kinesthetic information in bimanual movement control may induce problems associated with the different frames of reference that are used for these modalities, with visual feedback being used in an allocentric reference frame (i.e., extrinsic space oriented) and kinesthetic feedback in an egocentric frame of reference (i.e., body oriented) (cf., Beets et al., 2012; Hikosaka et al., 1999; Salesse, Oullier, & Temprado, 2005; Temprado, Swinnen, Carson, Tourment,

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& Laurent, 2003). Thus, although similar characteristics may be observed for different sensory modalities, these sources may also compete when they are to be used in guiding motor actions.

More important in the application of our findings to tasks in daily life, is the possibility that movements may be controlled differently in more complex tasks in which the two hands have different roles. In this regard, perceptual information may be much more important in achieving tasks goals. In the literature, a strong guiding influence of perception has been revealed for situations in which participants could rely on specific forms of visual feedback. When feedback of the individual hand movements is presented in such a way that it specifies an integrated bimanual task goal (such as the Lissajous plane in Chapter 4), otherwise impossible coordination patterns between the hands can be easily executed after some practice (e.g., Franz, Zelaznik, Swinnen, & Walter, 2001; Kovacs et al., 2010a; Mechsner, Kerzel, Knoblich, & Prinz, 2001). The observed dependence on perceptual information led some authors to conclude that motor control is organized in terms of perception (Mechsner, 2004; Mechsner et al., 2001). Indeed, when transformations are used to display a complex tasks into a more simple perceptual representation, this perceptual reference allows people to execute this task, and performance deteriorates significantly once this augmented feedback is removed (e.g., Kovacs, Buchanan et al., 2009; Kovacs & Shea, 2011; Maslovat et al., 2009).

Possibly, tasks in daily life are also controlled via abstract task goals that guide the individual hands in the motor actions that need to be performed. If indeed tasks are represented at a more abstract level for a specified task goal, the question arises how this may affect the different interlimb interactions that stabilize bimanual performance. Do these sources of interaction that have been found to stabilize phase relations between the hands also contribute to more complex coordination patterns between the limbs? If a pattern is represented at a more abstract level, it may be speculated that the distinct mechanisms of integrated timing of feedforward control signals and error correction based on kinesthetic afference are still operational, but now at a different representational level. (For unintentional phase entrainment such a dependence on task goal representation seems less likely, considering its presumably lower-level, more automatic nature.). Given the compelling results regarding the beneficial influence of simple task goal representations (Franz et al., 2001; Kovacs, Buchanan et al., 2009; Kovacs et al., 2010a; Kovacs, Buchanan, & Shea, 2010b; Mechsner et al., 2001), determining whether and how integrated timing and error correction are related to these representations would yield essential insights into the coupling between action and perception and open up ways to generalize the present results to more complex tasks in daily life.

Sources of interaction in coordination between persons

Thus far, the contribution of various sources of coupling has only been studied with respect to interlimb coordination tasks. However, it would be interesting to study how coordination tasks between persons are engendered by specific sources of coupling between moving limbs. Returning to the thought experiment outlined in the Chapter 1, executing bimanual tasks with two persons instead of one seems much more difficult than performing the same tasks with the two hands of a single person. Although coordination between the hands was indeed found to be inferior, studies examining coordination principles in rhythmic coordination between two persons revealed that similar coordination characteristics are present in such interpersonal coordination (e.g., Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007; Schmidt, Bienvenu, Fitzpatrick, & Amazeen, 1998; Schmidt et al., 1990).

Despite the reported similarities, the coordination between and within persons necessarily involves a different set of interaction sources. All three sources of interlimb interaction may be assumed to be involved in within-person coordination, whereas between-person coordination can only be stabilized by coupling processes that are based on visual (or other perceptual) feedback. As it has been shown that participants can track an external signal (Buekers, Bogaerts, Swinnen, & Helsen, 2000; Peper & Beek, 1998a; Wimmers, Beek, & van Wieringen, 1992) and become be entrained unintentionally to an external signal (Lopresti-Goodman, Richardson, Silva, & Schmidt, 2008; Schmidt & O'Brien, 1997; Schmidt, Richardson, Arsenault, & Galantucci, 2007; van Ulzen, Lamoth, Daffertshofer, Semin, & Beek, 2008), the contributions of error correction and phase entrainment appear to be sufficient in stabilizing coordination between persons. Integrated timing of the coordination pattern in a feedforward mode of control cannot occur however, possibly explaining why coordination between persons is less stable than coordination within a single person (Schmidt et al., 1998). Relating coupling processes of within-person and between-person coordination may further indicate the significance of perception and action coupling in specific coordination tasks.

