

2014

The Control of Amplitude and Direction in Bimanual Coordination

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THE CONTROL OF AMPLITUDE AND DIRECTION
IN BIMANUAL COORDINATION

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Kinesiology

by
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August 2014

ACKNOWLEDGMENTS

I would like to express my deepest gratitude to my advisor, Dr. Arend Van Gemmert, for the guidance and support during my study at LSU. His expertise, instruction and patience made this dissertation work possible. No matter how busy he was, he always has time to help me. His mentorship has built a solid foundation for my future research. He has played an integral role in my growth as a researcher and person.

I would like to thank Dr. Jan Hondzinski, for her support and encouragement. She has led me into the Taichi program for Parkinson's disease patients and opened the door towards my further study in exercise intervention for special populations. I would like to thank Dr. Gil Reeve, Dr. Katie Cherry, and Dr. Paul Mooney for serving on my committee. Their knowledge and insights have greatly increased my understanding of the theories and techniques within this dissertation. I appreciate all their suggestions and comments.

I would like to thank the Life Course and Aging Center, Lillian Oleson Scholarship, James J. Corbett Graduate Research Award, and Louisiana State University for providing the resources that have made this dissertation possible.

I would like to thank my parents and parents-in-law. I would not be where I am today without their unconditional love and support. Last but not least, I would like to thank my husband, Zhou, for his incredible patience and understanding. His support has made this degree a reality for me.

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ABSTRACT

Spatial coordination of bimanual movements is important when performing daily activities. Whereas, older adults and individuals with Parkinson's disease (PD) commonly show difficulties in temporally coordinating the hands in bimanual coordination tasks, the effects of aging and Parkinson's disease on the quality of spatial coordination between the hands are unclear. Thus, the present work investigated the impact of older age and PD on the spatial interference in a bimanual task in which 48 right hand-dominant participants (16 young adults, 16 older adults and 16 individuals with PD) drew simultaneously two lines with both hands with varied movement amplitudes (3 and 6 cm) and/or directions (horizontal and vertical). The dependent variables were amplitude error of the line drawn with the right hand (A-error-R), amplitude error of the line drawn with the left hand (A-error-L), directional error of the line drawn with the right hand (D-error-R) and directional error of the line drawn with the left hand (D-error-L).

The results showed that older adults were able to maintain a similar level of spatial accuracy on the dominant side as young adults, but they showed reduced spatial accuracy when using the non-dominant hand. Furthermore, advanced age altered the control of movement direction in the bimanual coordination task, but not the control of movement amplitude. These results indicate that, the effects of the use of a longer standard spatial code for movement amplitude did not change in older adults, but older age does alter the control of direction in bimanual movements. Individuals with Parkinson's disease and older adults showed similar levels of spatial accuracy, except for the directional accuracy of the lines drawn with the dominant hand; these lines showed angles with the target direction were increased about two degree in the PD group as compared to older control group. In summary, the quality of spatial

coordination declined only in part in older adults, and the decline in the quality of spatial coordination was not exacerbated in individuals with PD, indicating the divergent role of basal ganglia for the control of temporal and spatial aspects.

CHAPTER 1: INTRODUCTION

Spatial coordination in bimanual movements

Bimanual coordination is the simultaneous movements of two hands. When two hands produce different actions, the stability and accuracy of the performance declines (Franz, Eliassen, Ivry, & Gazzaniga, 1996; Eliassen, Baynes, & Gazzaniga, 1999; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Semjen, 2002). It has been suggested that temporal and spatial interference in bimanual coordination tasks have different origins (Franz, Eliassen, Ivry, & Gazzaniga, 1996; Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004). Specifically, it is suggested that spatial interference in bimanual coordination arises from the interaction or overlap between two spatial representations guiding spatial specifications of the task (i.e., one spatial code for movement amplitude on the right side of working space and another spatial code for the movement amplitude on the left side of working space) (Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003). On the other hand, there are at least two hypothesized origins for temporal interference. Temporal interference in discrete bimanual coordination tasks reflect our general limitation to represent a complex temporal relationship, which probably arises from an internal timing system in the cerebellum, whereas temporal interference in continuous bimanual coordination tasks arise from interactions between time-varying spatial representations on cortical level (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Franz, Eliassen, Ivry, & Gazzaniga, 1996; Semjen, 2002; Spencer, Semjer, Yang, & Ivry, 2006).

Only a few studies addressed the question whether direction and amplitude are interdependent in bimanual coordination. For instance, Swinnen, Dounskaia, Levin, and Duysens (2001) revealed some level of independence, as well as some degree of interdependent between

amplitude and directional parameters in bimanual coordination tasks, indicating that amplitude and direction are mediated by distinct but partially overlapping neural resources. In addition, brain imaging studies have shown that producing bimanual movements with different amplitude or direction activated similar cortical areas (i.e. bilateral superior parietal-premotor areas). However, additional bilateral networks are activated only when bimanual movements with different amplitudes are produced, while they are not activated when different directions are produced (Wenderoth, Debaere, Sunaert, & Swinnen, 2005). The studies of Swinnen and colleagues (Swinnen, Dounskaia, Levin, & Duysens, 2001; Wenderoth, Debaere, Sunaert, & Swinnen 2005) provided initial insights into the relationship between direction and amplitude in bimanual coordination tasks. However, these studies only analyzed the movement accuracy of each hand separately. Thus, they ignored important information about the quality of coordination between the two hands.

Bimanual coordination in older adults

Older adults are able to produce symmetric bimanual movements, while asymmetric bimanual movements have been shown to be challenging for them, especially when high movement speeds are required (Lee, Wishart, & Murdoch, 2002; Serrien, Swinnen, & Stelmach, 2000; Swinnen, Verschueren, Bogaerts, Dounskaia, Lee, Stelmach, & Serrien, 1998). Based on the attention allocation hypothesis, the age-related difficulties in asymmetric bimanual movements (i.e., a strong interference between the movements and a shift towards symmetric coordination) arise when the attention demands exceed the older adults' available attention resources (Lee, Wishart, & Murdoch, 2002). Another hypothesis for age-related difficulties observed in bimanual coordination is associated with the critical role of inter-hemispheric interactions through the corpus callosum for bimanual coordination. Recent studies suggest that the age-related declines

in corpus callosum quantity (i.e., callosal size) and quality (i.e., the integrity of the callosal microstructure) are key contributors to age-related difficulties in bimanual coordination (Fling, Walsh, Bangert, Reuter-Lorenz, Welsh, & Seidler, 2011; Fling, & Seidler, 2011).

Most studies investigating the impact of advanced age on bimanual coordination focused on the timing accuracy by applying “in-phase”, “anti-phase”, and “multi-phase” coordination patterns (Goble, Cocon, Van Impe, De Vos, Wenderoth, & Swinnen, 2010; Fling, Walsh, Bangert, Reuter-Lorenz, Welsh, & Seidler, 2011; Lee, Wishart, & Murdoch, 2002;), while it is suggested that temporal and spatial interference in bimanual coordination tasks have different origins (Franz, Elliassen, Ivry, & Gazzaniga, 1996; Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004). Therefore, a study is needed to investigate the impact of old age on spatial accuracy in a bimanual coordination tasks when the movement amplitude and movement direction are specified.

Parkinson’s disease in bimanual coordination

Several studies have reported that individuals with Parkinson’s disease (PD) show deficits in the control of bimanual movements (Johnson, Cunnington, Bradshaw, Philips, Lansek, & Rogers, 1998; Serrien, Steyvers, Debaere, Stelmach, & Swinnen, 2000; Swinnen, VanLangendonk, Verschueren, Peeters, Dom, & DeWeerd, 1997). The common findings in these studies were that individuals with PD perform with more error and variability when producing asymmetric movement than healthy controls, and they have a strong tendency to revert from asymmetric to symmetric coordination patterns. The majority of research investigating the influence of Parkinson’s disease on bimanual coordination did focus, like research in older adults, on temporal coordination and examined performance of bimanual tasks in “in-phase”, “anti-phase”,

and “multi-phase” coordinative patterns. The general finding of these studies (Johnson, Cunnington, Bradshaw, Philips, Lansek, & Rogers, 1998; Serrien, Steyvers, Debaere, Stelmach, & Swinnen, 2000; Swinnen, VanLangendonk, Verschueren, Peeters, Dom, & DeWeerd, 1997) is that one can observe impaired bimanual coordination in individuals with PD when they perform bimanual anti-phase or multi-phase movements. In contrast to the temporal accuracy aspects of bimanual coordination, spatial accuracy aspects of bimanual coordination in PD affected individuals have received much less attention, and as stated before, temporal and spatial interference in bimanual coordination tasks are assumed to have different origins (Franz, Elliassen, Ivry, & Gazzaniga, 1996; Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004). Therefore, a study is needed to explore the influence of Parkinson’s disease on spatial aspects of bimanual coordination tasks to provide a more comprehensive understanding of the role of basal ganglia in bimanual coordination.

Dissertation outline

Chapter 1 provides some basic background information with regard to the relationship between amplitude and direction in bimanual coordination, and how the performance in these bimanual tasks are affected by aging and/or Parkinson’s disease. **Chapter 2** presents a study in which the relationship between amplitude and direction was examined by analyzing the relative relationship between movement performances of the two hands in addition to the movement accuracy of each hand individually. **Chapter 3** presents a study examining the effects of aging on spatial accuracy in bimanual coordination. The results provide insight into the differential impact of advanced age on temporal and spatial control in bimanual movements. **Chapter 4** presents a study in which the influence of Parkinson’s disease was examined on spatial accuracy in bimanual coordination. Performance of individuals with Parkinson’s disease and healthy older

controls on a bimanual coordination task were compared to determine whether and how Parkinson's disease may impact control of bimanual movements, and possibly exacerbate the effects of aging on bimanual tasks. The studies outlined in chapter 2, 3, and 4 increase our understanding of spatial coordination for bimanual movements and the effects of aging and Parkinson's disease on tasks requiring simultaneous control of both hands. **Chapter 5** summarizes key findings of the aforementioned three studies, discusses limitation of the current work and indicates directions in future studies.

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CHAPTER 2: THE RELATIONSHIP BETWEEN AMPLITUDE AND DIRECTION IN BIMANUAL COORDINATION

Introduction

In our daily life, most motor skills using upper limbs require bimanual coordination, which is a simultaneously integrated action of the two hands. Research has mainly focused on the constraints in bimanual coordination. Some studies addressed the temporal interference in bimanual coordination (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Semjen, 2002; Spencer, Semjer, Yang, & Ivry, 2006). The timing assimilation effect has been observed during the production of discrete motor tasks, i.e., it was shown that people tend to initiate and terminate movements of the two hands synchronously, and continuous rhythmic tasks, i.e., it was shown that individuals have difficulty to maintain temporal stability when the two hands attempt to produce complex phases such as 1:2, 1:3, etc., There are at least two hypothesized origins for temporal interference. Temporal interference in discrete bimanual coordination tasks reflect our general limitation to represent a complex temporal relationship, which probably arises from an internal timing system in the cerebellum, whereas temporal interference in continuous bimanual coordination tasks arise from interactions between time-varying spatial representations on the cortical level (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Franz, Eliassen, Ivry, & Gazzaniga, 1996; Semjen, 2002; Spencer, Semjer, Yang, & Ivry, 2006).

