Research report

Directional constraints during bimanual coordination: The interplay between intrinsic and extrinsic directions as revealed by head motions

R.L.J. Meesen^{a,b}, N. Wenderoth^a, J.J. Temprado^c, S.P. Swinnen^{a,*}^a Motor Control Laboratory, Research Center for Motor Control and Neuroplasticity, Department of Biomedical Kinesiology, K.U.L., Tervuurse Vest 101, 3001 Leuven, Belgium^b REVAL Research Group, Department of Health Care Sciences, Provinciale Hogeschool Limburg, Guffenslaan 39, 3500 Hasselt, Belgium^c UMR 6152 “Mouvement & Perception”, Université de la Méditerranée et CNRS, Faculté des Sciences du Sport, 163 Avenue de Luminy, BP 910, 13288 Marseille, France

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Abstract

The role of directional compatibility was investigated during the production of in-phase and anti-phase coordination patterns involving both arms as well as the head. Our first aim was to compare the quality of coordination between both arms when symmetrical arm posture manipulations were used to disentangle muscle homology from the mutual direction of limb motions in extrinsic space. Findings revealed that in-phase coordination, characterized by the simultaneous activation of homologous muscle groups, was resistant to posture manipulations. Conversely, during anti-phase coordination, the influence of extrinsic direction became more prevalent whereby isodirectionality in extrinsic space contributed to stabilization of anti-phase coordination patterns. The second aim was to study the effect of periodic head movements upon the assembling of a coordinative synergy among the body segments. The findings demonstrated that the in-phase patterns were hardly affected by directionality of head motion. Conversely, the anti-phase patterns were more vulnerable to the directional influence of head movements, showing less accurate and stable coordination during non-isodirectional than isodirectional head motions. These observations underscore the robust nature of coordination patterns based on muscle homology, even in the absence of symmetric arm positions. Moreover, isodirectional head movements became easily integrated with the overall coordination pattern, whereas head–limb coupling was poor when the head moved anti-directional with the limbs.

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1. Introduction

In everyday life, we often manage to perform complicated coordination skills involving many joint and muscle combinations with little effort and high efficiency. Bernstein was already intrigued by this phenomenon which he referred to as the degrees-of-freedom problem [2]. His profound insights have inspired an intensive research program into the constraints that govern interlimb coordination. Constraints emerge within

the context of the performer and his surroundings and refer to basic rules that enable the central nervous system to control the many degrees-of-freedom evident in biological systems, including humans. Two basic coordination constraints have received prominent attention in the context of cyclical bimanual coordination tasks: the egocentric and the allocentric constraint.

On the one hand, the *egocentric constraint* refers to a preference for simultaneous activation of the homologous muscle groups (in-phase, relative phase $\Phi = 0^\circ$), often resulting in mirror-symmetric movements with respect to the body midline and corresponding to movements in opposite directions (non-isodirectional) in extrinsic space. However, these directional relationships depend on the particular task context (medio-lateral movements in the present case). When homologous muscles are activated in alternation (anti-phase, $\Phi = 180^\circ$), both limbs often move in the same direction (isodirectional)

* Corresponding author at: Motor Control Laboratory, Research Center for Motor Control and Neuroplasticity, Department of Biomedical Kinesiology, K.U.L., Tervuurse Vest 101, 3001 Leuven, Belgium. Tel.: +32 16 32 90 71; fax: +32 16 32 91 97.

E-mail address: Stephan.Swinnen@FABER.KULEUVEN.BE (S.P. Swinnen).

in extrinsic space. The anti-phase coordination mode is usually less stable than the in-phase mode, such that when cycling frequency is increased and a critical frequency is reached, a phase transition occurs from anti-phase towards in-phase movements [8,12]. The higher vulnerability of anti-phase as compared to in-phase coordination modes has been demonstrated extensively in the literature, using various intrinsic or extrinsic perturbations [4,5,13,25]. Conversely, in-phase coordination has proven to be highly resistant to such experimental perturbations.

On the other hand, the *allocentric constraint* refers to a general preference to move the limbs in the same direction in extrinsic space. Whereas this constraint was initially demonstrated during coordination of the nonhomologous limbs [1], more recent studies have also shown its effects during coordination of the homologous limbs, most notably during bimanual coordination [19,23–25]. More specifically, in-phase and anti-phase coordination patterns are produced more successfully when occurring in the same as compared to different directions in extrinsic space. However, the allocentric constraint is subordinate to the egocentric constraint under these circumstances, pointing to the dominance of muscle homology as an organizing principle during bimanual coordination [18,23]. Overall, these findings suggest that the mutual directional relations between simultaneous limb motions play a critical role during interlimb coordination. This question ultimately revolves around the impact of directional compatibility on interlimb coordination and, more generally, around the influence of spatial parameters in general [3,6,22]. The present study further explored the role of directional (in)compatibility during bimanual coordination. This was accomplished by means of two different experimental strategies that were developed across two experiments.