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Towards clinical applications

Finally, future experiments may be directed towards more functional applications when examining the sources of coupling that govern coordinative stability. For this purpose, changes in interlimb interaction across learning as well as development as described in the present thesis may be used as a reference for learning in young adults and as

a reference of typical development across childhood, in order to gain further insight into processes that accompany motor control in individuals with motor difficulties. Insight into possible limitations in the contributions of the different sources of interlimb interaction in these individuals may provide tools to generate proper rehabilitation or learning programs. A better understanding of limitations in for instance planning or the use of feedback may serve the specification of therapy goals and specific training programs. Whether motor disorders are accompanied by specific limitations in one or more of these interlimb interactions need to be determined in future studies.

Studying the different sources of interlimb interaction may for instance help to scrutinize the problems underlying developmental coordination disorder (DCD). It has been shown that in children with DCD in-phase and antiphase performance is poorer that in age-matched controls, presumably due to a weaker coupling between the hands (Volman & Geuze, 1998). Delineating the contributions of the different interlimb interactions in this group of children may therefore improve our understanding of the processes that are affected. In this regard, it has been shown that motor problems in DCD in general may be accompanied by problems in using proprioceptive feedback (Laszlo, 1998; Smyth & Mason, 1997), which may hamper the afference-based correction of errors. In addition, it has been suggested that DCD children have problems with the internal representation of their actions (for a review, see Gabbard & Bobbio, 2011). As a result children may experience difficulties in predicting consequences of their own actions (Gabbard & Bobbio, 2011; Van Waelvelde et al., 2006) and in integrating different sources of information to enhance performance (de Oliveira & Wann, 2010; Smits-Engelsman, Wilson, Westenberg, & Duysens, 2003). These studies suggest that general problems in motor control may arise as a result of difficulties associated with predicting sensory consequences of one's motor actions as well as integrating these sensory predictions with visual and kinesthetic feedback, in order to make adequate corrections to accomplish a task. So far, these difficulties have typically been studied in isolation, either focusing on the ability to use sensory feedback or on predictive control and planning. In this thesis an interesting interdependence of feedforward control and error correction was observed, which may be worthwhile studying in children with DCD. In addition, since the perception of kinesthetic afference is hampered in these children (Laszlo, 1998; Smyth & Mason, 1997), it may be interesting to study whether these impairments are differentially affecting error correction and phase entrainment, in order to understand how the intentional and unintentional effects of phase entrainment are affected.

CONCLUDING REMARKS

Stability of bimanual coordination is engendered by the contributions of various sources of interlimb interaction. The work reported in this thesis showed that changes in coordinative stability at short and longer time scales may be explained in terms of underlying sources of coupling between the limbs. Using a previously developed methodology we were able to distinguish between changes in the contributions of integrated timing of feedforward control signals, error correction based on kinesthetic afference, and phase entrainment by contralateral afference. Most interestingly, results showed that changes in the contributions of the interlimb interactions to coordinative stability are independent of the time scale over which they occur. In particular, at short and longer time scales alike, changes in integrated timing and error correction, but not in phase entrainment, were found to underlie changes in coordinative stability. Furthermore, the interesting interplay between integrated timing and error correction, as observed previously, was also revealed for changes in bimanual coordination at short and longer time scales, providing evidence for a predictive mode of control in stabilizing difficult bimanual coordination patterns. With respect to potential future directions of research, these results may be taken as an entry point for more detailed assessments of the underlying interaction processes and for the application of the research method in more functional settings.

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Summary

In rhythmical bimanual coordination, coordinative stability is determined by the coupling between the hands. When both hands move at the same relatively low frequency, two coordination patterns can be executed stably: in-phase coordination (i.e., mirror-symmetrical movements of the hands) and antiphase coordination (i.e., isodirectional movements of the hands). At higher frequencies only in-phase coordination can be performed stably. This difference in coordinative stability has been formally captured by the Haken-Kelso-Bunz model (HKB model), which consists of a pair of nonlinearly coupled nonlinear oscillators. Within this model, bimanual coordination is studied in terms of the relative phase between the oscillators (Φ) and its variability, which provides an index of coordinative stability. The HKB model captures the stable execution of in-phase ($\Phi = 0°$) and antiphase coordination ($\Phi = 180°$), as well as the essential role of movement frequency: when movement increases, coordinative stability of antiphase coordination decreases, culminating in a transition to in-phase coordination at a critical frequency. Extensions of this model were successful in accounting for influences of additional factors such as the difference between uncoupled frequencies of the moving limbs and handedness. Because the HKB model does not provide information regarding possible underlying processes, subsequent studies have focused increasingly on the link between the model and underlying system properties and processes.