Some other studies have focused on the spatial interference in bimanual coordination, which is the tendency of the two hands to produce movements with similar amplitude and/or in a mirror direction. These studies suggest that the spatial interference mainly result from the inter-hemispheric communication across the corpus callosum. For example, a series of bimanual coordination studies suggest that the spatial coupling relies highly on the cognitive representation

of the task (Mechsner, Kerzel, Knoblich, & Prinz, 2001; Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003): asymmetric bimanual coordination induce more lateral (left-dominant) cortical activation, and relies on the corpus callosum to share the goal representations with the other hemisphere (Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004). Moreover, the study of Eliassen, Baynes and Gazzaniga (1999) showed that the posterior region of the corpus callosum might be a major contributor to directional coupling in bimanual coordination tasks due to the observation that an epilepsy patient started to show spatial uncoupling in directional asymmetric bimanual task after the resection of the posterior region of corpus callosum.

Spatial interference occurs when people attempt to draw two different amplitudes. The different amplitudes for the right and left hand normally results in assimilation of movement lengths, such that the shorter amplitude tends to overshoot whereas the longer amplitude tends to undershoot (Franz, 1997; Swinnen, Dounskaia, Levin, & Duysens, 2001; Spijkers, & Heuer, 1995; Ryu, & Buchanan, 2004). Similar interference effects have been also observed in the directional incongruent conditions when the movement trajectories become mutually coupled (Franz, Eliassen, Ivry, & Gazzaniga, 1996; Eliassen, Baynes, & Gazzaniga, 1999; Wenderoth, Puttemans, Vangheluwe, & Swinnen, 2003; Wenderoth, Debaere, Sunaert, & Swinnen, 2005). Studies focused on spatial interference have investigated the constraining role of direction and amplitude separately. The relationship between amplitude and direction in bimanual coordination has received less attention. Only a few studies addressed the question of whether direction and amplitude are interdependent in bimanual coordination. For instance, a study of Swinnen, Dounskaia, Levin, and Duysens (2001) and a study of Wenderoth, Debaere, Sunaert and Swinnen (2005) revealed some level of independence, as well as some degree of interdependent

between amplitude and directional parameters in bimanual coordination, indicating that amplitude and direction are mediated by distinct but partially overlapping neural resources.

Swinnen, Dounskaia, Levin and Duysens (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, the left hand (the non-dominant hand) drew vertical lines, while the right hand (the dominant hand) drew lines in 8 different directions. They also asked participants to draw the movements at either 8 cm or 16 cm. For each hand, participants' performance of bimanual coordination 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. Wenderoth, Debaere, Sunaert and Swinnen (2005) applied functional magnetic resonance imaging (fMRI) on participants while they 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 a bimanual coordination task. It was shown that direction had an influence on the interference of amplitude. In addition, the brain imaging results 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, Dounskaia, Levin, & Duysens, 2001; Wenderoth, Debaere, Sunaert, & Swinnen 2005) provided initial insights for the relationship between direction and amplitude in bimanual coordination tasks. However, the two studies only

analyzed the movement accuracy of each hand separately. The important information of the quality of coordination between the two hands has not been examined. The quality of the bimanual coordination is represented by a relative relationship between the movements of the two hands (i.e. the ratio of movement length between the lines drawn with the right and the left hand and the relative angle between the movement directions of the two hands). To comprehensively understand the relationship between the direction and amplitude in bimanual coordination, the current study analyzes parameters representing the quality of coordination between the hands in addition to parameters showing movement accuracy of each hand separately in a bimanual task paradigm.

Methods

Participants

Sixteen young adults (20.69 ± 0.79 , range from 20 to 22) were recruited from the Baton Rouge community. All participants were asked to fill out a short questionnaire to determine eligibility of study participation. Anyone who indicated (i.e. self-reported) 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.

Apparatus

The apparatus included a WACOM Intuos digitizer tablet (12x18 inches), two digital pens (WACOM GP-100), a 1 by 18 inch wooden stick, and two 20 inch monitors (monitor-1 and monitor-2). The tablet recorded the X- and Y-position of each pen with a sampling rate of 100Hz and spatial resolution of 0.001cm. The wooden stick was placed on the vertical midline of the tablet to restrain the movement area of each hand, so the two pens and hands could not touch each other or cross over into each other's working area. 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 visual information of the movement of the hands. The experimental procedures were programmed in MovAlyzeR (NeuroScript LLC, Tempe, Arizona, USA) running on a PC (Dell Dimension 8400). The monitor-1 (which was the lower monitor) was placed approximately 80cm in front of the participants. Prior to the start of the go-stimulus, participants needed to study an example of the required movement directions and amplitudes shown on the lower monitor. After completion of the movements, monitor-2 (the upper monitor), which was placed right on top of the lower monitor, showed participants their actual movement trajectories (see Figure 2.1.).

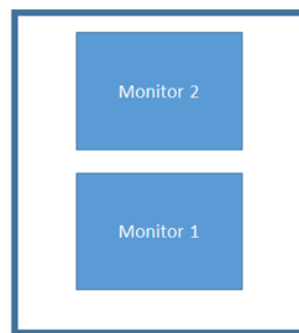


Figure 2.1. Monitors Configuration

Experimental design

The possible requirements for the movement amplitude for each hand were a short line (3cm) and a long line (6cm). Thus, there were four possible bimanual coordination tasks regarding the movement amplitudes: “Short-Short”, “Long-Long”, “Short-Long” and “Long-Short”.

Moreover, participants needed to draw two 3cm lines in the “Short-Short” condition, two 6cm lines in the “Long-Long” condition, a 3cm line with the left hand and a 6cm line with the right hand in the “Short-Long” condition, and a 6cm line with the left hand and a 3cm line with the right hand in the “Long-Short” condition. The target amplitude ratio between the right and the left line was 1 (3:3 or 6:6) for the “Short-Short” and “Long-Long” conditions, while the target amplitude ratio between the right and the left line was 2 (6:3) for the “Short-Long” condition and 1/2 (3:6) for the “Long-Short” condition (see Table 2.1.).

The possible requirements for movement direction for each hand were drawing a vertical line and a horizontal line. Thus, there were four possible movement direction targets for the bimanual coordination task. They were both hands drew lines straight away from the body, i.e., vertical lines (“Vertical-Vertical”), both hands drew perpendicular lines to the body away from the center, i.e., horizontal lines (“Horizontal-Horizontal”), the left hand drew a perpendicular line to the body going left away from the center, i.e., horizontal line, while the right hand drew straight away from the body, i.e., vertical line (“Horizontal-Vertical”), and the left hand drew straight away from the body, i.e., vertical line, while the right hand drew a line perpendicular to the body going right away from the center, i.e., horizontal line (“Vertical-Horizontal”). Thus, the target angle between the two lines was 0° for the “Vertical-Vertical” condition, 180° for the “Horizontal-Horizontal” condition, and 90° for the “Horizontal-Vertical” and “Vertical-Horizontal” conditions (see Table 2.1.).

Table 2.1. Experimental design

Target amplitudes \ Target directions	Vertical-Vertical	Horizontal-Horizontal	Vertical- Horizontal	Horizontal-Vertical
Short-short	x	— — o	— x	— o
Long-long	o	— — x	— o	— x
Short-long	x	— — o	— x	— o
Long-short	o	— — x	— o	— x

The current study used a 4 (four target amplitudes) \times 4(four target directions) nested design (see Table 2.1.). The four target amplitudes were “Short-Short”, “Long-Long”, “Short-Long”, and “Long-Short”. The four target directions were “Vertical-Vertical”, “Horizontal-Horizontal”, “Horizontal-Vertical”, and “Vertical- Horizontal”. In the pilot study, we found that completing the 16 conditions would take about 60-70 minutes and participants reported to be fatigued after about 30-40 minutes, therefore to avoid fatigue to be introduced as a confounding factor, the experimental design was adapted to limit fatigue to become a 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”) (see Table 2.1.).

Procedures

Participants sat comfortably in a chair in front of a table, where the tablet and monitors were placed. Participants were instructed to hold one pen in each hand with their normal pen grip and they were allowed to rest their arms on the tablet. Each trial contained three parts: presentation of two lines showing the required movements, producing the bimanual coordination task, and receiving feedback. A trial started when two home positions were shown on the lower monitor. After participants placed the right pen in the right home position and placed the left pen in the

left home position, the home positions disappeared and two lines showing the required movement trajectories was shown on the lower monitor. These lines, (one on the right one on the left side) showed the required movement directions and amplitudes. For instance, if the lines showed a 3cm vertical line on the left side and a 6cm 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 1/2. Participants were required to keep the tip of both pens in the home position while the lines showing the required movement directions and amplitudes were presented. The presentation of the lines indicating the required bimanual task was shown for a random duration between 5 and 8 seconds, after which it disappeared with a loud beeping sound indicating 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). During execution of the bimanual task no visual on-line feedback was provided. Furthermore, participants were instructed to draw the lines at their comfortable speed, and to only lift the pens up from the digitizer tablet after they had finished the movements. After the participant finished the bimanual task, the upper monitor 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 grey lines) to the required target movements (i.e., the black lines), and to note any differences between their executed movements and the target movements. The experimenter also provided knowledge of results verbally, by

stressing the differences between the lines, e.g., “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 to draw 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 her/him 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 8 trials in each condition. Participants completed all 8 trials of one condition before moving on to the next condition. The sequence of experimental conditions was randomized for every participant. If a trial was deemed invalid, the participant needed to redo the trial. A trial was deemed to be invalid when any of the following requirements were not met:

- Participant drew visually curved instead of straight lines.
- Participant did not wait for the go-signal to start the bimanual movement task.
- Participants started the movement after about 2 seconds or more.
- After movement initiation the participant paused with one or both hands before the bimanual movement task was completed.
- The participant moved only one hand, i.e., they did not move the hands simultaneously.
- The participant did not make a complete stop before the participant lifted one or both pens of the digitizer tablet.

Measurements and statistical analysis

First the movement data were low-pass filtered at 7 Hz with a 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. To estimate spatial accuracy for each hand six dependent variables were calculated; three for each hand. The first three dependent variables estimated amplitude error. The dependent variable for amplitude error for the line on the right (i.e., produced with the right hand) is A-error-R, which is calculated by using the formula:

$$\frac{[actual_amplitude(R) - target_amplitude(R)]}{target_amplitude(R)}. \text{ Positive A-error-R would indicate prolonged movement}$$

amplitudes produced with the right hand, while negative A-error-R would suggest shortened movement amplitudes produced with the right hand. Similarly to the estimation of amplitude error of the produced lines with the right hand, the amplitude error for the line on the left (i.e., produced with the left hand) is A-error-L, which is determined by using the formula:

$$\frac{[actual_amplitude(L) - target_amplitude(L)]}{target_amplitude(L)}. \text{ Positive A-error-L would indicate prolonged movement}$$

amplitudes produced with the left hand, while negative A-error-L would imply shortened movement amplitudes produced with the left hand. The dependent variable for ratio of amplitude error between the line on the right (i.e., produced with the right hand) and the line on the left (i.e., produced with the left hand) is A-error-Ratio, which is calculated by using the formula:

$$\frac{[\frac{amplitude(R)}{amplitude(L)} - target_ratio]}{target_ratio}. \text{ Positive A-error-Ratio would indicate prolonged movement amplitudes}$$

produced with the right hand, or shortened movement amplitudes produced by the left hand, or prolonged movement amplitude of the right hand and shortened movement amplitudes of the left hand. Negative A-error-Ratio would imply shortened movement amplitudes produced with the

right hand, or prolonged movement amplitudes produced with the left hand, or shortened movement amplitude of the right hand and prolonged movement of the left hand.

