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The control of amplitude and direction in a bimanual coordination task

Zhujun Pan[a,*], Arend W.A. Van Gemmert[b]

[a] Department of Kinesiology, Mississippi State University, Mississippi State, MS 39762, USA
[b] School of Kinesiology, Louisiana State University, Baton Rouge, LA 70803, USA

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ABSTRACT

Bimanual coordination requires task-specific control of the spatial and temporal characteristics of the movements of both hands. The present study focused on the spatial relationship between hand movements when their amplitude and direction were manipulated. In the experiment in question, participants were instructed to draw two lines simultaneously. These two lines were instructed to be drawn in mirror symmetric or perpendicular directions of each other while the length was instructed to be the same or different. The coordinative quality of amplitude control was compared when the task required symmetric and asymmetric bimanual spatial coordination patterns. Results showed that the amplitude accuracy decreased when different amplitudes and/or directions had to be generated simultaneously. The coordinative quality of direction was also compared when the task required symmetric and asymmetric bimanual spatial coordination patterns. Unlike amplitude, the direction accuracy was largely independent of coordination symmetry/asymmetry of direction or amplitude. The results suggest that the coordinative quality of amplitude control does not only interfere with amplitude asymmetry, but it also interferes with direction asymmetry. Moreover, in bimanual coordination amplitude control is more vulnerable to the influence of direction control demands than vice versa.

1. Introduction

Many voluntary actions involve bimanual coordination, that is, the simultaneous integration of movements of the two upper-limbs. When the two upper-limbs produce mirror or isomorphic actions, it is referred to as symmetric bimanual coordination, whereas it is called asymmetric bimanual coordination when different movements are required. Research has shown that tasks involving symmetrical movements of the two hands are relatively stable and precise, whereas the stability and accuracy of the performance usually declines when the action requires asymmetric bimanual coordination (Eliassen, Baynes, & Gazzaniga, 1999; Franz, Elliassen, Ivry, & Gazzaniga, 1996; Semjen, 2002; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). The difficulty of producing asymmetry bimanual movements has been denoted in the literature when discussing the “interferences” in bimanual coordination (Swinnen, Dounskaia, Levin, & Duysens, 2001). Traditionally, the tendency for symmetry (eg. In-phase movements) was defined as the co-activation of homologous muscles (Kelso, 1984). More recently, the emphasis has been shifting toward the role of perception and representation of action (Franz, Kerzel, Knoblich, & Prinz, 2001; Ivry, Diedrichsen, Spencer, Hazeline, & Semjen, 2004), and the possibly distinctive origins for different types of interferences (i.e. temporal vs. spatial interference; discrete vs. continuous movement interference) (Franz et al., 1996; Spencer et al., 2003).

* Corresponding author at: Department of Kinesiology, Mississippi State University, Mail Stop 6186, 241 McCarthy Gymnasium, Mississippi State, MS 39762, USA.
E-mail addresses: zp147@msstate.edu (Z. Pan), gemmert@lsu.edu (A.W.A. Van Gemmert).

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Temporal interference in bimanual coordination is the tendency to initiate and terminate movements of the two hands synchronously, and therefore it is difficult to produce complex movement phases (Haken, Kelso, & Bunz 1985; Kelso, Southard, & Goodman, 1979; Marteniuk, MacKenzie, & Baba, 1984; Semjen 2002; Semjen & Ivry, 2001). Spatial interference is the tendency of the two hands to produce movements with similar amplitude and/or in a mirror direction (Spijkers & Heuer, 1995; Wenderoth, Puttemans, Vangheluwe, & Swinnen, 2003). Ivry et al. (2004) reviewed interference reported in many bimanual coordination studies and identified an important discrepancy in temporal and spatial interference, suggesting distinct origins. There are two generally accepted hypotheses regarding the origins of temporal interference, depending on the type of motor task performed. Based on studies by Ivry and his colleagues (Franz et al., 1996; Semjen, 2002; Spencer, Semjer, Yang, & Ivry, 2006; Spencer et al., 2003), the temporal interference observed in discrete/discontinuous bimanual movements (i.e. simultaneously drawing one circle with each hand) is associated with an explicit representation of the temporal goal, which is constrained by the limited ability of the internal timing system in the cerebellum to represent complex temporal relationships. On the other hand these studies also showed that temporal interference in continuous tasks (i.e. simultaneously drawing repetitive circle with two hands) is not correlated with temporal interference observations in discontinuous tasks, and thus it is hypothesized that this pattern arises from interactions between time-varying spatial representations on the cortical level (Franz et al., 1996; Semjen, 2002; Spencer et al., 2003; Spencer et al., 2006). Spencer et al. (2003) found that patients with cerebellar damage exhibit deficits in discontinuous but not in continuous bimanual movements, providing evidence supporting a distinctive origin of temporal interference for discrete and continuous tasks. With respect to the spatial interference in bimanual coordination, which is the focus of the current study, a series of bimanual coordination studies imply that the spatial interference strongly relies on the cognitive representation of the task (Diedrichsen, Hazeltime, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003; Mechsner, Kerzel, Knoblich, & Prinz, 2001). As summarized by Ivry et al. (2004), asymmetric bimanual coordination induces primarily lateral (left-dominant) cortical activation and it relies on the corpus callosum to share the goal representations with the other hemisphere. Moreover, the study of Eliassen et al. (1999) showed that the posterior region of the corpus callosum might be a major contributor to directional coupling in bimanual coordination tasks due to an observation that an epilepsy patient started to show spatial uncoupling in a directional asymmetric bimanual task after the resection of the posterior region of the corpus callosum. In other words, two spatial representations guiding spatial specifications of the bimanual task are produced in the left (dominant) hemisphere for movements on the right and left side of the working space respectively. The spatial interference arises from the overlap between these two spatial representations (Diedrichsen et al., 2001; Diedrichsen et al., 2003).