Considering that bimanual coordination is governed by the coupling between the hands, it is relevant to determine the contributions of the underlying sources of interlimb interaction to the stability of bimanual coordination. In the literature, various candidate sources of interlimb coupling have been proposed. Using an established methodology, the research reported in the present thesis focused on three functionally defined sources of interlimb interaction. First, *integrated timing* reflects interaction processes related to feedforward timing of the efferent signals that specify the intended bimanual coordination pattern, without consideration of potential adjustments based on afferent feedback. Second, *error correction* reflects the intentional correction of relative phasing errors based on kinesthetic afference, resulting in stabilization of the intended bimanual coordination pattern. Third, *phase entrainment* pertains to the unintentional entraining influences stemming from contralateral afference, leading to unintended attraction towards specific phase relations between the limbs. Changes in the stability properties of bimanual coordination that occur as a function of task-related parameters like movement frequency and amplitude, learning, and development, should be related

to changes in interlimb interactions. The research reported in the present thesis thus aimed to elucidate how changes in coordinative stability are engendered by changes in the interlimb interactions underlying coordinative stability. In particular, we focused on changes in coordinative stability and interlimb coupling at both short (viz. movement frequency and amplitude) and longer time scales (viz. learning and development). In Chapters 2, 4, and 5 all three sources of interlimb interaction were investigated, while in Chapter 3 only phase entrainment was studied.

In Chapter 2, the influence of movement frequency on coordinative stability was examined in terms of the three sources of interlimb interaction of interest. To this end, five tasks involving passive and active movements of the hands were systematically compared. In each of these tasks, the different sources of interaction were assumed to be involved to a different extent. First, during unimanual coordination with a pacing signal (task UN) no sources of interlimb interaction were present. Second, for unimanual coordination in the presence of phase-shifted passive movements of the contralateral hand (task UNm), the active hand was entrained towards in-phase and antiphase coordination with the passively moving hand. Hence, comparison of UNm and UN served to tease apart the contribution of phase entrainment. Furthermore, when the actively moving hand tracked the passive movements of the contralateral hand, either in the presence of an auditory distracting signal (task KTa) or without such a signal (task KT), the coordination pattern between the hands was stabilized by interactions associated with error correction. Whereas interactions due to phase entrainment were present in both KTa and UNm interlimb, error correction was present in KTa but not in UNm. Hence, the influence of error correction could be assessed by comparing KTa to UNm. In addition, the robustness of the error correction process was examined by comparing KT and KTa, because this comparison revealed its susceptibility to the distracting influences of the auditory signal. Finally, during active bimanual coordination (task AB), participants executed active movements of both hands in a specified pattern, implying that in this task coordinative stability was also enhanced by integrated timing of the bimanual control signals. The contribution of integrated timing was assessed by comparing AB to KT, because in KT only phase entrainment and error correction were involved while AB involved all three sources of interaction. Finally, integrated timing was also assessed by comparing AB to UNm, because error corrections were found to be hardly involved in AB.

The effect of movement frequency was studied by systematic pairwise comparisons of the five tasks for three different frequencies for in-phase and antiphase coordination. The highest frequency was equal to the critical frequency of each participant, i.e., the

frequency at which the stability of antiphase coordination was lost. Results confirmed that bimanual coordination was stabilized by each of the three sources of interlimb interaction, with the differential stability of in-phase and antiphase coordination resulting predominantly from interactions associated with integrated timing. Moreover, at low frequencies integrated timing seemed sufficient to stabilize bimanual coordination, whereas a shift towards a more prominent role of error correction was observed at higher frequencies for the more difficult antiphase pattern. These results suggested that for low frequencies coordinative stability was mainly achieved by means of open-loop control of the bimanual pattern, whereas at the critical frequency stabilization of the pattern required a shift to closed-loop control in which relative phase errors were corrected based on kinesthetic afferent information. The contribution of phase entrainment was not influenced by movement frequency. Furthermore, the observation that also kinesthetic tracking involved coordinated bimanual muscle activity indicated that error corrections were more effective when bimanual control signals were generated. Presumably, in this manner a bimanual reference frame was generated that allowed for sensory predictions against which the actual kinesthetic afference could be compared.

Because both empirical results and theoretical considerations have suggested that larger movement amplitudes may induce stronger phase entrainment, this relation was scrutinized in Chapter 3. The central question was whether phase entrainment strength was influenced by movement amplitude as such or by the amplitude relation between the hands. For this purpose, a previously published dataset was re-analyzed and compared to the results of a new experiment. In both experiments, phase entrainment strength was determined by comparing the coordination of unimanual movements with a pacing signal (task UN) to the performance of the same task in the presence of distracting passive movements of the contralateral hand (task UNm). In the first experiment two amplitudes of the passive hand movements were imposed without having any restrictions on the amplitude of the actively moving hand. Since the active hand moved at the same amplitude in the two amplitude conditions, the amplitude relation between the hands was different in the two conditions. Specifically, the amplitude relation between the passive and active hand was 1:1.9 for the small amplitude and 1:1 for the large amplitude. In the second experiment the same movement amplitudes of the passively moving hand were used, but the amplitude relation was 1:1 between the two hands in both amplitude conditions. The results indicated that phase entrainment strength was only influenced by a change in the amplitude relation between the limbs (as obtained for Experiment 1) and not by amplitude as such (Experiment 2). These results suggested that entrainment

to the contralateral hand was not only influenced by the strength of afferent signals, but also by the susceptibility of the active hand movements to external influences.