The other three variables used to assess spatial accuracy estimated the directional accuracy of the movements. The movement direction was defined as the stroke angle (at peak velocity) in relation to the straight line between the centers of the starting position and the target circle. The D_error_R was determined by the angle between the target line and the line produced on the right by the right hand. Positive D_error_R would indicate that the right hand moved away from the center of the body, while a negative D_error_R would imply that the right hand moved toward the center of the body (see Figure 2.2.). Similarly, D_error_L was determined by the angle between the target line and the line drawn on the left with the left hand. Positive D_error_L would indicate that the left hand moved away from the center of the body, while negative D_error_L would suggest that the left hand moved toward the center of the body (see Figure 2.2.). The D_error_RL was determined by the angle between the line on the right (i.e., produced with the right hand) and the line on the left (i.e., produced with the left hand). Positive D_error_RL would indicate that the angle between the line on the right and line on the left is larger than required, while negative D_error_RL would suggest that the angle between the line on the right and line on the left is smaller than required.

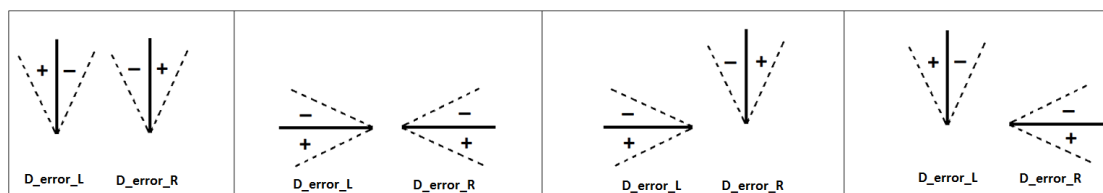


Figure 2.2. Interpretations for signs in D_error_R and D_error_L

The study focused on the effects of the different target amplitudes, target directions, and their compound effects on the control of amplitude and control of direction in bimanual

coordination. Therefore, the study applied analysis of variance (ANOVA) with target amplitudes (“Short-Short”, “Long-Long”, “Short-Long” and “Long-Short”) and target directions (“Vertical-Vertical”, “Horizontal-Horizontal”, “Horizontal-Vertical” and “Vertical- Horizontal”) as independent factors for each dependent variables. If any main effect or interaction proved to be significant ($\alpha \leq .05$), bonferroni corrected post-hoc analyses were applied to identify the locus of the significant interaction.









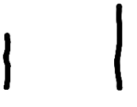


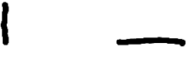




Results

Representative examples of left and right line drawing

Representative examples of the bimanual line drawings are displayed in Table 2.2. As can be observed in the Short-Short (SS) and Long-Long (LL) rows, the trajectory length on the right and left side are fairly similar across all directional conditions, showing accurate amplitude ratio in conditions which did required symmetric movement amplitudes. In conditions which required asymmetric amplitudes, the length of the short line was supposed to be half of the length of the long line. However, as shown in the Short-Long (SL) and Long-Short (LS) rows, the length of the short line generally exceeded the $\frac{1}{2}$ length of the long line, showing the occurrence of an interference effect on the amplitudes of the movements. Drawings with orthogonal directions can be found in Table 2.2. in the Horizontal-Vertical (HV) and Vertical-Horizontal (VH) columns. Although, visually not immediately evident, a close look reveals a general tendency to overshoot the vertical line in the HV and VH columns, thus indicating that direction influenced the accuracy of the amplitudes. The four columns of Table 2.2. give a general impression of accuracy of the angles between the two lines for all directional conditions. Nevertheless, when exam closely into the columns of VH, the drawings show that the horizontal lines are slightly

lean upwards (i.e. away from the body). The vertical lines in VH are not exactly vertical as required by the condition; instead, the vertical lines tend to rotate away from the horizontal line (the vertical left line in the LS-VH condition shows a clear tendency of rotating away from the horizontal right line). Thus, the bimanual drawings in the VH conditions show directional interference. In contrast, the movement directions visually seem to be similar in the SS, LL, SL, and LS conditions, thus suggesting a minimal effect of amplitude on direction accuracy.

Table 2.2. Representative example of left and right line drawing

	VV	HH	HV	VH
SS				
LL				
SL				
LS				

Note: “SS” is abbreviation for the target amplitude of “Short-Short” (both hands draw short lines); “LL” stands for the target amplitude of “Long-Long” (both hands draw long lines); “SL” stands for the target amplitude of “Short-Long” (the left hand draw a short line while the right hand draw a long line), and “LS” is abbreviation for the target amplitude of “Long-Short” (the left hand draw a long line while the right hand draw a short line). “VV” is abbreviation for the target direction of “Vertical-Vertical” (both hands draw vertical lines); “HH” stands for the target direction of “Horizontal-Horizontal” (both hands draw horizontal lines); “HV” stands for the target direction of “Horizontal-Vertical” (the left hand draw a horizontal line while the right hand draw a vertical line), and “VH” is abbreviation for the target direction of “Vertical-Horizontal” (the left hand draw a vertical line while the right hand draw a horizontal line).

Analysis of amplitude interferences

The analysis of amplitude interference includes three dependent variables; i.e., A-error-L, A-error-R, and A-error-Ratio. The analysis of the interference of amplitude contained three parts in which all three dependent variables are assessed. The first part was focused on the effects of target amplitude. The second part was focused on the effects of target direction. Finally, the last part was focused on the combined effects of target amplitude and target direction, i.e., the interaction of these factors.

The main effects of target amplitude on A-error-L, A-error-R and A-error-Ratio, and the post-hoc tests are presented in Table 2.3.. The results showed that the main effect of target amplitude was significant for all three variables. The means and standard deviations (SD) of A-error-L (the white bar), A-error-R (the gray bar), and A-error-Ratio (the black bar) for each target amplitude condition are presented in Figure 2.3..

The results of A-error-L show a general tendency to overshoot the lines drawn with the left hand. The A-error-L was significantly larger in the “Short-Long” conditions compared to the “Long-Long” and “Long-Short” conditions (see A-error-L in Table 2.3. and Figure 2.3.). The left hand produced a short line in the “*Short*-Long” condition, while it produced a long line in “*Long*-Long” and “*Long*-Short” condition. Therefore, the left hand overshoot the short line. The left hand’s tendency to overshoot the short line is especially strong when the target amplitudes were asymmetric. The post-hoc tests showed that A-error-R is significantly higher in “Short-Short” and “Long-Short” conditions compared to “Long-Long” and “Short-Long” conditions (see Table 2.3. and Figure 2.3.). No significant difference was found between the “Short-Short” and “Long-Short” conditions, or between the “Long-Long” and “Short-Long” conditions. The A-

error-R is close to zero in “Long-Long” and “Short-Long” conditions, whereas it is about 0.1 (i.e., 10% to long) in the “Short-Short” and “Long-Short” conditions. The right hand produced a shorter line (3cm) in the “Short-**Short**” and “Long-**Short**” condition, while it produced a long line (6cm) in the “Long-**Long**” and “Short-**Long**” conditions. The results of A-error-R indicate that the right hand produce accurate amplitudes when required to draw a long line, but it overshoots when it is required to draw a short line. This tendency does not seem to change as result of the symmetry/asymmetry of the target amplitudes.

The post-hoc tests showed significant differences on A-error-Ratio between the “Long-Short” and both the “Long-Long” and “Short-Long” conditions (see Table 2.3. and Figure 2.3.). When the right and left hand both draw short lines in the “**Short-Short**” condition the drawn lines are to long for both hands (see Figure 2.3.). In other words, the relatively accurate amplitude ratio in “Short-Short” condition is the result of an largely equal overshoot of the right and left hand. When both hands draw long lines in the “**Long-Long**” condition, the amplitude of the right line is quite accurate while the left line is slightly larger than the target. These combined effects result in a slight negative A-error-Ratio in “Long-Long” condition (see Figure 2.3.). In the “Short-Long” condition the right hand produced accurate amplitudes for the long lines, while the left hand overshoot the short lines, which resulted in negative A-error-Ratio in the “Short-Long” condition (see Figure 2.3.). In other words, the amplitude interfered in the asymmetric target amplitude when the condition is “Short-Long”. This is mainly caused by the overshoot of the short line with the left hand. In the “**Long-Short**” condition the right hand did overshoot the short line, while the left hand only showed a slight overshoot of the long line (see Figure 2.3.). These combined effects in the “Long-Short” condition suggest that even though the pattern is not exactly the same as in “Short-Long” condition, the amplitude interferes when the target

amplitudes are asymmetric, which in the “Long-Short” condition is mainly caused by a overshoot of the short line.

Table 2.3. Effects of target amplitudes on A-error-L, A-error-R

Target amplitude (main effect)				Post-hoc comparison			
A-error-L	F(3,112)	Sig.	η^2		LL	SL	LS
	4.441	.005*	.106	SS	.332	1.000	.154
				LL		.042*	1.000
				SL			.016*
A-error-R	F(3,112)	Sig.	η^2		LL	SL	LS
	11.013	<.001*	.228	SS	<.001*	.006*	1.000
				LL		1.000	<.001*
				SL			.001*
A-error-Ratio	F(3,112)	Sig.	η^2		LL	SL	LS
	9.047	<.001*	.195	SS	1.000	.062	.098
				LL		.798	.004*
				SL			<.001*

Note: “SS” is abbreviation for the target amplitude of “Short-Short” (both hands draw short lines); “LL” stands for the target amplitude of “Long-Long” (both hands draw long lines); “SL” stands for the target amplitude of “Short-Long” (the left hand draw a short line while the right hand draw a long line), and “LS” is abbreviation for the target amplitude of “Long-Short” (the left hand draw a long line while the right hand draw a short line).

Large absolute A-error-Ratio was found in the conditions which require asymmetric amplitudes (i.e. “Long-Short” conditions). Further analysis of the A-error-R and A-error-L illustrate that the large A-error-Ratio observed in asymmetric coordination is mostly caused by overshooting the short lines. Moreover, the tendency to overshoot short lines is not only found in the asymmetric conditions, but also shown in the symmetric “Short-Short” conditions. In previous studies, overshooting the short lines was deemed to be a consequence of amplitude interference in symmetric conditions (Swinnen, Dounskaia, Levin & Duysens, 2001; Wenderoth, Debaere, Sunaert, & Swinnen, 2005). However, the results of the current study seem to suggest

that the overshooting of short line is a general tendency in bimanual coordination, which effects are exacerbated in conditions that require asymmetric amplitudes.