In Experiment 1, arm posture was manipulated to disentangle muscle homology from isodirectionality of limb motions in extrinsic space. This resulted in a factorial combination of muscle homology and extrinsic direction during the production of cyclical arm motions around their cranio-caudal axis. Based on previous studies with different tasks, it was hypothesized that coordination patterns involving the simultaneous activation of homologous muscle groups would be performed with higher accuracy and stability than patterns based on nonhomologous muscle groups. Moreover, it was hypothesized that isodirectional movements would proceed with higher accuracy/stability than non-isodirectional movements.

In Experiment 2, head movements were added to determine their impact on bimanual coordination quality. As a single undivided segment positioned on top of the longitudinal body axis, the head occupies a unique position in the human body as a directional stabilizer/destabilizer but its role in interlimb coordination has hardly been explored (for exceptions see [9,10,15,16]).

A previous study already documented the impact of head movements on the quality of homologous limb coordination [16]. In the present study, head movements were added to bimanual coordination modes and their effects were assessed to address two specific questions. A first question pertained to the impact of the head on coordination when it moved isodirectionally versus non-isodirectionally with the upper limbs. Based on the allocentric constraint, it was hypothesized that

isodirectional head movements would have a stabilizing effect and non-isodirectional head movements a destabilizing effect on bimanual coordination. Secondly, we investigated the differential effect of moving either the head or one arm anti-directional to the other segments. This allowed us to assess whether head versus arm movements have a differential impact on multilimb coordination. These questions were addressed during the production of in-phase and anti-phase bimanual coordination modes.

2. Materials and methods

2.1. Participants

Eleven participants (8 females, 3 males) were involved in Experiment 1 (aged 19–27, mean 22 years) and 20 (12 females, 8 males) in Experiment 2 (aged 18–36, mean 26 years). All were right-handed as determined by the Oldfield questionnaire [17] and were paid for their participation. They were not previously involved in a similar experiment. None of them exhibited overt sensory-motor deficits and all were able to move their limbs within the full range of motion. They received information about the experimental procedures and provided written informed consent. The experiment was approved by the local Ethics Committee of Biomedical Research at K.U.Leuven and was performed in accordance with the standards of the 1964 Declaration of Helsinki.

2.2. Apparatus and task

The participants were positioned supine on a padded wooden table (breadth: 125 cm, length: 250 cm). The head and both upper limbs were attached to custom-built manipulanda that allowed rotations around the cranio-caudal axis of the respective segments. All limbs were attached to the manipulanda and were positioned in such a way that postural stability was minimally affected. Additionally, subjects were fixated by a belt spanning over the hip and clamping the body to the table. This prevented that postural instabilities occurred as a consequence of large reaction forces. Even at high frequencies, the participants were able to perform the motions in a stable fashion. Angular motions were registered by means of three incremental shaft encoders (Hengstler, 1000 counts per revolution, accuracy = 0.36° , sampling frequency = 200 Hz), mounted at the axis of rotation of each manipulandum (Fig. 1).

A computer was used to sample and record the data and to signal the start and end of a trial. Each trial lasted 15 s and consisted of two frequencies, paced by a real-time toolkit (KUKA-roboter, accuracy = 10^{-7} s). The first 5 s was paced at 1.58 Hz and was used as a warm up period, followed by 10 s at a frequency of 3 Hz for Experiment 1 and 2 Hz for Experiment 2. This implies that a full cycle (from leftward to rightward rotation, and vice versa) had to be produced in 333 and 500 ms in Experiments 1 and 2, respectively. The imposed frequencies differed between both experiments because the cycling frequency at which head movements can be made comfortably is lower than that for arm movements. Only the last 10 s of each trial was analyzed.

Participants were encouraged to move according to their full range of motion. The task required in-phase and/or anti-phase coordination patterns with the upper limbs (Fig. 2). The in-phase coordination mode was characterized by the simultaneous timing of activation of homologous muscle groups for both arms whereas the anti-phase mode required an alternated activation of the homologous muscles.

In Experiment 1, the position of the arms was manipulated, i.e., in adduction close to the legs or abducted at shoulder level, resulting in a modulation of the mutual direction between limb movements in extrinsic space (Fig. 2, panel A). This manipulation results in a factorial design to disentangle the influence of isodirectionality with respect to the egocentric versus allocentric space.