In Chapter 4 the effect of learning a new coordination pattern on the underlying interlimb interactions was examined, thereby assessing the changes in interlimb interactions at a longer time scale. Participants learned to execute a new bimanual coordination pattern (Φ = 90°) and changes in bimanual coordination were related to changes in the underlying contributions of integrated timing, error correction, and phase entrainment. For this purpose, participants executed the four tasks that involved the three interlimb interactions to a different extent, i.e., tasks AB, KT, UNm, and UN. Learning effects were assessed for in-phase and antiphase coordination, the practiced 90° pattern, and its mirror-symmetrical transfer pattern (Φ = 270°). In addition, bimanual performance and changes in the sources of interlimb interaction were compared for learning with an internal focus of attention, an external focus of attention closely related to the hand movements, and an external focus further away from the hand movements. Results showed that learning the 90° pattern involved changes in the contributions of integrated timing and error correction, whereas no changes were observed for phase entrainment. The changes in the contribution of integrated timing to the 90° pattern preceded the changes in error correction. In addition, the amount of error correction was found to increase only when integrated timing contributed to the stability and accuracy of the new pattern. These results suggested that error corrections were more effective when integrated timing provided a bimanual reference frame against which the kinesthetic feedback could be compared. Results were comparable for the three attentional focus groups. Performance of the 270° transfer pattern improved later than that of the practiced 90° pattern, suggesting that generalization to an abstract representation occurred at a slower rate than improvement of the practiced pattern itself.

Modifications of interlimb interactions were studied at an even longer time scale in Chapter 5, by examining the development of bimanual coupling from infanthood to adulthood. For this purpose, four groups were compared: 6/7-year olds, 10/11-year olds, 14/15-year olds, and young adults. Not only the temporal coupling between the hands was studied (again using tasks AB, KT, UNm, and UN), but also the spatial coupling between the hands using a bimanual line-circle drawing task. Results showed that although performance of the temporal coordination task improved over all age groups (thanks to an overall increase in coupling strength, as reflected by increased cycle duration correlation), the relative contributions of the three sources of interaction to the stability hardly changed over age. Only the absolute amount of error correction (as

indexed by the error correction correlation) was found to improve with development, suggesting enhanced use of kinesthetic afference with increasing age. Furthermore, the results revealed parallel improvement of in-phase and antiphase coordination over the age groups, thereby suggesting that the differential stability of in-phase and antiphase probably evolved before the age of 6/7 years. Spatial drawing performance (as indexed by drawing smoothness and consistency) was found to improve over all age groups. Spatial coupling of the hands improved after the age of 14/15 years, as evidenced by the fact that adults showed less deterioration of bimanual drawing performance than children when bimanual drawing of spatially incompatible shapes was compared to bimanual drawing of identical shapes and to unimanual drawing. These results were consistent with the anterior-posterior direction of myelination of the corpus callosum reported in the literature, with early improvements in the temporal coupling (mediated by the anterior corpus callosum) and later improvements in the spatial coupling of the hands (more closely related to the posterior corpus callosum).

In Chapter 6 the main findings and implications of the research reported in the thesis are discussed. A major finding across the experimental studies was that the changes in the contributions of the interlimb interactions to coordinative stability were independent of the time scale over which they occurred. The differences between the contributions of the three sources of interlimb interaction seemed to depend on the intention to perform a specific bimanual pattern, because marked changes in the contributions of integrated timing and error correction, but not in phase entrainment, were evident at both short and longer time scales. Furthermore, both at a short time scale (frequency) and at a longer time scale (learning) a tight relation between integrated timing and error correction was observed. These findings were interpreted as an indication of a form of predictive control that appeared to be employed, especially during difficult coordination tasks. In this mode of control, efference copies (resulting in a bimanual frame of reference) may be used to generate sensory predictions against which actual sensory feedback can be compared. Following this discussion, Chapter 6 continues with an evaluation of the theoretical assumptions regarding interlimb interactions underlying the methodology used in the present thesis as well as its limitations. Finally in closing, several suggestions are made with regard to future directions of research, inspired by the results and insights obtained regarding the contributions of integrated timing, error correction, and phase entrainment to the stabilization of bimanual coordination.