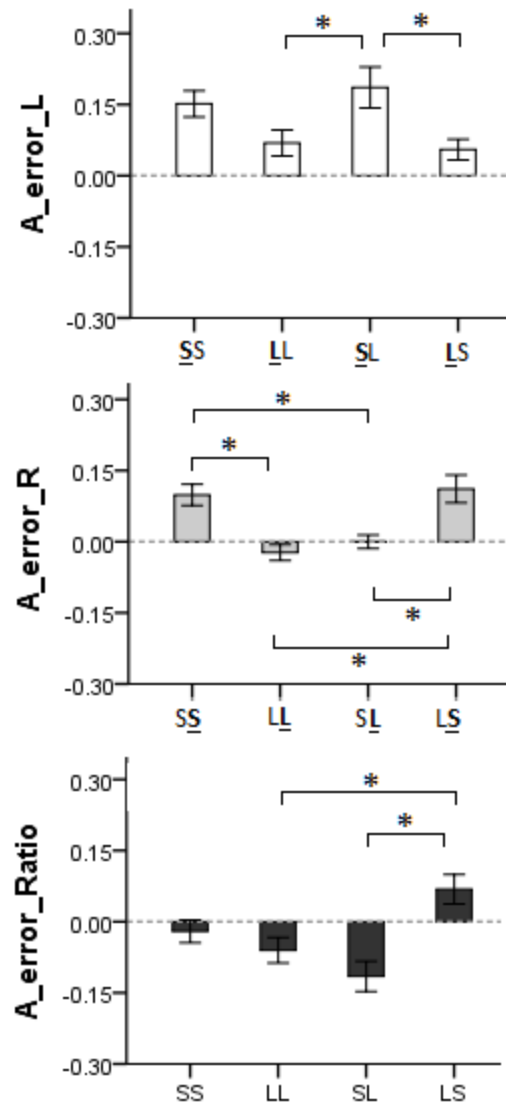


Figure 2.3. A-error-L, A-error-R and A-error-Ratio on different target amplitude

The main effect of target direction on A-error-L, A-error-R and A-error-Ratio, and the post-hoc tests for each variable are presented in Table 2.4.. Target direction proved to be significant for all three variables that represent the amplitude accuracy (see Figure 2.4.).

Table 2.4. Effects of target direction on A-error-L, A-error-R and A-error-Ratio

Target direction (main effect)				Post-hoc comparison			
A-error-L	F(3,112)	Sig.	η^2		HH	VH	HV
	4.898	.003*	.116	VV	1.000	.040*	1.000
				HH		.013*	1.000
				VH			.006*
A-error-R	F(3,112)	Sig.	η^2		HH	VH	HV
	6.428	<.001*	.147	VV	1.000	.425	.190
				HH		1.000	.004*
				VH			.001*
A-error-Ratio	F(3,112)	Sig.	η^2		HH	VH	HV
	11.965	<.001*	.243	VV	1.000	.001*	.216
				HH		.012*	.043*
				VH			<.001*

Note: “VV” is abbreviation for the target direction of “Vertical-Vertical” (both hands draw vertical lines); “HH” stands for the target direction of “Horizontal-Horizontal” (both hands draw horizontal lines); “HV” stands for the target direction of “Horizontal-Vertical” (the left hand draw a horizontal line while the right hand draw a vertical line), and “VH” is abbreviation for the target direction of “Vertical-Horizontal” (the left hand draw a vertical line while the right hand draw a horizontal line).

As can be seen in Figure 2.4., the left hand had a general tendency to overshoot the movement amplitude. The post-hoc tests for A-error-L showed that A-error-L in the “Vertical-Horizontal” condition was significant higher compared to the other three target directions (see Table 2.4. and Figure 2.4.). The target direction is asymmetric in “**Vertical**-Horizontal” in a way that the left hand needs to draw a vertical line while the right hand draws a horizontal line. The results of A-error-L suggest that, when two hands move in asymmetrical (i.e., orthogonal) directions, the left hand overshoots the required movement amplitude when the line needs to be drawn in a vertical direction. With respect to the A-error-R, the post-hoc tests shown that the A-error-R was significantly higher in “Horizontal-**Vertical**” conditions compared to “Horizontal-Horizontal” and “Vertical-Horizontal” conditions (see Table 2.4. and Figure 2.4.). The A-error-R

represents the amplitude deviation of the right line from the target line; a positive value of A-error-R would suggest longer amplitude than the amplitude of the target line. The results of A-error-R suggest that, like the left hand, the right hand tended to overshoot the vertical line, especially when the target directions of the two hands are asymmetrical (i.e., orthogonal).

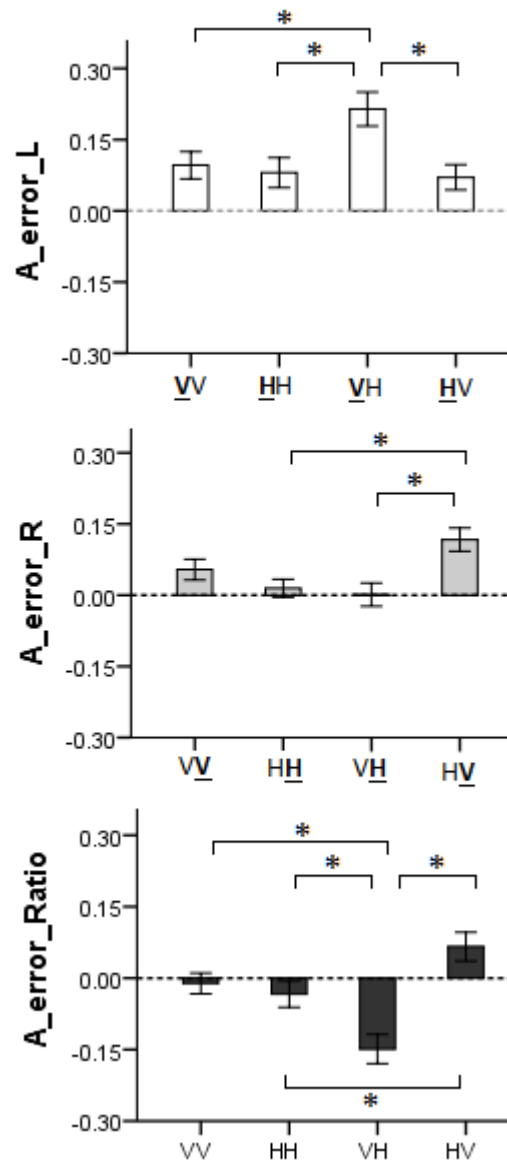


Figure 2.4. A-error-R, A-error-L and A-error-Ratio on different target directions

The post-hoc tests showed that the A-error-Ratio in the “Vertical-Horizontal” condition is significantly different from the A-error-Ratio in all other conditions. A-error-Ratio also significantly differed between “Horizontal-Horizontal” and the “Horizontal-Vertical” condition (see Table 2.4. and Figure 2.4.). As can be seen in Figure 2.4., the A-error-Ratio is close to zero in the “Vertical-Vertical” conditions due to the similar and relatively small overshoots with both hands. In the “Horizontal-Horizontal” condition, the A-error-Ratio is close to zero due to relatively accurate amplitude production of both hands (see Figure 2.4.). As can be seen in Figure 2.4., in the “Horizontal-Vertical” condition the right hand overshoots the vertical lines, while the overshoots of the drawn horizontal lines with the left hand are smaller. The positive A-error-Ratio in the “Horizontal-Vertical” condition is mainly the result of overshooting the vertical line with the right hand. The amplitude interference shown when the target directions are asymmetrical, i.e., in the “Horizontal-Vertical” and “Vertical-Horizontal” conditions are mainly caused by overshooting the vertical lines.

In general, the absolute A-error-Ratio is larger when the condition requires asymmetry of drawing direction between the hands (i.e. “Horizontal-Vertical” and “Vertical-Horizontal”) than when the condition requires symmetry of drawing direction between the hands (i.e. “Vertical-Vertical” and “Horizontal-Horizontal”). The findings for A-error-R and A-error-L illustrate that the larger A-error-Ratios observed in the asymmetric coordination conditions are mostly caused by overshooting of the required amplitudes of the vertical lines. It seems that the direction requirements affect the accuracy of the vertical amplitudes when the opposite hand is required to produce a horizontal movement at the same time. It is also worth noting that individuals have a tendency to overshoot the vertical lines as well when both hands have to move vertically (i.e., “Vertical-Vertical” conditions). It is possible that there is a general tendency of overshooting

vertical movements (i.e., movements away from the body) when performing a bimanual coordination task, while a requirement to produce asymmetrical (i.e., orthogonal) movement directions with the hands exacerbate the tendency to overshoot.

No significant interactions were found for the interaction target amplitude and target direction failed to reach significant for A-error-L, A-error-R and A-error-Ratio. Thus, indicating that target amplitude and direction interference on amplitude was not compound.

Analysis of direction interferences

Direction interference was assessed using the dependent variables D_error_L, D_error_R, and D_error_RL. Similarly to what was used to determine the interference on amplitude, interference on direction also contains three parts. The first part focuses on the effects of target direction on the interference of direction. The second part focuses on the effects of target amplitude on A-error-R, A-error-L and A-error-Ratio. And the last part focuses on the interactive effects of target direction and amplitude on the interference of direction.

Significant main effects of target direction were found for D_error_L and D_error_R, but not for D_error_RL (see Table 2.5.). Post-hoc tests were applied on D_error_L and D_error_R to compare the performance when required to move into different target directions (see Figure 2.5.).

Table 2.5. Effects of target direction on D_error_L, D_error_R and D_error_RL and post-hoc comparisons

Target direction (main effect)				Post-hoc comparison			
D_error_L	F(3,112)	Sig.	η^2		HH	VH	HV
	3.414	.020*	.084	VV	1.000	.077	1.000
				HH		.404	1.000
				VH			.022*
D_error_R	F(3,112)	Sig.	η^2		HH	VH	HV
	14.250	<.001*	.276	VV	1.000	<.001*	.465
				HH		<.001*	1.000
				VH			<.001*
D_error_RL	F(3,112)	Sig.	η^2				
	1.095	.354	.028				

Note: “VV” is abbreviation for the target direction of “Vertical-Vertical” (both hands draw vertical lines); “HH” stands for the target direction of “Horizontal-Horizontal” (both hands draw horizontal lines); “HV” stands for the target direction of “Horizontal-Vertical” (the left hand draw a horizontal line while the right hand draw a vertical line), and “VH” is abbreviation for the target direction of “Vertical-Horizontal” (the left hand draw a vertical line while the right hand draw a horizontal line).

D_error_L shows a positive value in “Vertical-Horizontal”, while its value is close to zero in the “Horizontal-Horizontal”, “Vertical-Vertical”, and “Horizontal-Vertical” conditions. The post-hoc tests showed that the D_error_L significantly differed between the “Horizontal-Vertical” and “Vertical-Horizontal” conditions (see Table 2.5. and Figure 2.5.). In the “**Vertical-Horizontal**” condition, the right hand draws a horizontal line, whereas the left hand draws a vertical line. The D_error_L values which are close to zero indicates that the left hand produce accurate movement directions in all conditions, except the “Vertical-Horizontal” condition which shows a positive value which means that the left hand tends to make drawing movements which produce lines that lean away from the midline of the body (i.e. the line drew by the left hand in the “Vertical-Horizontal” condition moved away from the line drew by the right hand). D-error-R showed a general tendency to become negative, so the vertical line tended to slant slightly

upward (i.e. slant towards the middle line of the body, see Figure 2.5.). The post-hoc tests revealed that the D_error_R is significantly higher in the “Vertical-Horizontal” condition compared to the other remaining target direction conditions (see Table 2.5. and Figure 2.5.). D_error_R shows a directional deviation of the line drawn with the right hand indicating that the right hand moves in an upward direction when drawing the horizontal line while the left hand draws a vertical line.