Spatial interference could occur when people draw two different amplitudes. The difference in amplitude between motions of the right and left hand normally results in an assimilation of movement lengths, i.e., the shorter amplitude tends to overshoot, whereas the longer amplitude tends to undershoot (Franz, 1997; Ryu & Buchanan, 2004; Spijkers & Heuer, 1995; Swinnen et al., 2001). Similar interference effects can also be observed in directional incongruent conditions where the directional trajectories become mutually coupled/mirrored (Eliassen et al., 1999; Franz et al., 1996; Wenderoth, Debaere, Sunaert, & Swinnen, 2005; Wenderoth et al., 2003). The majority of the studies focusing on spatial interference have investigated the constraining role of direction and amplitude separately and independently. Even so, interference findings in direction and amplitude were commonly discussed together without distinction between the two, which was based on an unverified assumption that direction and amplitude follow the same pattern of interference. In the domain of bimanual coordination, the relationship between amplitude and direction is largely unknown; even though it is of theoretical importance in comprehensively understanding the mechanisms of bimanual coordination. A few studies have tried to investigate whether direction and amplitude are controlled independently or interdependently in bimanual coordination. For instance, the studies of Swinnen et al. (2001) and Wenderoth et al. (2005) revealed some level of interdependence, as well as some degree of independence between amplitude and directional parameters in bimanual coordination, indicating that amplitude and direction are mediated by distinct but partially overlapping neural resources.

Swinnen et al. (2001) studied the spatial assimilation effect in a drawing task with different drawing directions and amplitudes for the right and the left hand. In their study, participants were asked to draw with the left hand (which in this study was synonymous for the non-dominant hand) vertical lines, while they drew with the right hand (i.e., in this study the dominant hand) lines in eight different directions. They also asked participants to draw the lines either 8 cm or 16 cm long. For each hand, participants' performance executed during the bimanual task was compared to performance of the same task executed unimanually. The results suggested that amplitude regulates the directional interference, whereas direction only partly affects amplitude interference. To further understand the relationship between amplitude and direction, Wenderoth et al. (2005) applied a functional magnetic resonance imaging (fMRI) protocol while participants performed a bimanual drawing task in which the movement direction and amplitude was manipulated per condition. Performance of each hand was analyzed. The behavioral results supported the interdependence of direction and amplitude in bimanual coordination tasks. It was shown that direction had an influence on the interference of amplitude. In addition, the brain imaging data showed that producing bimanual movements with different amplitude or different direction activated similar cortical areas (i.e. bilateral superior parietal-premotor areas). However, additional bilateral networks (i.e. bilateral dorsolateral prefrontal cortex, the anterior cingulate gyrus, and the supramarginal gyrus) are activated only when bimanual movements with different amplitudes are produced, while they are not activated when different directions are produced.

The studies of Swinnen and colleagues (Swinnen et al., 2001; Wenderoth et al. 2005) provided initial insights into the relationship between direction and amplitude in bimanual coordination tasks. The two studies analyzed the movement accuracy of each hand separately by comparing performance of each hand in a bimanual task to performance of the same hand when the task was performed unimanually. This analysis protocol only indirectly studied the quality of coordination between the two hands. The present study involves an analysis of the parameters representing the quality of coordination between the hands in different coordinative conditions directly, with the aim to more thoroughly understand the relationship between the direction and amplitude in bimanual coordination tasks.