Samenvatting

Stabiliseren van bimanuele coördinatie:
Veranderingen in tussenledemaatinteracties

Tijdens het uitvoeren van ritmische bewegingen van twee handen (bimanuele coördinatie) wordt de stabiliteit van de coördinatie bepaald door de koppeling tussen de handen. In dit proefschrift is bimanuele coördinatie onderzocht door middel van ritmische flexie-extensie bewegingen van de twee handen, waarbij de handen met dezelfde frequentie bewegen. Bij een voldoende lage bewegingsfrequentie kunnen zonder specifieke training twee coördinatiepatronen stabiel worden uitgevoerd: in-fasecoördinatie (spiegelsymmetrische bewegingen van de handen) en tegenfasecoördinatie (bewegingen van de handen in dezelfde richting). Op hogere frequenties kan alleen het in-fasepatroon stabiel worden uitgevoerd. Dit verschil in coördinatieve stabiliteit is onder meer onderzocht vanuit het perspectief van de coördinatiedynamica, waarin benadrukt wordt hoe bimanuele patronen ontstaan als gevolg van de koppeling tussen de handen. Bimanuele coördinatie kan worden begrepen op basis van het Haken-Kelso-Bunz-model (HKB-model), dat bestaat uit twee niet-lineair gekoppelde niet-lineaire oscillatoren. Vanuit dit perspectief wordt bimanuele coördinatie bestudeerd aan de hand van de relatieve fase tussen de oscillatoren (Φ) en de variabiliteit hiervan, die een maat voor de coördinatieve stabiliteit. Het HKB-model beschrijft de stabiele uitvoering van in-fase- ($\Phi = 0°$) en tegenfasecoördinatie ($\Phi = 180°$), evenals de rol van bewegingsfrequentie: als de bewegingsfrequentie geleidelijk wordt verhoogd, neemt de stabiliteit van tegenfase geleidelijk af totdat bij een kritieke frequentie een plotselinge overgang (transitie) plaatsvindt van tegenfase- naar in-fase-coördinatie. Uitbreidingen van het model bleken bovendien een accurate beschrijving te geven van de invloed van specifieke factoren, zoals het verschil in de ongekoppelde frequenties (eigenfrequenties) van de gecoördineerde ledematen en handvoorkeur. Omdat het HKB-model geen informatie verschaft over mogelijke onderliggende processen, heeft vervolgonderzoek zich in toenemende mate gericht op het verband tussen dit model en de onderliggende structuren en processen.

Aangezien bimanuele coördinatie bepaald wordt door de koppeling tussen de handen, is het relevant om de bijdragen van de onderliggende bronnen van tussenledemaatinteractie aan de stabiliteit van de coördinatie te achterhalen. In de

literatuur zijn verschillende bronnen van koppeling tussen de handen geopperd, die de bimanuele coördinatie kunnen beïnvloeden. Door gebruik te maken van een bestaande methode, richtte het in dit proefschrift beschreven onderzoek zich op drie functioneel gedefinieerde bronnen van tussenledemaatinteractie. De eerste bron, *geïntegreerde timing*, weerspiegelt de processen die gerelateerd zijn aan 'open-loop' timing van de stuursignalen van beide handen die het intentionele bimanuele patroon specificeren, zonder rekenschap te geven van mogelijke aanpassingen die gebaseerd zijn op feedback over de bewegingsuitvoering (afferente [10] feedback). De tweede bron, *foutcorrectie*, verwijst naar intentionele correcties van waargenomen fouten in het coördinatiepatroon (c.q. de relatieve fase) op basis van kinesthetische[11] informatie, resulterend in stabilisatie van het bimanuele coördinatiepatroon. *Fase-aantrekking*, ten slotte, weerspiegelt niet-intentionele invloeden van afferentie van de andere hand, die zich uiten in aantrekking tot bepaalde faserelaties tussen de handen. Deze tussenledemaatinteracties kunnen worden onderscheiden op basis van twee eigenschappen: intentionaliteit (d.w.z., of een bepaald bimanueel coördinatiepatroon wordt nagestreefd of niet) en afhankelijkheid van afferentie. Zowel geïntegreerde timing als foutcorrectie zijn intentioneel, terwijl alleen foutcorrectie en fase-aantrekking afhankelijk zijn van afferentie.

De veranderingen in de stabiliteit van bimanuele coördinatie die optreden als gevolg van taakgerelateerde parameters zoals bewegingsfrequentie en –amplitude, leren en ontwikkeling, moeten gepaard gaan met veranderingen in tussenledemaatinteracties. Het doel van het in dit proefschrift beschreven onderzoek was daarom om te achterhalen hoe veranderingen in de stabiliteit van de coördinatie voortvloeien uit veranderingen in de onderliggende tussenledemaatinteracties. Het onderzoek richtte zich hierbij op veranderingen in stabiliteit en tussenledemaatinteracties op zowel korte (variatie in taakparameters als frequentie en amplitude) als langere tijdschalen (leren en ontwikkeling). In de hoofdstukken 2, 4 en 5 worden alle drie interactiebronnen onderzocht, terwijl in Hoofdstuk 3 alleen fase-aantrekking wordt onderzocht.