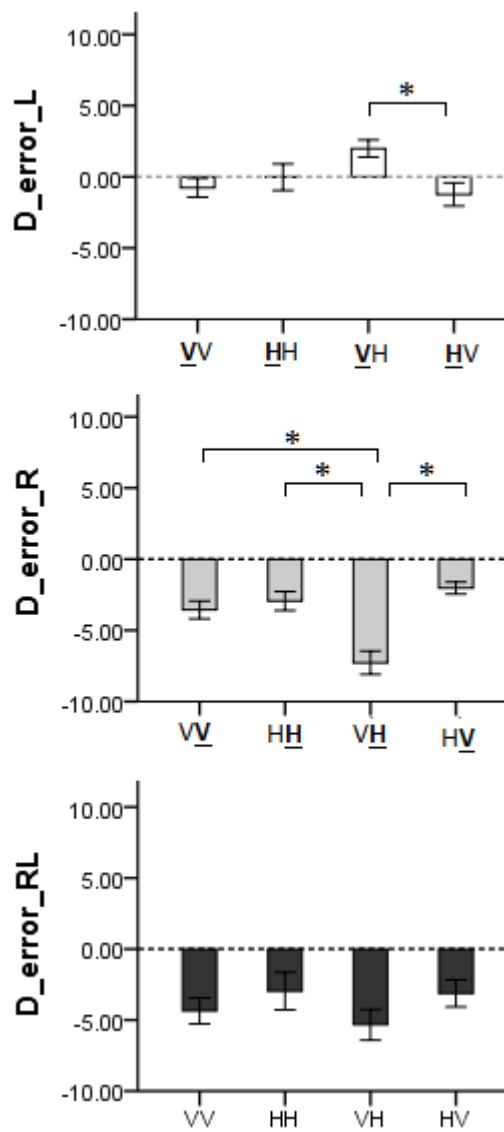


Figure 2.5. D_error_R, D_error_L and D_error_RL on different target directions

D_error_RL showed no significant effects as result of varying the target direction. The D_error_RL is negative for all target directions (see Figure 2.5.) indicating that the angle between the right and left line is smaller than required. This result is mainly caused by the negative values of D-error-R. In other words, when drawing two lines simultaneously, one has a tendency to reduce the relative angle by orienting the line drawn with the right hand towards the line drawn with the left hand. In Figure 2.5. it can be seen that in the “Vertical-Horizontal” conditions the lines drawn with the right hand lean about 10 degrees to the line drawn with the left hand, while the line drawn with the left hand tends to tilt downward, i.e., lean away from the line drawn with the right hand. This pattern of results may occur because the left hand tries to compensate for the big directional error of the right hand. This compensation mechanism may explain why the angle between the lines drawn with the right and left hand (i.e., D_error_RL) in the “Vertical-Horizontal” conditions does not become significantly different from the angle relationships (i.e., D_error_RL) in all other target directions.

A significant effect main effect of target amplitude was only found on D_error_R, while D_error_L, and D_error_RL were not significantly affected by target amplitude (see Table 2.6. and Figure 2.6.). Post-hoc tests were applied to determine which of the target amplitude conditions were significant different for D_error_R (see Figure 2.6.).

It was shown that D_error_R is negative in all target amplitude conditions, implying the general tendency of the right hand draw lines that lean to the line drawn with the left hand (see Figure 2.6.). The post-hoc tests showed that D_error_R was significantly larger in “Long-Short” conditions compared to D_error_R in “Short-Long” conditions (see Table 2.6.). The post-hoc tests showed that D_error_R was significantly larger in “Long-Short” conditions compared to

D_error_R in “Short-Long” conditions (see Table 2.6. and Figure 2.6.). In both these conditions the two hands are required to make bimanual movements that have asymmetric amplitudes. In Figure 2.5., it can be seen that in these asymmetric amplitude conditions the directional movement error of the right hand is larger when this hand is required to draw a line with smaller amplitude than the directional movement error of the right hand when this hand is required to produce larger movement amplitude. In contrast, D-error-L is shown to be close to zero in all target amplitude conditions (see Figure 2.6.). Moreover, no significant difference was found between the different target amplitudes for D-error-L. The results of D_error_L imply that the left hand (i.e., the non-dominant hand for all participants) in general is quite capable to producing movements with an accurate direction regardless of the amplitude requirements (see Figure 2.6.).

Table 2.6. Effects of target amplitude on D_error_L, D_error_R and D_error_RL

Target amplitude (main effect)				Post-hoc comparison			
D_error_L	F(3,112)	Sig.	η^2				
	0.376	.771	.010				
D_error_R	F(3,112)	Sig.	η^2				
	4.995	.003*	.118		LL	SL	LS
				SS	1.000	.585	.224
				LL		1.000	.060
				SL			.002*
D_error_RL	F(3,112)	Sig.	η^2				
	1.509	.216	.039				

Note: “SS” is abbreviation for the target amplitude of “Short-Short” (both hands draw short lines); “LL” stands for the target amplitude of “Long-Long” (both hands draw long lines); “SL” stands for the target amplitude of “Short-Long” (the left hand draw a short line while the right hand draw a long line), and “LS” is abbreviation for the target amplitude of “Long-Short” (the left hand draw a long line while the right hand draw a short line).

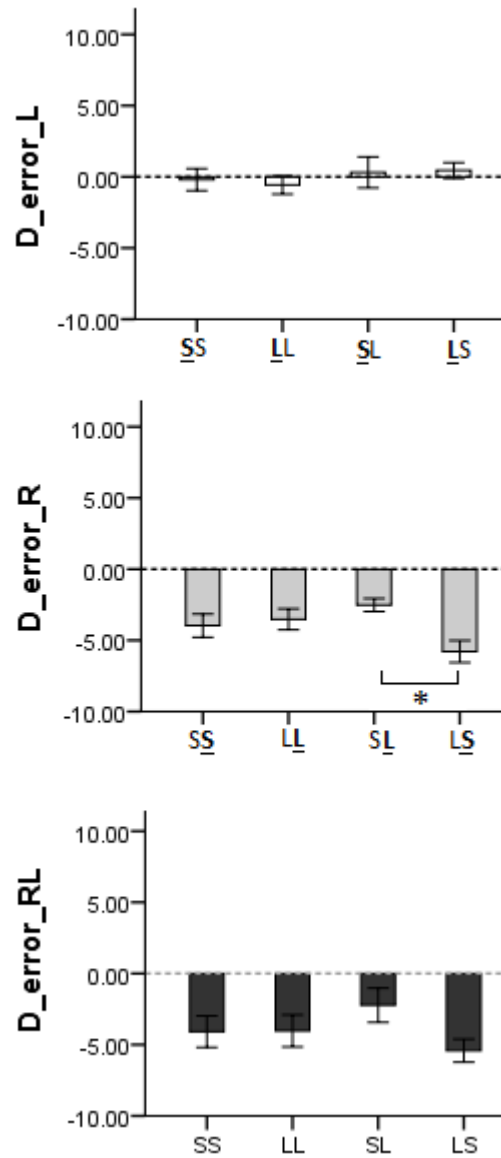


Figure 2.6. D_error_R, D_error_L and D_error_RL on different target amplitudes

The target amplitude does not seem to have a strong influence on the angle between the movement directions of each hand. The angle between the lines drawn with the right and left hand tends to be smaller than required irrespective of the amplitude requirements. Moreover, the results also show that especially movements with the left hand are resistant to interference as result of target amplitude requirements for both hands. Only movement direction of the right hand seem to be affected by the target amplitude requirements if the amplitude conditions are

asymmetric between the two hands, and smaller rather than longer amplitude requirements for the right hand seem to affect the directional error (i.e., larger directional errors were found in the “Long-Short” than in the “Short-Long” condition).

None of the target direction by amplitude interactions proved to be significant for any of the variables, i.e., D_error_R, D_error_L, and D_error_RL. This lack of significance for interactive effects indicates that there is no compounding effect of target direction and amplitude on the directional interference between the two hands.

Discussion

The discussion is divided into two parts. The first part focuses on the mechanisms of the interference of amplitude and direction in bimanual coordination tasks. The discussion of this part is based on the main effects of target amplitude conditions on the interference between the two hands on amplitude, and the main effects of target direction conditions on the interference between the two hands on direction. The second part focuses on the inter-dependence of amplitude and direction in bimanual coordination tasks. The discussion of this part is based on the main effects of target direction conditions on the interference between the hands on amplitude, the main effects of target amplitude on the interference between the hands on direction, and the interactive effects of target amplitude and direction on the interference of the two hands on amplitude and direction.

Amplitude interference and direction interference

A-error-Ratio quantifies the accuracy of amplitude ratio between the lines drawn with right and left hand, which represents the quality of the coordination between hands. The results of A-error-

Ratio revealed that participants experience substantial interference between the hands on the accuracy of matching the required amplitude conditions that require amplitudes that differ between the hands (i.e., asymmetric amplitude conditions). A-error-R and A-error-L represent the accuracy of amplitude of the drawn lines with the right and left hand respectively. These two variables added to the findings of A-error-Ratio that the asymmetry requirement of amplitudes between the two hands mainly results in an overshoot of the hand required to make a short movement when the other hand is required to draw a long line. In addition, an overshoot of the hand drawing the short line is also observed when the required amplitudes of the two hands are both short, i.e., one of the two symmetric conditions. Taken together, these results imply that overshooting short line in a paradigm with two movement amplitudes is a general tendency when bimanual coordination is required (i.e. in conditions of “Short-Short”, “Short-Long” and “Long-Short”). The tendency of overshooting shorter movements is exacerbated when the amplitude requirements are incompatible between the right and left sides (i.e. in conditions of “Short-Long” and “Long-Short”).

D-error-RL represented one of the accuracy measures for coordination movement direction between the two hands. It revealed that the interference of direction between the two hands was not affected by the asymmetry/symmetry of the movement direction requirements of the two hands. However, comprehensive analysis of D-error-R, D-error-L, and D-error-RL showed that some interference between the two hands occurred when the direction requirement of the movements of the two hands were asymmetric due to a requirement of moving with the right hand to draw a horizontal line to right away from the midline and perpendicular to the body while the left hand had to draw a vertical line, i.e., moving the pen straight away from the body. The directional interference of the directional performance requirements of the left hand on the

directional performance accuracy of the right hand did not lead to interference that resulted in an angle change between of the movement directions compared to the required angle between the two the target movement direction requirements of the two hands. The latter finding, probably occurred due a compensation of the movement direction performed with the left hand, which increased the angle between the two lines produced by the two hands in the condition of “Vertical-Horizontal” to compensate for the movement direction error made with the right hand in the “Vertical-Horizontal” condition. This phenomenon was observed to be strongest for the “Vertical-Horizontal” conditions.