In Experiment 2, head movements were included and the positions of the arms were manipulated in such a way that directionality in extrinsic space was disentangled from muscle homology, such that three experimental conditions of in-phase and anti-phase coordination were obtained: (a) the head moved isodirectionally with the arms (head iso) (Fig. 2, panel B 1 and 2), (b) the

Fig. 1. Top-view of the experimental set-up showing the registration methodology.

head moved non-isodirectionally with the arms that were moved in the same direction (head non-iso) (Fig. 2, panel B 3 and 4), and (c) the head moved isodirectionally with one arm and non-isodirectionally with the other arm, or, one arm moved in a direction that differed from the isodirectional head–arm couple (limb non-iso) (Fig. 2, panel B 5 and 6). Each task condition consisted of 4 registered trials, resulting in a total of 16 trials for Experiment 1 and 24 trials for Experiment 2. A practice session preceded the experimental session to ensure that participants were able to perform all required coordination patterns.

2.3. Procedure

At the start of the experiment, participants were informed about the experimental procedure and the different task conditions. They were instructed to rotate their arms and, if required, their head (Experiment 2) without interruption, using the full range of motion and following the pace provided by the metronome at 180 beats per minute (Experiment 1) and 120 beats per minute (Experiment 2). The pace was lowered in Experiment 2 to allow par-

ticipants to make comfortable head movements. Following the instructions, the participants performed a short practice trial for each condition to ensure that these were well understood. If the instructions were not sufficiently clear, the conditions were demonstrated by moving the participants' limbs passively. The order of the trials was counterbalanced across subjects. Following the "ready" command from the experimenter, an auditory cue indicated the start of a trial.

2.4. Data analyses

The data analyses focused on the quality of interlimb coordination, as determined by means of the relative phase. Through subtraction of the phase angles of two signals measured simultaneously, a quantification of the relation between these signals is obtained. This difference in phase angle, also referred to as the relative phase (Φ), characterizes the coordination pattern observed between two segments [8]. Relative phase was calculated using the formula $\Phi = \theta_1 - \theta_2 = \tan^{-1}[(dX_1/dt)/X_1] - \tan^{-1}[(dX_2/dt)/X_2]$ adapted from Kelso et al. [14], whereby θ_1 refers to the phase angle of the first segment at each sample, X_1 is the position of the segment after rescaling the interval $[-1, 1]$ for each oscillation cycle, and dX_1/dt is the normalized instantaneous velocity. The same notation, with 2 as the subscript, applies to the motion of the other segment. This formula provides a continuous estimate of relative phase. Subsequently, the phase error represented by the absolute deviation from the target relative phase ($\Phi = 0^\circ$ for in-phase or $\Phi = 180^\circ$ for anti-phase) was computed to obtain a measure of coordinative accuracy. To determine relative phase consistency, the S.D. scores of relative phase were computed across each trial and averaged across trials belonging to the same condition.

In summary, two analyses were done. First, the relative phasing between limbs was computed for the trials of Experiments 1 and 2. Secondly, the coordination between the moving head and limbs was determined for the trials of Experiment 2.

2.5. Statistical analyses

In Experiment 1, the statistical analyses focused on the quality of coordination between the limbs. The absolute error (AE) and standard deviation (S.D.) of relative phase were analyzed by means of 2×2 (coordination mode $\times$ direction) analyses of variance (ANOVA). Coordination mode referred to the in-phase versus anti-phase pattern, whereas direction referred to limb movements in the same versus different directions in extrinsic space.

In Experiment 2, the statistical analyses were divided into two parts, i.e., the quality of coordination between the limbs and between the head and limbs. With respect to interlimb coordination, two analyses were conducted. First, a 2×2 (head direction $\times$ coordination mode) ANOVA with repeated measures on both factors was applied to task conditions 1–4 (Fig. 2, panel B 1–4). Head direction consisted of two levels, referring to head rotations in the same (head iso) versus different (head non-iso) directions as compared to both arms. This analysis focused on the role of head direction on interlimb coordination. Second, a 2×2 (segment direction $\times$ coordination mode) ANOVA was applied to conditions 3–6 (Fig. 2, panel B 3–6). Segment direction consisted of two levels whereby either the head moved non-isodirectionally with the isodirectional arm–arm couple (head non-iso) or one arm moved non-isodirectionally with the isodirectional head–arm couple (limb non-iso). The latter analysis compared the effect of incompatible head versus arm movements on the quality of coordination. The same analyses were applied to the coordination data between the head and limbs. In the latter case, data were averaged across both body sides because statistical analysis did not reveal any differences between the left and right side. The level of significance was set at $\alpha = 0.05$.