Hoofdstuk 2 presenteert een onderzoek waarin werd onderzocht hoe veranderingen in coördinatieve stabiliteit als gevolg van veranderingen in de bewegingsfrequentie samenhangen met veranderingen in de onderliggende bronnen van tussenledemaatinteractie. Om de relatieve bijdragen van deze bronnen aan de coördinatieve stabiliteit te onderzoeken, werden vijf verschillende taken bestaande uit passieve en actieve bewegingen systematisch vergeleken. Deze taken waren zo gekozen, dat de mate waarin de interactiebronnen een rol speelden verschilden. Ten

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10   Afferentie: de aanvoer van neurale signalen naar het zenuwstelsel toe die sensorische informatie bevatten.
11   Kinesthesie: de waarneming van de eigen beweging.

eerste, bij unimanuele coördinatie met een auditieve metronoom (taak UN) zijn geen bronnen van tussenledemaatinteractie betrokken. Ten tweede, tijdens unimanuele coördinatie met de metronoom in de aanwezigheid van tijd-verschoven passieve bewegingen van de andere hand (taak UNm), wordt de actieve hand aangetrokken tot in-fase- of tegenfasecoördinatie met de passieve hand. Door taken UNm en UN te vergelijken kan de bijdrage van fase-aantrekking onderzocht worden. Tijdens de derde taak werden de bewegingen van de actieve hand gecoördineerd met passieve bewegingen van de andere hand. Omdat de handen niet zichtbaar waren, moesten de actieve handbewegingen afgestemd worden op basis van kinesthetische informatie over de bewegingen van de passieve hand (het zogenoemde 'kinesthetic tracking', KT). Op basis van deze signalen werd het coördinatiepatroon gestabiliseerd door middel van foutcorrectie. Door de uitvoering van deze taak te vergelijken met die van taak UNm kon de stabiliserende bijdrage van foutcorrecties worden vastgesteld. Bovendien werd de robuustheid van het foutcorrectieproces onderzocht door de invloed van een afleidend auditieve signaal te bestuderen. Hiertoe werd de kinesthetische volgtaak uitgevoerd zowel in de aanwezigheid van een tijd-verschoven metronoomsignaal (KTa) als zonder een dergelijk signaal (KT). Ten slotte, tijdens actieve bimanuele coördinatie (taak AB) voerden proefpersonen actieve bewegingen van beide handen uit in een gespecificeerd patroon, zodat coördinatieve stabiliteit in deze taak ook werd bepaald door geïntegreerde timing van de bimanuele aansturingsignalen. De bijdrage van geïntegreerde timing werd onderzocht door taak AB te vergelijken met taak KT, omdat in taak KT alleen fase-aantrekking en foutcorrectie betrokken waren terwijl in taak AB alle drie de bronnen van tussenledemaatinteractie aan de stabiliteit konden bijdragen. Omdat foutcorrecties minder prominent aanwezig bleken te zijn in taak AB, werd geïntegreerde timing ook onderzocht door AB te vergelijken met UNm.

In Hoofdstuk 2 werd de invloed van bewegingsfrequentie op de tussenledemaat-interacties bestudeerd door deze vijf taken systematisch te vergelijken voor zowel in-fase- als tegenfasecoördinatie, uitgevoerd op drie verschillende bewegingsfrequenties. De hoogste frequentie was gelijk aan de kritieke frequentie zoals vastgesteld voor elke proefpersoon: de frequentie waarop de uitvoering van het tegenfasepatroon niet langer stabiel was en een overgang plaatsvond naar het in-fasepatroon. Resultaten bevestigden dat bimanuele coördinatie werd gestabiliseerd door elk van de drie tussenledemaatinteracties, waarbij het verschil in stabiliteit tussen in-fase en tegenfase vooral te wijten was aan verschillen in de stabiliserende werking van geïntegreerde timing. Bovendien bleek geïntegreerde timing op zichzelf voldoende om in-fase en tegenfase stabiel uit te voeren op lage bewegingsfrequenties, terwijl de invloed van

foutcorrectie prominenter zichtbaar werd als het moeilijkere tegenfasepatroon werd uitgevoerd met een hoge frequentie. Deze resultaten suggereerden dat in de buurt van de kritieke frequentie 'open-loop' motorische sturing niet voldoende was om coördinatieve stabiliteit te waarborgen, waardoor een overgang plaatsvond naar een vorm van 'closed-loop' sturing waarbij fouten in de relatieve fase gecorrigeerd werden met behulp van kinesthetische afferente informatie. De bijdrage van fase-aantrekking werd niet beïnvloed door de bewegingsfrequentie. Hoewel tijdens de volgtaak de ene hand passief werd bewogen, werd voor deze hand toch gecoördineerde spieractiviteit waargenomen. Deze bevinding suggereerde dat foutcorrecties effectiever konden worden uitgevoerd indien naar beide handen sturingssignalen werden gestuurd. Het lijkt waarschijnlijk dat op deze manier een bimanueel referentiekader werd gegenereerd, op basis waarvan sensorische verwachtingen konden worden opgesteld waarmee de actuele afferente signalen werden vergeleken.