A series of studies (Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003) demonstrated the occurrence of spatial interference when spatially the hand movements were incompatible, especially when the bimanual movements were symbolically cued. Symbolic cueing is a cueing condition, in which target shapes are presented to participants whose task is reproduce these shapes. The action is represented as direction-based trajectories in the symbolic cueing condition. A cueing condition, in contrast to a symbolic cueing condition, is called in this line of research direct cueing. Instead of presenting target shapes, the direct cue decomposes the shapes into multiple target locations (i.e., direct cues), so that participants only need to move from one direct cue to the next to reproduce the required shapes. The actions are specified as target locations in direct cued conditions. Thus, the present study applied a paradigm similar to what is called in this literature a symbolic cueing condition; i.e., a sample with a specific target amplitude and direction is presented to participant before s/he can start the reproduction. 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 are requested when asymmetric movements of two

hands are required (e.g., one spatial code for the 3 cm movement length requirement for the right hand and another spatial code for the 6 cm movement length requirement for 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, Diedrichsen, Spencer, Hazeline, & Semjen, 2004). The notion that spatial interference arises at the representative level is supported by studies (Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003) showing the elimination of reaction time costs in incongruent trials when the movements are cued directly, as well as studies (Mechsner, Kerzel, Knoblich, & Prinz, 2001; Bogaerts, Buekers, Zaal, & Swinnen, 2003; de Oliveira, & Barthelemy, 2005) which showed spatial interference in incongruent trials are reduced when transformed visual feedback is provided in such a way that the sensory information becomes symmetric.

The results of the interference between the two hands on movement amplitude in the current study support the representational basis of spatial interference discussed above; i.e., when movement amplitudes are symbolically cued, the interference of the movement amplitudes between the two hands occurred only in the asymmetric conditions. This finding of results occurs probably due to an overlap between the various spatial codes for the different movement amplitude requirements for the right and left hand. In accordance with previous studies (Sherwood, & Nishimura, 1992; 1997; Sherwood, 1994), results from the present study showed that the interference of movement amplitude performance between the hands occurred in the asymmetric coordination conditions mainly as results of an overshoot of the hand with the shorter movement requirement. This finding implies that the effects of the spatial codes are not equivalent. It seems that the spatial code for shorter movements are vulnerable to the influence of spatial code for longer movements, while the spatial code for the longer movements are barely

affected by the spatial code for shorter movements. We hypothesize that, for discrete bimanual tasks that are cued symbolic, the movement system selects a the longer movement extent as a standard for the spatial codes of the disparate movement amplitudes, while the spatial code for the shorter movement extent is derived from the selected standard. In other words, in the current study the original spatial codes were specified for the 6cm movement amplitude requirements, while the spatial code for the production of the 3cm movement amplitude requirement is simply coded as half the length of the 6 cm selected standard. This hypothesis would also explain the relatively accurate movement amplitudes in all conditions when longer movement amplitudes were required, while movement amplitude productions tended to overshoot all required movement amplitudes when they were required to be short.

Direction interference occurred on the right side when the right hand was required to draw a horizontal line moving away from the midline of the body and the left hand was required to draw a vertical line moving straight away from the body at the same time. From the perspective of the representational basis of spatial interference, multiple spatial codes are needed to be generated for these two different movement directions. The overlap between the various spatial codes results in a directional constraint in the orthogonal trials. Similar to the explanation suggested for the interference of amplitude production between the hands, the effects between the directional codes are not equivalent. The line drawn with the right hand showed an interference effect of the movement direction required for the line drawn with the left hand. Moreover, the horizontal line drawn with the right hand was drawn with an upward direction thus the angle was reduced between the lines drawn with the left and right hands in the “Vertical-Horizontal” condition. On the other hand, the directional bias of the left hand in “Vertical-Horizontal” condition is not believed to be a consequence of the spatial interference occurring as

result of the movement direction requirement of the right hand, because the movement direction of the left hand increases the angle between the lines drawn with the two hands. Therefore, we hypothesize that in discrete bimanual coordination tasks when the directions are cued symbolical, the left hand compensate only when necessary for a directional error if the right hand movement directions are inaccurate, while the left hand is able to maintain directional accuracy when no compensation to maintain angle accuracy between the drawn lines of both hands is needed. In the current study all participants were right handed, therefore, it is suggested that the non-dominant hand is proficient in directional control. Thus, the non-dominant hand is not only accurate to control direction, it is also capable to adjust direction to compensate for inaccurate direction control of the dominant hand by constraining the angle requirements. The proficiency of the non-dominant hand system in directional control has been also reported in previous studies (Pan, & Van Gemmert, 2013a; 2013b) which showed that adapting to a visual rotation distortion was more proficiently adapted to by the non-dominant hand system than the dominant hand system. It is possible that, due to the proficiency in directional control, the non-dominant side generates more robust spatial codes, which are hardly affected by other spatial codes. On the other hand, the spatial codes for movement direction of the dominant movement system seem to be less sturdy, resulting in directional influences on the dominant side when trials require directionally incongruent bimanual coordination.

Interdependence between amplitude and direction

The control of amplitude and direction in bimanual coordination tasks has been shown to be at least in part independently specified. This notion has been supported by behavioral data (Swinnen, Dounskaia, Levin, & Duysens, 2001) as well as data obtained in a study investigating brain activity (Wenderoth, Debaere, Sunaert, & Swinnen, 2005). In the present study,

significant main effects of target amplitude conditions were found on variables representing the interference of amplitude production of the two hands in a bimanual coordination task, whereas interactive effects of target amplitude and direction conditions failed to approach significant levels. These findings indicate that some degree of independence of amplitude and direction control exists, since the effects of amplitude and direction requirements on the interference of movement amplitude between the two hands did not show a compounding effect. Similarly, significant main effects of target direction were found on the interference of direction between the movements of both hands in the bimanual coordination tasks, whereas also compounding effects of target direction and amplitude requirements of the two hands were not found as suggested by the non-significant interaction between target direction and amplitude conditions findings for the directional interference variables.

With respect to the effects of the directional requirements on control of amplitude, A-error-Ratio revealed that amplitude interference between the two hands in bimanual coordination is larger when the required directions for the two hands result in asymmetric coordination (i.e., “Horizontal-Vertical” and “Vertical-Horizontal” conditions) compared to amplitude interference when the conditions require directionally symmetric bimanual coordination (i.e., “Vertical - Vertical” and “Horizontal -Horizontal” conditions). This observation indicates the evident influence of direction on the control of amplitude in bimanual coordination tasks. The influence of direction on movement amplitude has also been reported in the study of Wenderoth, Debaere, Sunaert and Swinnen (2005), who showed that amplitudes on the right side were 4 degrees (4% of maximal amplitude) larger when the direction requirements resulted in an incompatible coordination pattern compared when the direction requirements resulted in a compatible coordination pattern. Additional analysis of A-error-R and A-error-L in the present study

illustrates that the movement amplitude interference between the hands when the conditions requires an asymmetric directional movement pattern is mainly caused by overshoot of the movement producing the vertical lines (i.e., a movement straight away from the body) when the opposite hand is required to produce a movement resulting in a horizontal line (i.e., a movement away from the midline and perpendicular to the body). Further analysis revealed that the overshoot of the movement amplitudes when producing vertical lines also occurs when both hands move in directional symmetry straight away from the body, thus producing both vertical lines (i.e., “Vertical-Vertical” conditions). These observations indicate a general tendency to overshoot vertical drawn lines in bimanual tasks, whereas the requirements to produce a movement pattern in which the movement directions are orthogonal do exacerbate this tendency. The study of Swinnen, Dounskaia, Levin and Duysens (2001) showed influence of amplitude on movement direction. In the current study, movement amplitude did show to affect to some degree directional accuracy; this effect was limited only to the right side. In contrast to the findings in the current study for the drawn lines with the right hand, drawn lines with the left hand were found to be directionally accurate across all amplitude conditions.

In accordance with previous studies (Swinnen, Dounskaia, Levin, & Duysens, 2001; Wenderoth, Debaere, Sunaert, & Swinnen 2005), the present study showed that directional and amplitude variables are at some level of independent, while at the same time also some interdependency between these variables was shown in the bimanual coordination tasks. These findings support the notion that amplitude and direction are mediated by distinct but partially overlapping neural resources. Specifically, Wenderoth, Debaere, Sunaert and Swinnen (2005) revealed that asymmetric amplitude coordination and asymmetric direction coordination do recruit similar bilateral superior parietal-premotor networks, while the interference due to

amplitude requirements additionally activate the bilateral dorsolateral prefrontal cortex, the anterior cingulate gyrus, and the supramarginal gyrus. The finding that interference of amplitude requirements and directional requirements do recruit similar cortical areas does indicate that spatial codes for amplitude and direction arise from the same or 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 spatial codes for a movement producing a long line), but it also happens between codes for different parameters (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 the parameters of movement amplitude and the spatial codes for parameters of movement direction, which arise from the shared cortical areas of the bilateral superior parietal-premotor network. Moreover, the finding that the interference between the limbs of amplitude instead of direction do activate additional cortical areas suggest that the spatial codes generated for different amplitudes in bimanual movements is more taxing compared to spatial codes generated for different directions. Additional cortical area recruitment for amplitude control may be associated or even the result of a higher demand for attention resources when controlling amplitude than when controlling direction. Thus movement direction control may request less attention resources than movement amplitude control. The higher demand for attention resources to control amplitude as compared to attentional resources needed to control direction may explain the observation that amplitude is evidently affected by direction, whereas direction is only partially affected amplitude in the present study. One possibility is that the goal to produce an accurate directional relationship between hands is preferred by the

movement system above the goal to produce an accurate amplitude ratio between hands when attention resource are limited, since directional control require less attentional resources than amplitude control. Thus, the motor system adheres to the rule to allocate first resources to control the least demanding part of the task and if resources are left to allocate them to the more demanding part of the task to ensure that at least one part of the task is performed accurate.

In summary, the current study found that spatial interference between the hands occurs in a bimanual task when the trials require moving the hands according to a spatially incompatible pattern. Further analysis revealed that the spatial interference between the hands in a bimanual task is not equivalent: the amplitude of movements with the hand producing the short lines were more vulnerable to the influence of the movements of the hand producing the long lines, while the movement direction of the dominant hand was easier affected by the direction of the dominant hand. The present study also showed that, in a bimanual coordination task when movement amplitude and direction are manipulated, directional requirements regulate the interference between the hands on movement amplitude, and amplitude requirements only influence to some degree the interference of the non-dominant on the dominant hand on movement direction and not vice versa. The interdependence between amplitude and direction in bimanual movements is probably due to overlap between the spatial codes for the parameters of movement amplitude control and the spatial codes for parameters of movement direction control, which arise from the shared cortical areas in the bilateral superior parietal-premotor network.

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CHAPTER 3: THE EFFECTS OF AGING ON SPATIAL ACCURACY IN BIMANUAL COORDINATION

Introduction

Many daily activities such as feeding oneself and buttoning a shirt require coordination between the two hands. Bimanual tasks which require mirror movements of the right and left limb are referred to as symmetric bimanual coordination tasks, whereas bimanual tasks relying on independent control of each hand are referred to as asymmetric bimanual coordination tasks. Studies have reported that older adults are able to produce symmetric bimanual movements, while asymmetric bimanual movements have been shown to be challenging for them, especially when high movement speeds are required (Lee, Wishart, & Murdoch, 2002; Serrien, Swinnen, & Stelmach, 2000; Swinnen, Verschueren, Bogaerts, Dounskaia, Lee, Stelmach, & Serrien, 1998).