2. Methods

2.1. Participants

Eighteen young adults (20.69 ± 0.79 (mean ± standard deviation, range 20–22) were recruited from the Baton Rouge community. All participants were asked to fill out a short questionnaire to determine eligibility to participate in the study. Anyone who indicated to have a history of neurological problems, had current vision and/or hearing problems, and/or was unable to use a pen due to a dexterity problem, was excluded from participation. All participants were right hand dominant, which was defined by having a laterality quotient of 0.6 or higher on the Edinburgh Handedness Inventory (Oldfield, 1971). Upon arrival participants read and signed the informed consent form. The protocol of the study was approved by the Human Subjects Institutional Review Board of Louisiana State University.

2.2. Apparatus

A WACOM Intuos digitizer tablet (12 × 18 inches), two digital pens (WACOM GP-100), a 1 by 18 in. wooden stick, and two 20 in. monitors (monitor-1 and monitor-2) were used to capture movements, display stimuli, and present feedback. The tablet recorded the X- and Y-position of each pen (one in each hand) with a sampling rate of 100 Hz and spatial resolution of 0.001 cm. The wooden stick was placed on the vertical midline of the tablet to constrain the movement area of the pen manipulated with each hand. This protocol was used to avoid the possibility that the hands would touch each other or movements would cross over into the working area of the other hand. The digitizer and hands were covered by a box with an opening for the hands and a small curtain in front of the opening to block vision of the hands and pen during the bimanual task. The experimental procedures were programmed in MovAlyzeR (NeuroScript LLC, Tempe, Arizona, USA) running on a PC (Dell Dimension 8400) with a customized MatLab program that was integrated to display the recorded movements after each trial. Monitor-1 was placed approximately 80 cm in front of the participants, while Monitor-2 was placed above Monitor-1. Prior to the start of the go-stimulus, participants needed to study an example of the required movement direction and amplitude shown on Monitor-1. After completion of the bimanual coordination task, Monitor-2 gave participants feedback about their actual movement trajectories.

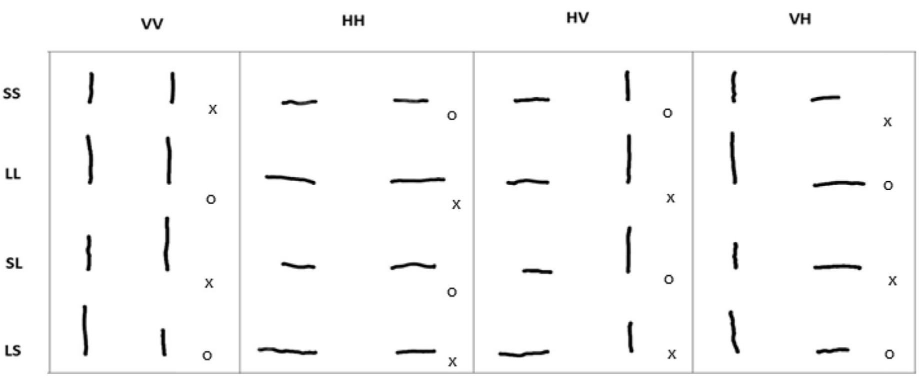
2.3. Experimental design

Participants were required to make with each hand either a short line (3 cm) or a long line (6 cm). Thus, four bimanual coordination tasks regarding the movement amplitudes were possible: “Short-Short”, “Long-Long”, “Short-Long” and “Long-Short”. The target amplitude ratio between the right and the left line was 1 for the “Short-Short” (3 cm:3 cm) and “Long-Long” (6 cm:6 cm) conditions, while the target amplitude ratio between the right and the left line was 2 for the “Short-Long” (6 cm:3 cm) condition and 1/2 for the “Long-Short” (3 cm:6 cm) condition. The possible requirements for the movement direction for each hand were drawing a vertical line (i.e., moving straight forward away from the body) and a horizontal line (i.e., moving from the left to the right for the right hand and moving from the right to the left for the left hand). Thus, there were four possible movement direction conditions for the bimanual coordination task: “Vertical-Vertical”, “Horizontal-Horizontal”, “Horizontal-Vertical”, and “Vertical-Horizontal”. These conditions resulted in 3 different target angles between the two lines: i.e., 0° for the “Vertical-Vertical” condition, 180° for the “Horizontal-Horizontal” condition, and 90° for the “Horizontal-Vertical” and “Vertical-Horizontal” conditions (see Table 1).

These 4 amplitude and 4 direction conditions resulted in 16 variations of the bimanual coordination task. In a pilot study, it was

Table 1

Experimental design (a representation of performance of the left and right hand for each condition).