3. Results

The results of Experiments 1 and 2 will be discussed consecutively. The absolute error and standard deviation of relative phase ($AE\Phi$ and $S.D.\Phi$) were used to quantify coordination accuracy and stability, respectively. A complete statistical report of all dependent measures is provided in Tables 1 and 2.

Fig. 2. Overview of the experimental conditions for Experiment 1 (panel A) and Experiment 2 (panel B).

Table 1

Results of the statistical analysis of Experiment 1 (coordination between limbs, relative phase) with respect to $AE\Phi$ and $S.D.\Phi$ with respect to the homologous limbs

	d.f.	F	
		AE	S.D.
Coordination mode	1–10	39.54***	58.72***
Direction	1–10	8.82*	6.86*
Coordination mode $\times$ direction	1–10	5.22*	7.77*

* $p < .05$.

*** $p < .001$.

3.1. Experiment 1: effect of symmetrical limb position manipulations on interlimb coordination

The 2×2 (coordination mode $\times$ direction) ANOVA revealed significant main effects for coordination and direction with respect to $AE\Phi$ and $S.D.\Phi$ (Table 1).

In general, scores were lower during in-phase ($AE\Phi = 14.96^\circ$, $S.D.\Phi = 12.38^\circ$) than during anti-phase coordination ($AE\Phi = 47.39^\circ$, $S.D.\Phi = 39.88^\circ$). Both measures were also lower during isodirectional ($AE\Phi = 27.13^\circ$, $S.D.\Phi = 23.39^\circ$) than during non-isodirectional coordination of the limbs ($AE\Phi = 35.21^\circ$, $S.D.\Phi = 28.88^\circ$). Also the interaction between

Table 2

Results of the statistical analysis of Experiment 2 (relative phase) with respect to $AE\Phi$ and $S.D.\Phi$ during coordination of the homologous limbs (A) and coordination between head and limbs (B)

	d.f.	<i>F</i>	
		AE	S.D.
(A) Coordination between both arms			
Head direction × coordination mode			
Head direction	1–17	9.44**	33.58***
Coordination mode	1–17	2.65	5.50*
Head direction × coordination mode	1–17	8.16**	9.58**
Segment direction × coordination mode			
Segment direction	1–17	8.61**	21.23***
Coordination mode	1–17	6.55*	5.67*
Segment direction × coordination mode	1–17	0.91	1.47
(B) Coordination between the head and the limbs			
Head direction × coordination			
Head direction	1–17	144.00***	85.32***
Coordination mode	1–17	0.26	9.74**
Head direction × coordination mode	1–17	8.49**	31.55***
Segment direction × coordination			
Segment direction	1–17	95.29***	69.46***
Coordination mode	1–17	15.37***	0.04
Segment direction × coordination mode	1–17	26.08***	57.21***

* $p < .05$.** $p < .01$.*** $p < .001$.

both factors reached significance for both measures and is displayed for $S.D.\Phi$ in Fig. 3. Whereas the adopted direction did not differentially affect the in-phase coordination mode ($p > 0.05$), it had a significant effect on anti-phase coordination ($p < 0.05$). Anti-phase coordination was performed with higher accuracy and consistency when the limbs moved in the same as compared to different directions. This suggests that anti-phase coordination was more sensitive to extrinsic directional constraints than in-phase coordination. The same pattern was observed in the results obtained for $AE\Phi$ (not shown).

Fig. 3. Interaction between direction and coordination mode with respect to $S.D.$ of relative phase ($p = 0.019$) between the limbs (Experiment 1).

3.2. Experiment 2: effects of head movements on interlimb coordination

We will first focus on the coordination between the homologous limbs and subsequently on the coordination between the head and limbs (head–limb coordination) (Fig. 2B, conditions 1–4).

3.2.1. Interlimb coordination

Conditions 1–4 (Fig. 2B) were analyzed by means of a 2×2 (head direction $\times$ coordination mode) ANOVA on the coordination performance between the arms as indicated by $AE\Phi$ and $S.D.\Phi$ (see Table 2A).

The main effect of head direction was significant for both measures, showing more stable and accurate coordination between both arms when the head moved in the same (head iso: $AE\Phi = 17.10^\circ$, $S.D.\Phi = 17.69^\circ$) than in the opposite direction as compared to both arms (head non-iso: $AE\Phi = 21.23^\circ$, $S.D.\Phi = 27.48^\circ$). The main effect for coordination mode was only significant for $S.D.\Phi$, showing more stable coordination when the limbs were moved according to the in-phase ($S.D.\Phi = 20.94^\circ$) as compared to the anti-phase mode ($S.D.\Phi = 24.23^\circ$).