One hypothesis for the age-related difficulties in bimanual coordination is associated with attention resources. Based on the attention allocation hypothesis, when a task requires symmetric bimanual movements, older adults access more attention resources to achieve a similar level of performance that young adults can accomplish with less attention. When a task requires asymmetric bimanual movements, additional extra attention resources are required for older adults to achieve the mutual goal. Therefore, the age-related difficulties in asymmetric bimanual movements (i.e. strong interferences and a shift towards symmetric coordination) arise when the attention demands exceed the older adults' available attention resources (Lee, Wishart, & Murdoch, 2002). Indeed, greater neural activation was found for older compared to younger adults in bimanual movements, even though older adults' movement frequency was evidently slower than the movement frequency of young adults. Moreover, positive correlations between task performance and increased brain activation in the supplementary motor area (SMA) and the

left secondary somatosensory cortex imply that at least some of the age-related over-activation has a compensatory mechanism (Goble, Cocon, Van Impe, De Vos, Wenderoth, & Swinnen, 2010). An alternative hypothesis for age-related difficulties in bimanual coordination is based on the critical role of inter-hemispheric interactions for bimanual coordination. Many studies have shown that production of integrated bimanual movements relies on the inter-hemispheric communication across the corpus callosum, which is the major connection for information sharing between two hemispheres (Eliassen, Baynes, & Gazzaniga, 1999; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Franz, Eliassen, Ivry, & Gazzaniga, 1996; Kennerley, Diedrichsen, Hazeltine, Semjen, & Ivry, 2002). Recent studies suggested that the age-related declines in corpus callosum quantity (i.e., callosal size) and quality (i.e., the integrity of the callosal microstructure) are key contributors to age-related difficulties in bimanual coordination (Fling, Walsh, Bangert, Reuter-Lorenz, Welsh, & Seidler, 2011; Fling, & Seidler, 2011).

Most studies investigating the impact of advanced age on bimanual coordination focused on the timing accuracy by applying “in-phase”, “anti-phase”, and “multi-phase” coordination patterns (Goble, Cocon, Van Impe, De Vos, Wenderoth, & Swinnen, 2010; Fling, Walsh, Bangert, Reuter-Lorenz, Welsh, & Seidler, 2011; Lee, Wishart, & Murdoch, 2002; Bangert, Reuter-Lorenz, Walsh, Schachter, & Seidler, 2010; Wishart, Lee, Murdoch, & Hodges, 2000). For example, the study of Lee, Wishart and Murdoch (2002) applied a bimanual task, in which participants either moved two handles (one for each hand) perpendicular to the body away from or towards the center of the body to produce an in-phase coordination pattern, or moved the two handles in the same direction to produce an anti-phase coordination pattern. Similarly, the study of Goble, Cocon, Van Impe, De Vos, Wenderoth and Swinnen (2010) applied a wrist coordination task, in which the in-phase pattern was defined as midline symmetric wrist

flexion/extension, while the anti-phase pattern was defined as midline asymmetric wrist flexion/extension. In contrast to temporal accuracy, spatial accuracy in bimanual coordination tasks performed in an aging population has received much less attention. It has been suggested that temporal and spatial interference in bimanual coordination tasks have different origins (Heuer, 1993; Franz, Eliassen, Ivry, & Gazzaniga, 1996; see also for a review Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004). Specifically, the spatial interference in bimanual coordination arises from the interaction or overlap between the multiple spatial representations for spatial specifications (i.e. one spatial code for movement amplitude on the right side and another spatial code for the movement amplitude on the left side) (Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003). On the other hand, there are at least two hypothesized origins for the temporal interference. The temporal interference in discrete bimanual coordination reflects our general limitation to represent complex temporal relationship, which probably arises from an internal timing system in the cerebellum, whereas the temporal interference in continuous bimanual coordination arise from interactions between time-varying spatial representation on the cortical level (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Franz, Eliassen, Ivry, & Gazzaniga, 1996; Semjen, 2002; Spencer, Semjer, Yang, & Ivry, 2006). For example, the study of Franz, Eliassen, Ivry and Gazzaniga (1996) found that split-brain patients, who have resection of the corpus callosum as treatment for epilepsy, show strong temporal coupling, but do not show evident spatial interference in spatially incongruent conditions (i.e., the task required that the right hand had to draw a three sides box with the opening on the upper side, while the left hand had to draw another three sides box with the opening on the left side), indicating that at least there is a partial disassociation between temporal and spatial control in bimanual coordination.

Even though studies for young adults included temporal and spatial interferences, most previous studies investigated the impact of advanced age on temporal interference in bimanual coordination. Therefore, the present study investigated the impact of old age on spatial interference in a bimanual coordination task when the movement amplitude and movement direction are specified.

Methods

Participants

Sixteen older adults (67.69 ± 6.89 ; range from 49 to 78) were recruited from the Baton Rouge community in addition to 16 young adults (20.69 ± 0.79 ; range from 20 to 22) from study one. All participants were asked to fill out a short health history questionnaire. 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). All older participants scored higher than 25 (out of a maximum of 30) on the Mini Mental State Exam (MMSE) (Folstein, Folstein, & McHugh, 1975). Anyone who indicated (i.e. self-reported) 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. No participants were excluded from participation in the present study. 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.

Apparatus

The apparatus included a WACOM Intuos digitizer tablet (12x18 inches), two digital pens (WACOM GP-100), a 1 by 18 inch wooden stick, and two 20 inch monitors (monitor-1 and

monitor-2). The tablet recorded the X- and Y-position of each pen with a sampling rate of 100Hz and spatial resolution of 0.001cm. The wooden stick was placed on the vertical midline of the tablet to restrain the movement area of each hand, so the two pens and hands could not touch each other or cross over into each other's working area. 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 visual information of the movement of the hands. The experimental procedures were programmed in MovAlyzeR (NeuroScript LLC, Tempe, Arizona, USA) running on a PC (Dell Dimension 8400). The monitor-1 (which was the lower monitor) was placed approximately 80cm in front of the participants. Prior to the start of the go-stimulus, participants needed to study an example of the required movement directions and amplitudes shown on the lower monitor. After completion of the movements, monitor-2 (the upper monitor), which was placed right on top of the lower monitor, showed participants their actual movement trajectories (see Figure 2.1.).

Experimental design

The possible requirements for the movement amplitude for each hand were a short line (3cm) and a long line (6cm). Thus, there were four possible bimanual coordination tasks regarding the movement amplitudes: "Short-Short", "Long-Long", "Short-Long" and "Long-Short".

Moreover, participants needed to draw two 3cm lines in the "Short-Short" condition, two 6cm lines in the "Long-Long" condition, a 3cm line with the left hand and a 6cm line with the right hand in the "Short-Long" condition, and a 6cm line with the left hand and a 3cm line with the right hand in the "Long-Short" condition. The target amplitude ratio between the right and the left line was 1 (3:3 or 6:6) for the "Short-Short" and "Long-Long" conditions, while the target amplitude ratio between the right and the left line was 2 (6:3) for the "Short-Long" condition and 1/2 (3:6) for the "Long-Short" condition (see Table 2.1.).

The possible requirements for movement direction for each hand were drawing a vertical line and a horizontal line. Thus, there were four possible movement direction targets for the bimanual coordination task. They were both hands drew lines straight away from the body, i.e., vertical lines (“Vertical-Vertical”), both hands drew perpendicular lines to the body away from the center, i.e., horizontal lines (“Horizontal-Horizontal”), the left hand drew a perpendicular line to the body going left away from the center, i.e., horizontal line, while the right hand drew straight away from the body, i.e., vertical line (“Horizontal-Vertical”), and the left hand drew straight away from the body, i.e., vertical line, while the right hand drew a line perpendicular to the body going right away from the center, i.e., horizontal line (“Vertical-Horizontal”). Thus, the target angle between the two lines was 0° for the “Vertical-Vertical” condition, 180° for the “Horizontal-Horizontal” condition, and 90° for the “Horizontal-Vertical” and “Vertical-Horizontal” conditions (see Table 2.1.).

The current study used a 4 (four target amplitudes)*4(four target directions) nested design (see Table 2.1.). The four target amplitudes were “Short-Short”, “Long-Long”, “Short-Long”, and “Long-Short”. The four target directions were “Vertical-Vertical”, “Horizontal-Horizontal”, “Horizontal-Vertical”, and “Vertical- Horizontal”. In the pilot study, we found that completing the 16 conditions would take about 60-70 minutes and participants reported to be fatigued after about 30-40 minutes, therefore to avoid fatigue to be introduced as a confounding factor, the experimental design was adapted to limit fatigue to become a 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”) (see Table 2.1.).

Procedures

Participants sat comfortably in a chair in front of a table, where the tablet and monitors were placed on. Participants were instructed to hold one pen in each hand with their normal pen grip and they were allowed to rest their arms on the tablet. Each trial contained three parts: presentation of two lines showing the required movements, producing the bimanual coordination task, and receiving feedback. A trial started when two home positions were shown on the lower monitor. After participants placed the right pen in the right home position and placed the left pen in the left home position, the home positions disappeared and two lines showing the required movement trajectories was shown on the lower monitor. These lines, (one on the right one on the left side) showed the required movement directions and amplitudes. For instance, if the lines showed a 3cm vertical line on the left side and a 6cm 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 in the home position while the lines showing the required movement directions and amplitudes were presented. The presentation of the lines indicating the required bimanual task was shown for a random duration between 5 and 8 seconds, after which it disappeared with a loud beeping sound indicating 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). During execution of the bimanual task no visual on-line feedback was provided. Furthermore, participants were instructed to draw the lines at their comfortable speed, and to only lift the pens up from the digitizer tablet after they had finished the movements. After the

participant finished the bimanual task, the upper monitor 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 grey lines) to the required target movements (i.e., the black lines), and to note any differences between their executed movements and the target movements. The experimenter also provided knowledge of results verbally, by stressing the differences between the lines, e.g., “the right line is too short relative to the left line” and “the angular difference between two lines is too small”. This verbally given knowledge of results together with the visual presentation of the result in comparison to the required movements was provided to help participants to improve their performance on the next trial.

A practice session was provided before the experimental session started. First, the experimenter explained the procedures to the participants and asked participants to practice to draw 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 her/him 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 8 trials in each condition. Participants completed all 8 trials of one condition before moving on to the next condition. The sequence of experimental conditions was randomized for every participant. If a trial was deemed invalid, the participant needed to redo the trial. A trial was deemed to be invalid when any of the following requirements were not met:

- Participant drew visually curved instead of straight lines.
- Participant did not wait for the go-signal to start the bimanual movement task.
- Participants started the movement after about 2 seconds or more.
- After movement initiation the participant paused with one or both hands before the bimanual movement task was completed.
- The participant moved only one hand.
- The participant did not make a complete stop before the participant lifted one or both pens of the digitizer tablet.