Note: Rows: SS: Short-Short (i.e., the left hand is required to draw a short line, and so is the right hand); LL: Long-Long; SL: Short-Long; LS: Long-Short; Columns: VV: Vertical-Vertical (i.e., the left hand is required to draw a vertical line, and so is the right hand); HH: Horizontal-Horizontal; HV: Horizontal-Vertical; VH: Vertical-Horizontal.

determined that participants became fatigued after about 30–40 min, while it took about 60–70 min to perform all 16 variations when they had to repeat 8 trials for each condition, which was determined to be the minimum amount of trials per condition to measure reliably the performance capabilities of participants. Therefore, the experimental design was adapted to avoid fatigue (as much as possible) as a confounding factor. The experimental design chosen resulted in having half of the subjects completing 8 conditions (marked as "X"), while the other half of the subjects completed the remaining 8 conditions (marked as "O"), i.e., each participant completed 64 trials. The 8 conditions were selected for diverse combinations of amplitude and direction requirements.

2.4. Procedures

Participants sat comfortably in a chair in front of a table on which a tablet and the two monitors were placed. Participants were instructed to hold one pen in each hand with their normal pen grip. Each trial contained three sequential parts: presentation of two lines showing the required movements, producing the bimanual coordination task, and receiving feedback. A trial started when two circles, indicating the start positions, were shown on Monitor-1. After participants placed the right pen in the right start position and the left pen in the left start position, the circles (i.e., start positions) disappeared and two lines showing the required movement trajectories were shown on Monitor-1. These lines, one on the right and one on the left side, showed the required movement direction and amplitude for each hand. For instance, if the lines showed a 3 cm vertical line on the left side and a 6 cm horizontal line on the right side (the "Short-Long" amplitude and "Vertical-Horizontal" direction condition), it meant that the participant needed to produce a short vertical line on the left with the left hand and a long horizontal line on the right with the right hand, i.e., the two lines would require to have a 90° angle and an amplitude ratio of a ½. Participants were required to keep the tip of both pens within the area depicted by the circles indicating the start positions while the lines were shown which specified the required movement directions and amplitudes (it should be noted that the participants were required not to move the pens while the lines were shown). The presentation of the lines indicating the required bimanual coordination task was shown for a random duration between 5 and 8 s. When the lines disappeared, a loud beeping sound was presented which indicated that the participant should start the bimanual movement task. The participants were instructed to start the bimanual movement task as soon as possible after they heard the beep (i.e., go-signal); however it was emphasized that the hands had to start at the same time; even if this would mean that the reaction would be slower. During execution of the bimanual task no visual feedback was provided about the movements. Furthermore, participants were instructed to draw the lines at their comfortable speed. Moreover participants were reminded that the hands had to start and stop moving at the same time (i.e., they were not allowed to sequence the movements or to hold one pen while the other pen was still moving). In addition they were asked not to lift the pen from the digitizer tablet unless they had finished the bimanual drawing task. After the participant finished the bimanual task, Monitor-2 provided visual feedback of the performed drawing movements together with the required target movements. The movements produced by the participant with both hands were represented by two gray lines (i.e., one for each hand) and the required target movements were represented by two black lines. Participants were instructed to compare their actual movements (i.e., the gray lines) to the required target movements (i.e., the black lines), and to note differences, if any, between their executed movements and the target movements. The experimenter also provided knowledge of results verbally, by stressing performance of each line as well as the relationship between the lines, e.g., "the right line is too long relative to the left line", "the right line is too short relative to the left line" and "the angular difference between two lines is too small".

A practice session was provided before the experimental session started. First, the experimenter explained the procedures to the participants and asked participants to practice drawing two lines with the two hands simultaneously on the tablet till the participant felt familiar with the equipment. After they felt familiar with the equipment, the participant was allowed to get familiar with each of the 8 conditions assigned to him/her by allowing him/her to perform one trial of each condition. This performance of one practice trial for each condition was done to make sure that the participant would understand what was required when presented with the lines before each trial in each of the different conditions. In the experimental session, the participant performed blocks of 8 trials per condition for the grand total of 64 experimental trials. The sequence of assigned 8 conditions (either 8 conditions marked as "X" or 8 conditions marked as "O" conditions) was randomized for every participant.

A trial was excluded for further analysis if any of the following requirements were not met: 1) Participant did not wait for the go-signal to start the bimanual movement task; 2) The movements of the participant had not started within 2 s of go-signal; 3) After movement initiation the participant paused with one or both hands before the bimanual movement task was completed; 4) The participant moved only one hand, i.e., they did not move the hands simultaneously; 5) The participant did not make a complete stop before the participant lifted one or both pens of the digitizer tablet.