Aangezien zowel empirische resultaten als theoretische overwegingen hebben gesuggereerd dat de effecten van fase-aantrekking groter zijn naarmate de bewegingen met een grotere amplitude worden uitgevoerd, werd in Hoofdstuk 3 de relatie tussen bewegingsamplitude en fase-aantrekking onderzocht. De centrale vraag hierbij was of de sterkte van fase-aantrekking beïnvloed werd door de amplitude als zodanig of door de amplituderelatie tussen de handen. Om dit te onderzoeken werd een gepubliceerde dataset nader geanalyseerd en vergeleken met de resultaten van een nieuw experiment. In beide experimenten werd de sterkte van fase-aantrekking bepaald in termen van de mate waarin de coördinatie van unimanuele bewegingen met een metronoom werd beïnvloed door de aanwezigheid van passieve bewegingen van de andere hand. Hiertoe werden taken UN en UNm vergeleken. In het eerste experiment werd de passieve hand met twee verschillende amplitudes bewogen zonder instructies met betrekking tot de bewegingsamplitude van de actieve hand. Deze actieve hand bleek in beide condities met dezelfde amplitude te bewegen. Hierdoor werd de amplituderelatie tussen de handen beïnvloed. Voor de kleine amplitude was de relatie tussen de amplitude van passieve en actieve hand 1:1.9 en voor de grote amplitude 1:1. In het tweede experiment werd de passieve hand met dezelfde amplitudes bewogen, maar ditmaal moest de actieve hand met een overeenkomstige amplitude bewegen. De amplitude relatie tussen de handen was dus 1:1 voor beide condities. De resultaten gaven aan dat de sterkte van fase-aantrekking alleen beïnvloed werd door een verandering in de amplituderelatie tussen de handen, en niet door amplitude op zich. Deze resultaten toonden aan dat fase-aantrekking niet alleen afhankelijk was van de sterkte van afferente signalen (afhankelijk van de bewegingsamplitude), maar ook van de vatbaarheid van de actieve hand voor

externe invloeden.

In Hoofdstuk 4 werden veranderingen in tussenledemaatinteracties op een langere tijdschaal onderzocht door de invloed van het leren van een nieuw coördinatiepatroon op de tussenledemaatinteracties te bestuderen. Proefpersonen leerden een nieuw coördinatiepatroon uit te voeren (Φ = 90°) en veranderingen in bimanuele coördinatie werden gerelateerd aan de veranderingen in de onderliggende bijdragen van geïntegreerde timing, foutcorrectie en fase-aantrekking. Hiertoe voerden proefpersonen vier taken uit waarin de drie tussenledemaatinteracties in verschillende mate aanwezig waren: taak AB, KT, UNm en UN. Leereffecten werden onderzocht voor in-fase- en tegenfasecoördinatie, het geleerde coördinatiepatroon (Φ = 90°) en het spiegelsymmetrische patroon (Φ = 270°). Daarnaast werd de invloed van het richten van de aandacht onderzocht door drie situaties te vergelijken: een interne aandachtsfocus, een externe focus van aandacht sterk gerelateerd aan de bewegingen van de handen, en een externe focus van aandacht die verder was verwijderd van de handbewegingen. De resultaten toonden aan dat het leren van de 90°-faserelatie leidde tot veranderingen in de bijdragen van geïntegreerde timing en foutcorrectie, terwijl er geen verandering plaatsvond in de fase-aantrekking. De verandering in de bijdrage van geïntegreerde timing aan 90° ging vooraf aan de veranderingen in foutcorrectie. Bovendien nam de mate van foutcorrectie alleen toe in situaties waarbij geïntegreerde timing ook bijdroeg aan de stabiliteit en nauwkeurigheid van het coördinatiepatroon. Deze resultaten gaven aan dat foutcorrecties het meest effectief waren wanneer op basis van geïntegreerde timing een bimanueel referentieframe kon worden gevormd waarmee de actuele kinesthetische feedback kon worden vergeleken. De resultaten waren vergelijkbaar voor de drie groepen met een verschillende aandachtsfocus. De uitvoering van het 270°-coördinatiepatroon verbeterde later dan de uitvoering van het geoefende 90°-patroon. Dit resultaat gaf aan dat de generalisatie van het geoefende patroon langzamer verliep dan het leren van het patroon zelf.