The head direction $\times$ coordination mode interaction reached significance for $AE\Phi$ and $S.D.\Phi$. The results revealed that anti-phase coordination was more sensitive to the directional influence of head rotation than in-phase coordination (Fig. 4).

While the anti-phase pattern was performed slightly better than the in-phase pattern during isodirectional head move-

Fig. 4. Interaction between head direction and coordination mode with respect to AE and S.D. of relative phase ($p = 0.019$), with respect to the homologous limbs. The respective experimental conditions are depicted in the lower panel.

ments, it was performed worse when non-isodirectional head movements were produced. Post hoc analyses showed that only a significant difference between both head conditions was observed for the anti-phase but not for the in-phase coordination mode: $p < 0.0002$ for S.D. Φ , and $p < 0.025$ for AE Φ . This suggests again the higher vulnerability of anti-phase coordination to directional (in)compatibility effects induced by the head.

For conditions 3–6 (Fig. 2B), the data were analyzed by means of a 2×2 (segment direction $\times$ coordination mode) ANOVA on AE Φ and S.D. Φ separately (see Table 2, panel A). Segment direction consisted of two levels referring to either the head that moved in opposition to both arms or the arm that moved in opposition to the head and the other arm. Both main effects reached significance for AE Φ and S.D. Φ . The main effect for segment direction suggested a greater disturbance of stability and accuracy between both arms when the head (AE $\Phi = 22.18^\circ$, S.D. $\Phi = 27.48^\circ$) as compared to the arm (AE $\Phi = 17.76^\circ$, S.D. $\Phi = 18.38^\circ$) was moved in opposite directions. This suggests that the head direction had a powerful influence on coordination of the homologous arms.

The main effect of coordination mode also reached significance for both measures: lower error scores were obtained during in-phase (AE $\Phi = 17.37^\circ$, S.D. $\Phi = 20.48^\circ$) than anti-phase coordination (AE $\Phi = 22.57^\circ$, S.D. $\Phi = 25.38^\circ$). The interaction effects did not reach significance. Overall, anti-phase coordination was again more sensitive to directional interference,

whereas in-phase coordination appeared to be more resistant to these manipulations, presumably because it benefited from homologous muscle coupling.

3.2.2. Head–limb coordination

The analysis of head–limb coordination focused on the quality of coordination between the head and limbs and was conducted for conditions 1–4 and 3–6 separately. The results of the statistical analysis are presented in Table 2B. With respect to conditions 1–4, the head direction $\times$ coordination mode ANOVA revealed a significant main effect for head direction, implying increasing AE Φ and S.D. Φ scores when the head moved in the opposite as compared to the same direction as both arms. Mean scores were AE $\Phi = 32.63^\circ$, S.D. $\Phi = 25.72^\circ$ for the head-iso condition and AE $\Phi = 64.64^\circ$, S.D. $\Phi = 43.41^\circ$ for the head non-iso condition. The main effect of coordination mode also reached significance for S.D. Φ . The coordination mode $\times$ head direction interaction reached significance for both AE Φ and S.D. Φ measures (see Table 2B) and is shown in Fig. 5. The main result is that both AE Φ and S.D. Φ scores increased from the condition with isodirectional to non-isodirectional head movements. Additionally, we found that non-isodirectional head movements lead to an increase of both AE Φ and S.D. Φ scores for anti-phase coordination, whereas for in-phase coordination there was a large increase of AE Φ and only a moderate increase of S.D. Φ . This latter difference between the AE Φ and S.D. Φ measurement might result from the fact that AE Φ reflects a complex combination of the constant error and the standard deviation. In other

Fig. 5. Interaction between head direction and coordination mode with respect to AE ($p=0.006$) and S.D. of relative phase ($p=0.000$) for head–limb coordination. The respective experimental conditions are depicted in the lower panel.

Fig. 6. Interaction between segment-direction and coordination mode with respect to AE and S.D. of relative phase for head–limb coordination. The respective experimental conditions are depicted in the lower panel.

words, it can be assumed that non-isodirectional head movements induced a constant phase offset in the in-phase pattern of the arms.

However, the most important result of the coordination mode $\times$ head direction interaction is that both the in-phase and the anti-phase coordination pattern deteriorated when the head moved non-isodirectionally as compared to isodirectional.