2.5. Measurements and statistical analysis

First the movement data were low-pass filtered at 7 Hz with a dual-pass 4th order butterworth filter, after which the onsets and offsets of pen-tip movements were estimated by a fixed criterion of 5% of the peak velocity in the absolute velocity profile. Since the present study main interest was in the coordinative quality between two hands, only variables representing movement coordination were analyzed. Specifically, one innovation of our study is that we used a measure allowing us to measure how coordination is between hands is affected when the direction and/or amplitude is changed within a hand independently of the other hand, i.e., amplitude and direction ratio errors. The ***Amplitude Ratio Error*** was calculated by using the formula:

Table 2
Amplitude error statistics.

	Amplitude Ratio Error			Post-hoc comparison			
Target amplitude	F(3,128)	Sig.	η^2		LL	SL	LS
	6.213	.001*	.127	SS	1.000	.005*	.129
				LL		.003*	.096
				SL			1.000
Target direction	F(3,128)	Sig.	η^2		HH	HV	VH
	16.718	<.001*	.282	VV	.041*	<.001*	<.001*
				HH		.150	<.001*
				HV			.609
Interaction	F(9,128)	Sig.	η^2				
	2.05	.039*	.126				

$\left|\frac{\left[\frac{amplitude(R)}{amplitude(L)} - target\ ratio\right]}{target\ ratio}\right|$. ***Direction Error*** was used to specify the coordinative quality of the direction. The formula used for ***Direction Error*** was $|observedangletargetangle|$. The observed angle was obtained by connecting the onset and offset of each line and computing the angular difference between the two connected lines.

To understand the role of amplitude and direction symmetry on amplitude control, ***Amplitude Ratio Error*** was entered into a two-way ANOVA with the factors target amplitude ("Short-Short", "Long-Long", "Short-Long" and "Long-Short"), and target direction ("Vertical-Vertical", "Horizontal-Horizontal", "Horizontal-Vertical" and "Vertical- Horizontal"). ***Direction Error*** was entered into a two-way ANOVA with the same factors to analyze the influence of direction and amplitude on direction control. If a main effect or interaction proved to be significant ($\alpha \leq 0.05$), bonferroni corrected post hoc analyses were applied.

3. Results

3.1. Amplitude accuracy in different coordinative patterns

The results of the amplitude contained three parts: the main effects of target amplitude on amplitude accuracy, the main effects of target direction on amplitude accuracy, and the interactive effects of amplitude and direction, i.e., the interaction of these factors, on amplitude accuracy.

The statistical results are presented in Table 2. The effect of target amplitude was significant; subsequent post hoc tests revealed that the ***Amplitude Ratio Error*** was greater in the SL (Short-Long) condition compared to in the SS (Short-Short) and LL (Long-Long) conditions. As shown in Fig. 1A, conditions requiring asymmetric amplitudes (i.e., SL and LS) resulted in greater ***Amplitude Ratio Error*** than conditions with symmetric amplitudes (i.e., SS and LL). No significant difference was found between the SS and LL conditions. The greatest ***Amplitude Ratio Error*** was shown in the SL condition, indicating simultaneously drawing the long line with the right hand and the short line with the left hand induced a strong bimanual interference.

Target direction significantly influenced ***Amplitude Ratio Error***. Post-hoc analysis showed less ***Amplitude Ratio Error*** for the VV (Vertical-Vertical) condition than the HH (Horizontal-Horizontal), HV (Horizontal-vertical), and VH (Vertical-horizontal) conditions. Furthermore, ***Amplitude Ratio Error*** was significant smaller for the HH condition compared to the VH condition (see Fig. 1B). In general, conditions requiring asymmetric directions (i.e., HV and VH) induced larger ***Amplitude Ratio Error*** than conditions requiring symmetric directions (i.e., VV and HH). The VV condition was associated with the least ***Amplitude Ratio Error***, implying that drawing two vertical lines simultaneously does influence amplitude accuracy least in a bimanual coordination task.

Significant interactive effects on target amplitude and target direction were found (see Table 2). As shown in Fig. 2A, both amplitude symmetry and direction symmetry influenced the amplitude accuracy in a way that conditions requiring asymmetric amplitudes increased ***Amplitude Ratio Error*** and conditions requiring asymmetric directions amplified ***Amplitude Ratio Error***. Fig. 2B presents ***Amplitude Ratio Error*** in each of the 16 (4 * 4) coordinative conditions. The ***Amplitude Ratio Error*** fell within the range of 0.1–0.2 in the majority of the conditions, indicating that the produced amplitude ratio between the right and left side was 10–20% different from the target ratio in those conditions. The lowest ***Amplitude Ratio Error*** (less than 5%) was observed in the LL + VV condition, in which participants drew simultaneously two vertical lines with the same long amplitude. This indicates that drawing two long vertical lines is the easiest coordination task when accuracy of the movement amplitude is considered. The highest ***Amplitude Ratio Error*** (more than 25%) was found in SL + VH and LS + HV conditions. Thus, it implies that maintaining amplitude accuracy is most difficult when the coordination pattern requires drawing simultaneously a small vertical line with one hand and a long horizontal line with the other hand. In other words, high bimanual interference for amplitude accuracy arises in these two conditions.