Veranderingen in tussenledemaatinteracties werden onderzocht op de langste tijdschaal in Hoofdstuk 5, waarin de veranderingen tijdens de ontwikkeling van de bimanuele coördinatie van kind tot volwassene onder de loep werd genomen. Hiertoe werden vier groepen vergeleken: 6/7-jarigen, 10/11-jarigen, 14/15-jarigen en jongvolwassenen. Niet alleen werd de temporele koppeling tussen de handen onderzocht voor de taken AB, KT, UNm en UN, ook werd de spatiële koppeling tussen de handen onderzocht door middel van een bimanuele lijn-cirkel-tekentaak. Ondanks een verbetering in de temporele coördinatietaak over alle leeftijdsgroepen (dankzij een toename in de koppelingssterkte, die tot uiting kwam in een toegenomen correlatie

tussen de cyclusduur van beide handen), veranderde de relatieve bijdrage van de drie bronnen van tussenledemaatinteractie nauwelijks over de leeftijden. Alleen de mate van foutcorrectie (zoals vastgesteld door middel van de foutcorrectie-correlatie) verbeterde met de ontwikkeling, wat duidde op een beter gebruik van kinesthetische feedback met toenemende leeftijd. Daarnaast toonden de resultaten aan dat in-fase- en tegenfasecoördinatie tegelijkertijd verbeterden over de bestudeerde leeftijdsgroepen. Dit duidde erop dat het verschil in stabiliteit tussen in-fase en tegenfase waarschijnlijk al voor de leeftijd van 6/7 jaar was ontstaan. De uitvoering van de tekentaak verbeterde in termen van vloeiendheid en consistentie over alle leeftijdsgroepen. Spatiële koppeling van de handen verbeterde vooral na de leeftijd van 14/15 jaar, aangezien de volwassenen een minder sterke afname in hun prestatie vertoonden dan de kinderen wanneer tegelijkertijd twee verschillende vormen werden getekend in vergelijking met het tekenen van twee dezelfde vormen en het tekenen met één hand. De volwassenen lieten dus minder interferentie zien tussen de bewegingen van de handen dan de kinderen tijdens het tekenen van twee verschillende vormen. Uit een vergelijking met neurologische en neurofysiologische studies, bleek dat onze resultaten overeenkwamen met de achterwaartse richting van myelinistatie[12] van het corpus callosum, waarvan het voorste gedeelte betrokken lijkt bij de temporele koppeling en het achterste deel bij de spatiële koppeling van bimanuele bewegingen.

In Hoofdstuk 6 werden de belangrijkste bevindingen van het proefschrift en de implicaties ervan besproken. Een cruciale algemene observatie was dat de veranderingen in de bijdragen van de verschillende tussenledemaatinteracties onafhankelijk bleken te zijn van de tijdschaal waarover deze veranderingen plaatsvonden. De verschillen in de bijdragen van de drie tussenledemaatinteracties leken met name samen te hangen met de intentie om een specifiek bimanueel patroon uit te voeren, aangezien vooral de bijdragen van geïntegreerde timing en foutcorrectie veranderden op zowel korte als langere tijdschalen, terwijl weinig verandering werd waargenomen voor fase-aantrekking. Een andere interessante observatie was de hechte relatie tussen geïntegreerde timing en foutcorrectie, die werd gevonden voor veranderingen in coördinatieve stabiliteit op zowel een korte tijdschaal (frequentie) als een langere tijdschaal (leren). Deze relatie werd geïnterpreteerd als een indicatie van een vorm van predictieve sturing, die vooral tijdens moeilijkere coördinatietaken gebruikt leek te worden. Hierbij zou een kopie van het stuursignaal dat naar de handen gaat (een efferentiekopie) gebruikt worden om sensorische voorspellingen te maken, waarmee de actuele sensorische feedback

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12   Myelinisatie: een proces waarbij de stof myeline gevormd wordt rondom zenuwvezels, waardoor signalen sneller vervoerd worden.

vergeleken kan worden. Vervolgens werden in Hoofdstuk 6 enkele theoretische aannames ten aanzien van tussenledemaatinteracties besproken, die de basis vormden voor de gebruikte methodologie en werd ingegaan op de beperkingen hiervan. Tot slot werden enkele suggesties geopperd voor toekomstig onderzoek, geïnspireerd door de gevonden resultaten met betrekking tot de rol van geïntegreerde timing, foutcorrectie en fase-aantrekking bij de stabilisatie van bimanuele coördinatie.

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"I can no other answer make but thanks, and thanks."

William Shakespeare

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