Analysis of conditions 3–6 resulted in a significant main effect for segment direction: higher $AE\Phi$ and $S.D.\Phi$ scores were found during the condition with non-isodirectional head movements ($AE\Phi = 64.64^\circ$, $S.D.\Phi = 43.41^\circ$) as compared to the non-isodirectional limb movements ($AE\Phi = 33.92^\circ$, $S.D.\Phi = 28.78^\circ$). Thus, the coupling between the head and both arms was more accurate and consistent when the head was moved isodirectionally with one arm and non-isodirectionally with the other (limb non-iso) as compared to non-isodirectionally with both arms (head non-iso). The main effect of coordination mode was only significant for $AE\Phi$, demonstrating that head–limb coordination was less accurate during in-phase ($AE\Phi = 56.12^\circ$) than during anti-phase coordination of the arms ($AE\Phi = 42.44^\circ$).

The interaction effect reached significance for both measurements (Fig. 6). With respect to $AE\Phi$, head–limb coordination showed lower error scores when the arm moved non-isodirectionally with the remaining two segments (limb non-iso) as compared to the head (head non-iso) but the decreases in error were more pronounced during anti-phase than during in-phase coordination. In other words, $AE\Phi$ scores pertaining to head–limb coordination decreased from the condition with non-isodirectional head movements with both limbs (head non-iso) to the condition with isodirectional head movements with one of both limbs (limb non-iso) and this effect was more pronounced during anti-phase coordination.

With respect to $S.D.\Phi$, the interaction conveyed that head–limb coordination was less consistent during anti-phase than during in-phase coordination when the head moved non-isodirectionally with the two arms, whereas, the opposite effect was obtained when the arm moved non-isodirectionally with a head–limb couple. In other words, whereas head–limb coordination was not much affected by the direction of the arm or head segment during in-phase coordination, $S.D.\Phi$ decreased (improved) dramatically from the head non-iso to the limb non-iso condition during anti-phase coordination. Thus, head–limb coordination improved when the head was isodirectionally coupled with one of both arms as compared to non-isodirectional head motions with both arms.

4. Discussion

Research on interlimb coordination has demonstrated that direction plays an important role in the organization and control of coordination patterns. However, it is still a matter of debate whether direction should be understood within the context of an intrinsic or extrinsic reference frame. Neural coding of spatial features of movement and their associated reference frames is one of the most dominant themes within the

motor neurosciences. It is also an important topic within the context of interlimb coordination because directional compatibility comes into play when more than one limb is moved. In this respect, we have referred to two general principles: egocentric and allocentric [23,24]. The first refers to the longitudinal axis of the body as an intrinsic organizing principle whereby simultaneous limb movements towards and away from the body midline are more preferred than other patterns. This is often associated with the simultaneous timing of activation of homologous muscle groups. The allocentric constraint refers to a general preference to move the limbs in the same direction in extrinsic space. An important question that requires further attention pertains to the generalizability of these principles as well as their potential interactions. Moreover, combining movements of the limbs with other body segments prompt us to consider their degree of directional compatibility.

In the present study, we used two experimental strategies to explore the role of directional constraints in interlimb coordination. First, use was made of posture manipulations to dissociate between muscle homology and directionality in extrinsic space. Second, head movements were added to patterns of bimanual coordination to investigate their impact on the quality of interlimb coordination as well as head–limb coordination.

4.1. Dissociating muscle homology and directionality in extrinsic space

Consistent with previous studies [4,18,20,21,24], Experiment 1 demonstrated that in-phase coordination between the arms was generally more accurate and consistent than anti-phase coordination. By comparing the adducted and abducted limb postures, it was possible to disentangle directionality in extrinsic space from muscle homology. More specifically, bimanual in-phase patterns with the limbs in adducted versus abducted posture were associated with non-isodirectional and isodirectional movements in extrinsic space, respectively. The converse arrangement was obtained during anti-phase coordination, i.e., the adducted posture was associated with isodirectional and the abducted posture with non-isodirectional movements. The findings revealed that in-phase coordination, characterized by the simultaneous activation of homologous muscle groups, was resistant to posture manipulations. This suggests that direction in extrinsic space did not have a prominent effect on the accuracy/stability of interlimb coordination characterized by neuromuscular coupling. Conversely, anti-phase coordination was performed more successfully when associated with isodirectional as compared to non-isodirectional motions in extrinsic space. Thus, the influence of extrinsic direction became more prevalent in the absence of muscle homology whereby isodirectionality in extrinsic space contributed to stabilization of anti-phase coordination patterns. These observations are generally consistent with earlier work in which the interplay between both coordination constraints was demonstrated during bimanual circle drawing, with the egocentric constraint dominating over the allocentric constraint [23,24].