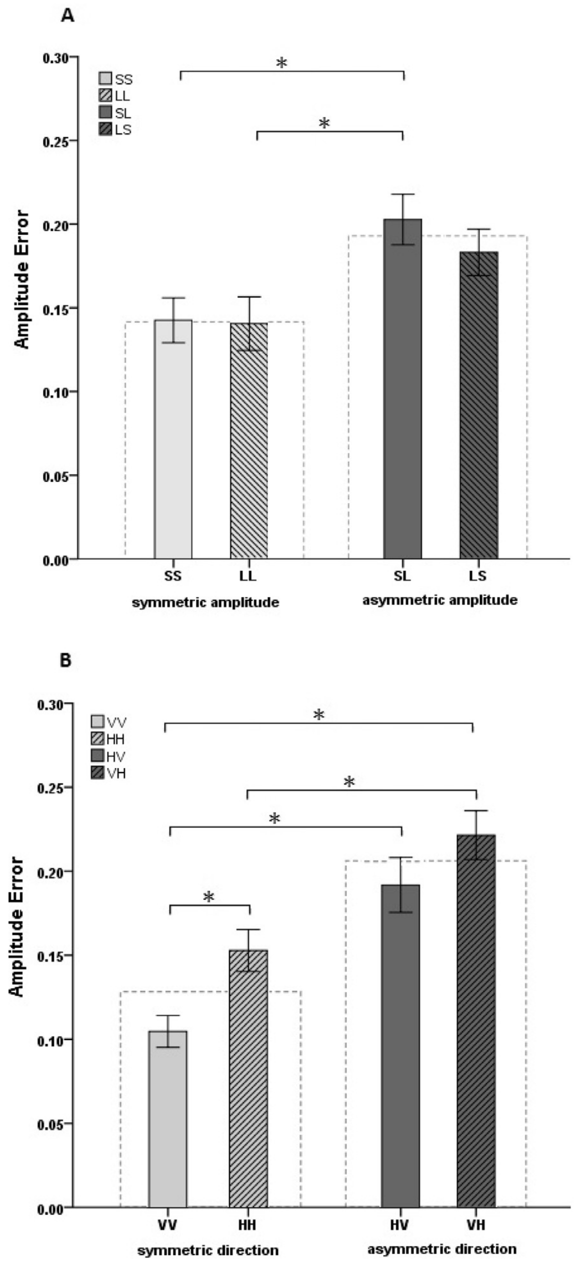


Fig. 1. Mean (Standard Error, SE) ***Amplitude Ratio Error*** as function of amplitude requirement condition (Panel A); SS (gray bar), LL (Gray bar with line filling), SL (black bar), and LS (black bar with line filling). Mean (SE) ***Amplitude Ratio Error*** as function of direction requirement condition (Panel B); VV (gray bar), HH (Gray bar with line filling), HV (black bar) and VH (black bar with line filling).

3.2. Direction accuracy in different coordinative patterns

To understand how different coordinative patterns affect direction accuracy in bimanual coordination, we analyzed the main effects of target direction on direction accuracy, the main effect of target amplitude on direction accuracy and their interactive effects.

The statistical results are presented in Table 3. The factor target direction did not significantly influence ***Direction Error***. ***Direction Error*** proved to be similar for the VV, HH, HV, and VH conditions. The interaction between the required direction and amplitude conditions failed to reach significance for ***Direction Error*** as well. However, the main effect of amplitude requirements proved to be significant. Post-hoc tests revealed that the ***Direction Error*** was lower in the LL condition when compared to in the SS conditions, even though ***Direction Error*** did not significantly differ between the SL and LS, and these asymmetric amplitude coordination conditions also did not significantly differ from either the SS or LL condition (see Fig. 3).

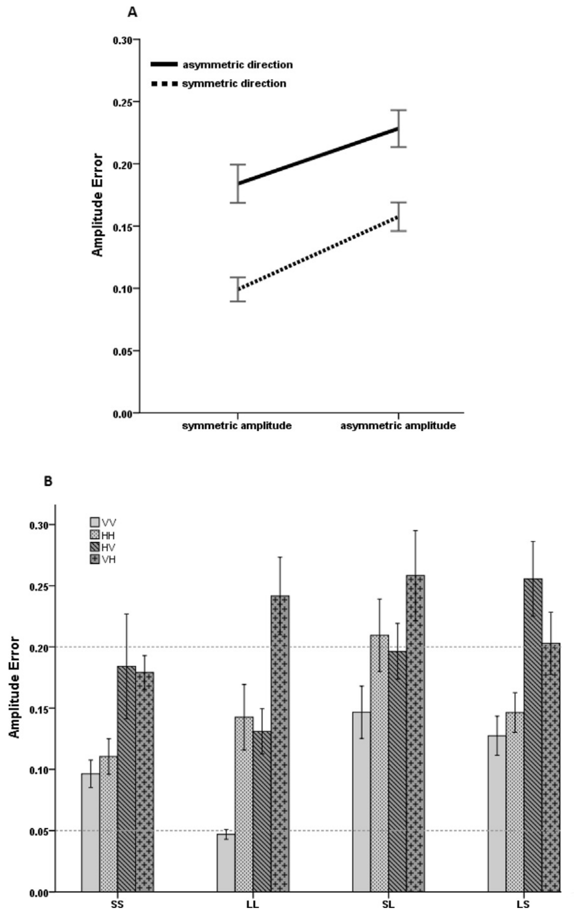


Fig. 2. Mean (SE) ***Amplitude Ratio Error*** as function of bimanual symmetry condition (Panel A). Mean (SE) ***Amplitude Ratio Error*** as function of the 16 bimanual spatial requirement conditions (Panel B).

Table 3
Direction error statistics.

	Direction Error			Post-hoc comparison			
Target direction	F(3,128)	Sig.	η^2				
	1.612	.190	.036				
Target Amplitude	F(3,128)	Sig.	η^2		LL	SL	LS
				SS	.006*	1.000	.296
	4.002	.009*	.086	LL		.182	1.000
				SL			1.000
Interaction	F(9,128)	Sig.	η^2				
	0.308	.971	.021				

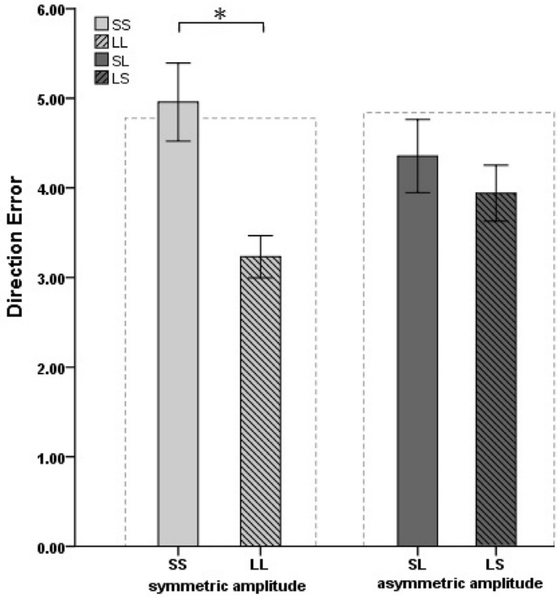


Fig. 3. Mean (SE) ***Direction Error*** as function of amplitude requirement condition; SS (gray bar), LL (Gray bar with line filling), SL (black bar) and LS (black bar with line filling).

4. Discussion

The present study aimed to understand the relationship between amplitude and direction in bimanual coordination. In a dedicated experiment, participants produced bimanual movements with the same and different amplitudes and along the same direction and along perpendicular directions of each other. The accuracy of movement amplitude and direction under different coordinative conditions were quantified. The results revealed that the amplitude accuracy declined when the spatial characteristics of the movements differed. An additional decline in amplitude accuracy was found when participants were required to make movements that differed in both amplitude and direction from each other. These findings suggest a relationship between the amplitude and direction in bimanual coordination when amplitude accuracy is considered. In contrast to the findings for the accuracy on amplitude, the directional accuracy was largely unaffected by either type of spatial incompatibility, indicating independence of directional control in bimanual coordination. Therefore, in accordance with the results of previous studies (Swinnen et al., 2001; Wenderoth et al. 2005), the present study showed a different pattern of results for bimanual interference of amplitude and direction, suggesting some level of interdependence as well as some level of independence in bimanual coordination between the control of amplitude and direction.