4.2. The influence of head motions on bimanual coordination

In Experiment 2, the influence of head movements on bimanual coordination was studied with special emphasis on the mediating role of directional (in)compatibility. Our principal objectives were (1) to compare the influence of isodirectional versus non-isodirectional head motions on bimanual coordination, and (2) to compare the differential influence of head versus arm motions as a directional (de)stabilizer on the quality of coordination.

With respect to the first question, arm position was manipulated in such a way that the influence of head motion direction on bimanual coordination could be studied with directionally comparable in-phase and anti-phase movements (Fig. 2, conditions 1–4). More specifically, by modulating arm posture, we obtained in-phase (muscle homology) and anti-phase (no muscle homology) coordination patterns that were both characterized by isodirectional movements in extrinsic space and therefore only differed with respect to the timing of activation of the homologous muscle groups. The impact of head movements that were either isodirectional versus non-isodirectional with the bimanual limb patterns was studied.

The findings demonstrated that the in-phase patterns were hardly affected by directionality of head motion. Conversely, the anti-phase patterns were slightly more accurate and stable than in-phase during isodirectional head motions but clearly less accurate and stable during non-isodirectional head motions. These observations underscore the robust nature of coordination patterns based on muscle homology, even in the absence of symmetric arm positions. Conversely, anti-phase patterns were more vulnerable to directional relationships among body segments in extrinsic space. When the head moved along with both arms, an isodirectional relation between the head and arms was preferred above a non-isodirectional relationship. These observations were also supported by the analysis of the coordination between the head and each of the upper limbs: $AE\Phi$ and $S.D.\Phi$ scores were lower during isodirectional than non-isodirectional head motions. In other words, isodirectional head movements became easily integrated with the overall coordination pattern, whereas head–limb coupling was poor when the head moved anti-directional with the limbs. The present results are generally consistent with earlier work addressing the impact of head motions on the quality of coordination between the homologous limbs (upper or lower) [16]. However, postures were symmetrical in the latter study, such that in-phase patterns were associated with non-isodirectional movements and anti-phase patterns with isodirectional movements. Consequently, the quality of in-phase (mirror symmetric) homologous limb patterns was affected by addition of head movements whereas anti-phase patterns were not. This is because the head rotated in the same direction in extrinsic space as both limbs during anti-phase coordination, whereas this solution was not possible during in-phase coordination. These findings point to the important role of extrinsic direction on interlimb coordination.

In a second analysis, the influence of head versus arm motions within the three-segment coordination pattern was determined.

For this purpose, we compared whether coordination between the limbs was differentially affected when either the head or one limb moved anti-directional with the other two segments (Fig. 2, conditions 3–6). The findings revealed that bimanual coordination was much less stable and accurate when the head as compared to the arm was moved anti-directionally with the remaining segments. This was confirmed during both the in-phase and anti-phase coordination modes. This was also reflected by the analysis of head–limb coupling, which was much less stable and accurate when the head was moved non-isodirectionally with the other segments, as compared to the arm (Fig. 6). Thus, non-isodirectional head movements lead to a more pronounced disruption of head–limb coupling than non-isodirectional arm movements. This destabilizing effect of non-isodirectional head movements was particularly pronounced during anti-phase coordination.

In summary, the present findings revealed that direction is a principal constraint during the generation of patterns of multilimb coordination. This is not surprising because single cell recording studies have pointed to the modulation of neuronal activity as a function of movement direction [7,11]. Furthermore, it has been shown that bimanual movements with incompatible directional specifications induce increased activity in a parieto-premotor network, relative to compatible directional specifications [26]. This points to the recruitment of extra neural resources to cope with or overcome directional interference between the limbs. Whereas converging directional relationships hardly impose increased demands on the central nervous system, incompatible directions between movement segments will require additional neural resources in cortical areas involved in spatial planning and organization of movement, unless these motions can be integrated into a unified command structure for all effectors. During bimanual coordination, direction can be interpreted within the context of intrinsic and extrinsic reference frames. Intrinsic directional relationships between limbs that are supported by simultaneous activation of homologous muscle groups are very prominent and promote a high degree of coordinative stability. However, when muscle homology is given up, direction in extrinsic space starts playing a more critical role: higher coordinative accuracy and stability is obtained when limbs move in the same direction in extrinsic space. Addition of head movements plays an important role in the balance between directional compatibility versus incompatibility. Overall, the findings support a coalition between egocentric and allocentric coordination constraints whereby the balance between both constraints is mediated by head motions. One has to keep in mind, though, that these findings were obtained for the specific task used in the present experiment. Further research on other head–limb coordinations tasks is needed to confirm the present findings.