A series of studies (Diedrichsen et al., 2001; Diedrichsen et al., 2003) demonstrated the occurrence of spatial interference when hand movements were spatially incompatible, especially when the bimanual movements were symbolically cued. Symbolic cueing in these experiments were conditions in which target shapes were presented to participants whose task was to reproduce these shapes. Thus the action was represented as direction-based trajectories in the symbolic cueing condition. In contrast to these symbolic cueing conditions, these studies also used a cueing condition which can be characterized as a direct cueing condition. Instead of presenting the target shapes, when direct cues are used the shapes are decomposed into multiple target locations (i.e., direct cues), so that participants only need to move from one target location to the next to reproduce the required shapes. Thus, the current study applied a paradigm which used conditions similar to what has been called symbolic cueing conditions; i.e., a sample with a specific target amplitude and direction was presented to participants before they could start the reproduction of the sample. It is hypothesized that, in symbolic cueing conditions, a single spatial code is needed to produce symmetric/mirror movements of the right and left hand. On the other hand, generation of multiple spatial codes is required when asymmetric movements of two hands are needed (e.g., one spatial code for the small movement length requirement of the right hand and another spatial code for the long movement length requirement of the left hand). Spatial interference observed in asymmetric movements arises from the interaction or overlap between the various spatial codes (see for a review Ivry et al., 2004). The notion that spatial interference arises at the representation level is supported by studies (Diedrichsen et al., 2001; Diedrichsen et al., 2003) showing the elimination of reaction time costs in incongruent trials when the movements are cued directly, as well as studies (Bogaerts, Buekers, Zaal, & Swinnen, 2003; de Oliveira, & Barthelemy, 2005; Mechsner et al., 2001) which showed that incongruent trials result in a reduction of spatial interference when transformed visual feedback is provided in such a way that the sensory information becomes symmetric.

A study of Wenderoth et al. (2005) revealed that amplitude and direction are mediated by distinct but partially overlapping neural resources. Specifically, when a task requires coordination resulting in amplitude asymmetry the superior parietal-premotor networks recruited bilaterally are similar as the networks recruited when a task requires coordination resulting in directional asymmetry. However, in contrast to tasks with directional coordination asymmetry, the interference due to amplitude requirements require additional bilateral activation of dorsolateral prefrontal cortex, the anterior cingulate gyrus, and the supramarginal gyrus. The finding that interference of amplitude and directional requirements would result in the recruitment of similar cortical areas (Wenderoth et al., 2005) does indicate that spatial codes for amplitude and direction arise from the same (or at least partially the same) cortical areas. Therefore, the overlap of spatial codes do not only occur between codes for different values within one parameter (i.e., the overlap between the spatial codes for a movement producing a short line and one producing a long line), but it also occurs between codes for different spatial characteristics (i.e., the overlap between the spatial code for a movement producing a short line and the spatial code for producing a vertical line). In other words, interdependence between amplitude and direction in bimanual movements is due to the interactive effect between the spatial codes for movement amplitude characteristics and the spatial codes for movement direction characteristics, which arise from the use of shared cortical areas of the bilateral superior parietal-premotor network. Moreover, it is possible that the spatial codes generated for movement amplitudes are more demanding as compared to spatial codes generated for movement directions, making the spatial codes for amplitude control more vulnerable to be influenced by other factors (i.e., additional demand due to directional requirements). Thus our findings provide behavioral evidence supporting previous imaging studies (e.g., Wenderoth et al., 2005) which suggest that bimanual demands of amplitude characteristics as compared to bimanual demands of directional characteristics require activation of additional cortical areas.

In addition, we found that movement amplitude accuracy was highest when the coordinative pattern required the two hands to draw two long vertical lines. We hypothesize that the movement system selects a standard for each spatial characteristic and derives the spatial codes of the standard for all spatial requirements of the bimanual coordination task. In the current study, we believe that the movement system uses the long vertical line as the standard for all movements; therefore, the spatial codes needed for horizontal lines and for short lines are derived from the standard resulting in more accurate performance measures when the requirement is long and the direction is vertical as compared drawings including short lines; such as bimanual movements requiring short (i.e., half the long line) and/or horizontal lines which proved to be less accurate than fore mentioned vertical long lines. This hypothesis is speculative and thus requires further investigation to determine whether people tend to use certain movement lengths as the standard unit when requirements for various movement lengths are possible.

In summary, the present study revealed a mix of interdependencies and independencies between amplitude and direction characteristics in bimanual coordination. This supports the notion that spatial codes do not only interfere with each other when the spatial demands are asymmetric for the same spatial characteristic, but the spatial codes also interfere when the asymmetry demands are caused by different spatial characteristics. In addition, the current study also showed that the influence of amplitude on direction and vice versa is not equivalent. Amplitude control in bimanual coordination tasks is more vulnerable to the influence of direction control demands than direction control is affected by amplitude control demands. This indicates that bimanual control of amplitude is more demanding than bimanual control of direction.

Conflict of interest statement

No potential conflict of interest was reported by the authors.

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