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References

- [1] Baldissera F, Cavallari P, Civaschi P. Preferential coupling between voluntary movements of ipsilateral limbs. *Neurosci Lett* 1982;34:95–100.
- [2] Bernstein N. The coordination and regulation of movements. Oxford: Pergamon Press; 1967.
- [3] Bogaerts H, Swinnen SP. Spatial interactions during bimanual coordination patterns: the effect of directional compatibility. *Motor Control* 2001;5:183–99.
- [4] Byblow WD, Summers JJ, Semjen A, Wuyts IJ, Carson RG. Spontaneous and intentional pattern switching in a multisegmental bimanual coordination task. *Motor Control* 1999;3:372–93.
- [5] Carson RG, Thomas J, Summers JJ, Walters MR, Semjen A. The dynamics of bimanual circle drawing. *Q J Exp Psychol A* 1997;50:664–83.
- [6] Fuchs A, Jirsa VK. The HKB model revisited: how varying the degree of symmetry controls dynamics. *Hum Movement Sci* 2000;19:425–49.
- [7] Georgopoulos AP, Ashe J, Smyrnis N, Taira M. The motor cortex and the coding of force. *Science* 1992;256:1692–5.
- [8] Haken H, Kelso JA, Bunz H. A theoretical model of phase transitions in human hand movements. *Biol Cybern* 1985;51:347–56.
- [9] Heuer H, Klein W. Involuntary rotations of a steering device induced by voluntary rotations of the head and maintained eccentric head positions. *J Motor Behav* 1999;31:248–64.
- [10] Heuer H, Klein W. Structural constraints on the coordination of concurrent rotations of the head and a steering device. *Motor Control* 1999;3:39–66.
- [11] Kakei S, Hoffman DS, Strick PL. Muscle and movement representations in the primary motor cortex. *Science* 1999;285:2136–9.
- [12] Kelso JA. Phase transitions and critical behavior in human bimanual coordination. *Am J Physiol* 1984;246:R1000–4.
- [13] Kelso JAS. Dynamic patterns: the self-organization of brain and behavior. Cambridge, MA: MIT Press; 1995.
- [14] Kelso JAS, Scholz JP, Schoner G. Nonequilibrium phase-transitions in coordinated biological motion—critical fluctuations. *Phys Lett A* 1986;118:279–84.
- [15] Klein W, Heuer H. The effects of eccentric head positions on leftward and rightward turns of a handle-bar. *Acta Psychol (Amst)* 1999;103:311–29.
- [16] Meesen R, Levin O, Wenderoth N, Swinnen SP. Head movements destabilize cyclical in-phase but not anti-phase homologous limb coordination in humans. *Neurosci Lett* 2003;340:229–33.
- [17] Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 1971;9:97–113.
- [18] Park H, Collins DR, Turvey MT. Dissociation of muscular and spatial constraints on patterns of interlimb coordination. *J Exp Psychol Hum Percept Perform* 2001;27:32–47.
- [19] Salesse R, Oullier O, Temprado JJ. Plane of motion mediates the coalition of constraints in rhythmic bimanual coordination. *J Motor Behav* 2005;37:454–64.
- [20] Semjen A, Summers JJ, Cattaert D. Hand coordination in bimanual circle drawing. *J Exp Psychol Hum Percept Perform* 1995;21:1139–57.
- [21] Summers JJ, Byblow WD, Bysouth-Young DF, Semjen A. Bimanual circle drawing during secondary task loading. *Motor Control* 1998;2:106–13.
- [22] Swinnen SP, Dounskaia N, Duysens J. Patterns of bimanual interference reveal movement encoding within a radial egocentric reference frame. *J Cogn Neurosci* 2002;14:463–71.
- [23] Swinnen SP, Jardin K, Meulenbroek R, Dounskaia N, HofkensVanDen-Brandt M. Egocentric and allocentric constraints in the expression of patterns of interlimb coordination. *J Cogn Neurosci* 1997;9:348–77.
- [24] Swinnen SP, Jardin K, Verschueren S, Meulenbroek R, Franz L, Dounskaia N, et al. Exploring interlimb constraints during bimanual graphic performance: effects of muscle grouping and direction. *Behav Brain Res* 1998;90:79–87.
- [25] Temprado JJ, Swinnen SP, Carson RG, Tourment A, Laurent M. Interaction of directional, neuromuscular and egocentric constraints on the stability of preferred bimanual coordination patterns. *Hum Mov Sci* 2003;22:339–63.
- [26] Wenderoth N, Debaere F, Sunaert S, Van Hecke P, Swinnen SP. Parieto-premotor areas mediate directional interference during bimanual movements. *Cerebral Cortex* 2004;10:1–11.