Measurements and statistical analysis

First the movement data were low-pass filtered at 7 Hz with a 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. To estimate spatial accuracy for each hand four dependent variables were calculated; two for each hand. The first two dependent variables estimated amplitude error for each hand. The dependent variable for amplitude error for the line on the right (i.e., produced with the right hand) is A-error-R, which is calculated by the formula:

$$\frac{[actual_amplitude(R) - target_amplitude(R)]}{target_amplitude(R)}$$
. Positive A-error-R would indicate prolonged movement

amplitudes produced with the right hand, while negative A-error-R would suggest shortened movement amplitudes produced with the right hand. Similarly to the estimation of amplitude error of the produced lines with the right hand, the amplitude error for the line on the left (i.e., produced with the left hand) is A-error-L, which is determined by using the formula:

$$\frac{[actual_amplitude(L) - target_amplitude(L)]}{target_amplitude(L)}$$
. Positive A-error-L would indicate prolonged movement

amplitudes produced with the left hand, while negative A-error-L would imply shortened

movement amplitudes produced with the left hand. The other two variables used to assess spatial accuracy estimated the directional accuracy of the movements of each hand. The movement direction was defined as the stroke angle (at peak velocity) in relation to the straight line between the centers of the starting position and the target circle. The D_error_R was determined by the angle between the target line and the line produced on the right by the right hand. Positive D_error_R would indicate that the right hand moved away from the center of the body, while a negative D_error_R would imply that the right hand moved toward the center of the body (see Figure 2.2). Similarly, D_error_L was determined by the angle between the target line and the line drawn on the left with the left hand. Positive D_error_L would indicate that the left hand moved away from the center of the body, while negative D_error_L would suggest that the left hand moved toward the center of the body (see Figure 2.2).

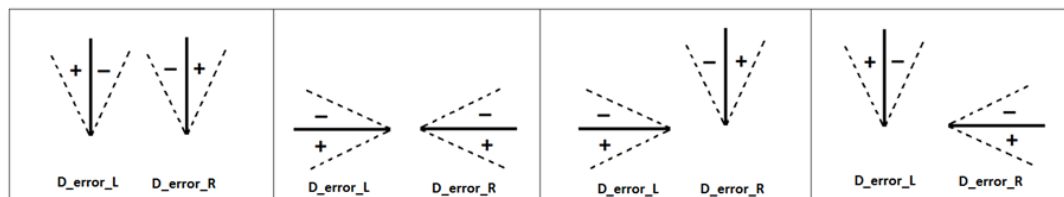


Figure 2.2. Interpretations for signs in D_error_R and D_error_L

The study focused on the effects age, and how the manipulations of target amplitude, target direction, and the spatial congruency of the required movements of both hands (i.e., amplitude congruency and direction congruency) would affect each of the dependent variable. Therefore, the independent factors used were: age-group, (i.e., young and older adults), target length (short and long), amplitude congruency (symmetric and asymmetric amplitude), target direction (vertical and horizontal), and direction congruency (symmetric and asymmetric direction). Therefore, the dependent variables were separately entered in a five factors (i.e., group, target length, amplitude congruency, target direction, direction congruency) analysis of

variance (ANOVA). If an interaction proved to be significant, bonferroni corrected post-hoc analyses were applied to identify the locus of the significant interaction.

Results

The present study investigated the effects of age on spatial coordination in bimanual movements. To estimate the accuracy of spatial coordination in the bimanual movement tasks, two sets of two dependent variables were analyzed, each focused on a different aspect of spatial accuracy (i.e., amplitude and directional accuracy). Therefore, to investigate the influence of age on spatial coordination, the results section is divided in two separate sections, i.e., one focused on amplitude and one focused on direction.

Analysis of amplitude accuracy

The amplitude error of the line drawn with the right hand, A-error-R showed a significant main effect for target length ($F(1,224) = 50.463, p < .001, \eta^2 = .184$) and target direction ($F(1,224) = 34.880, p < .001, \eta^2 = .135$), but the factor of age-group did not reach significance ($F(1,224) = 0.110, p = .741, \eta^2 = .000$; see Figure 3.1., panel A). Also amplitude congruency ($F(1,224) = 1.828, p = .178, \eta^2 = .008$) and direction congruency ($F(1,224) = 2.098, p = .149, \eta^2 = .009$) did not show a significant main effect. Even though age-group did not show a main effect, the interactions of age-group*target length* target direction* direction congruency ($F(1,224) = 5.929, p = .016, \eta^2 = .026$), and age-group*target length*amplitude congruency*target direction* direction congruency ($F(1,224) = 12.390, p < .001, \eta^2 = .052$) showed significance, see Figure 3.1., panels B and C. No other interactions reached statistical significance. In summary, these results suggest that there is no main age effect or an age associated congruency effect when using the dominant (right) hand. Both young and older adults overshoot the short line and they overshoot the vertical

lines, but the compound effects between amplitude length (overshooting the short line) and the direction (overshooting the vertical line) was only found in older adults.

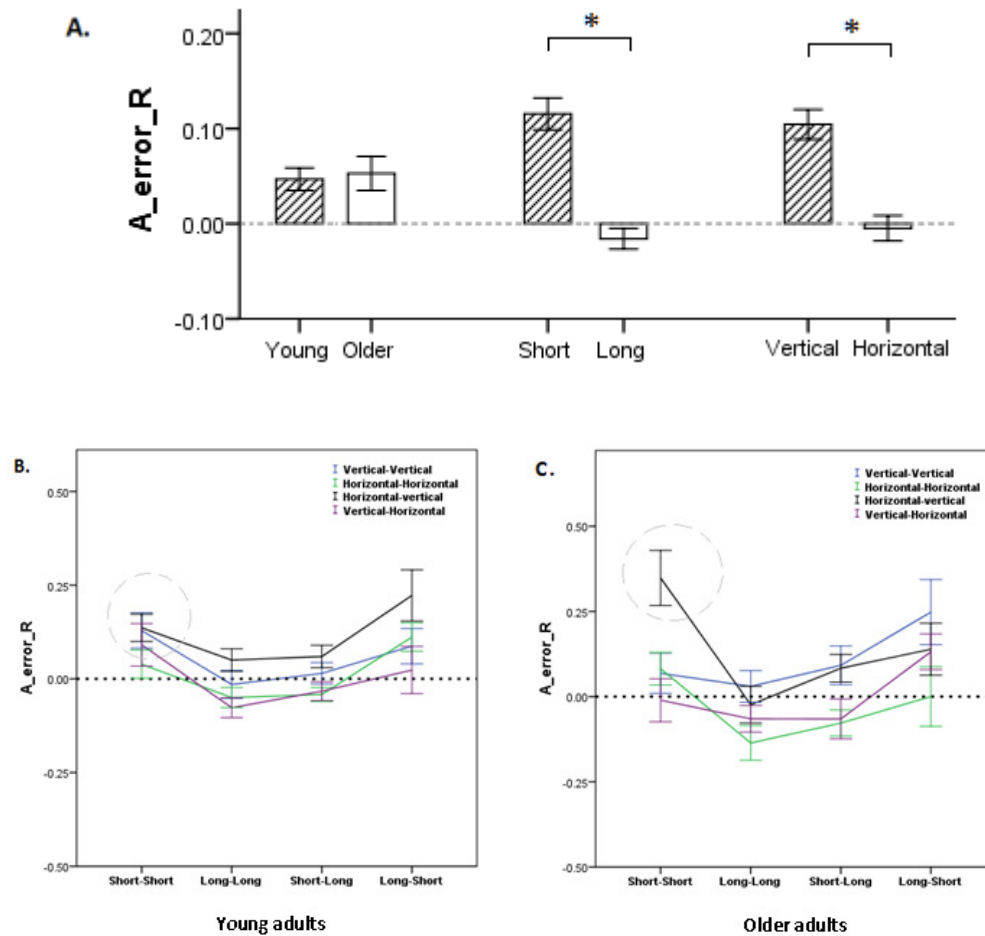


Figure 3.1. Panel A showed similar level of amplitude error in young and older groups. In accordance with findings of our previous study, larger A-error-R was found when the right hand drawing a short line compared to drawing a long line, showing the dominant hand overshoot the short line. On the other hand, the A-error-R was close to zero when drawing a horizontal line, while showed bigger than 10% of overshooting when the right hand was drawing a vertical line. Amplitude congruency and direction congruency had no effect on A-error-R. There was also no compound effects of amplitude length and orientation because the interaction of amplitude length*orientation was non-significant. Panel B and Panel C showed that when the right hand need to draw a short vertical line (**Short-Short** and **Horizontal-vertical**), while the left hand need to draw a short horizontal line (**Short-Short** and **Horizontal-vertical**), older adults showed evidently larger A-error-R than young adults, indicating compound effect of amplitude length and orientation in older adults, but not young adults.

The amplitude error of the line drawn with the left hand, A-error-L, showed a significant main effect for age-group ($F(1,224) = 6.489, p = .012, \eta^2 = .028$), target length ($F(1,224) = 45.084, p < .001, \eta^2 = .168$), target direction ($F(1,224) = 4.852, p = .029, \eta^2 = .021$) and direction congruency ($F(1,224) = 11.087, p < .001, \eta^2 = .047$), see Figure 3.2. None of the interactions reached significance for A-error-L. In summary, an effect of age was found for A-error-L, however, none of the independent variables interacted with age-group on A-error-L.

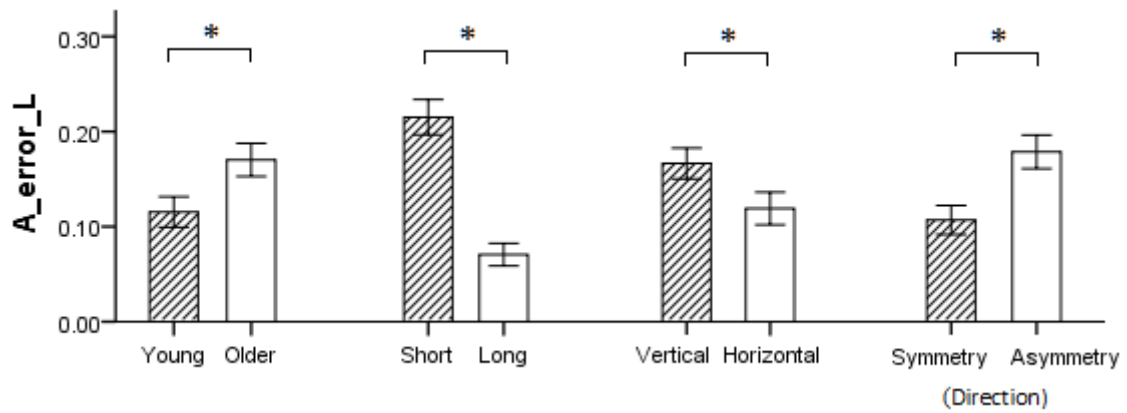


Figure 3.2. Older adults showed larger A-error-L than young adults. Larger A-error-L was found when the left hand drawing a short line compared to when drawing a long line. Larger A-error-L was also found when the left hand draws vertical line compared to when drawing a horizontal line. Furthermore, A-error-L was larger when the direction congruency was asymmetric compared to symmetric.

Analysis of direction accuracy

The direction error of the line drawn on the right with the right hand, D-error-R, did not reveal a significant main effect of age-group ($F(1,224) = 2.978, p = .086, \eta^2 = .013$). However, D-error-R was significantly affected by target direction ($F(1,224) = 51.215, p < .001, (\text{partial-}\eta^2) = .186$) and target length ($F(1,224) = 4.983, p = .027, \eta^2 = .022$), Figure 3.3., panel A.

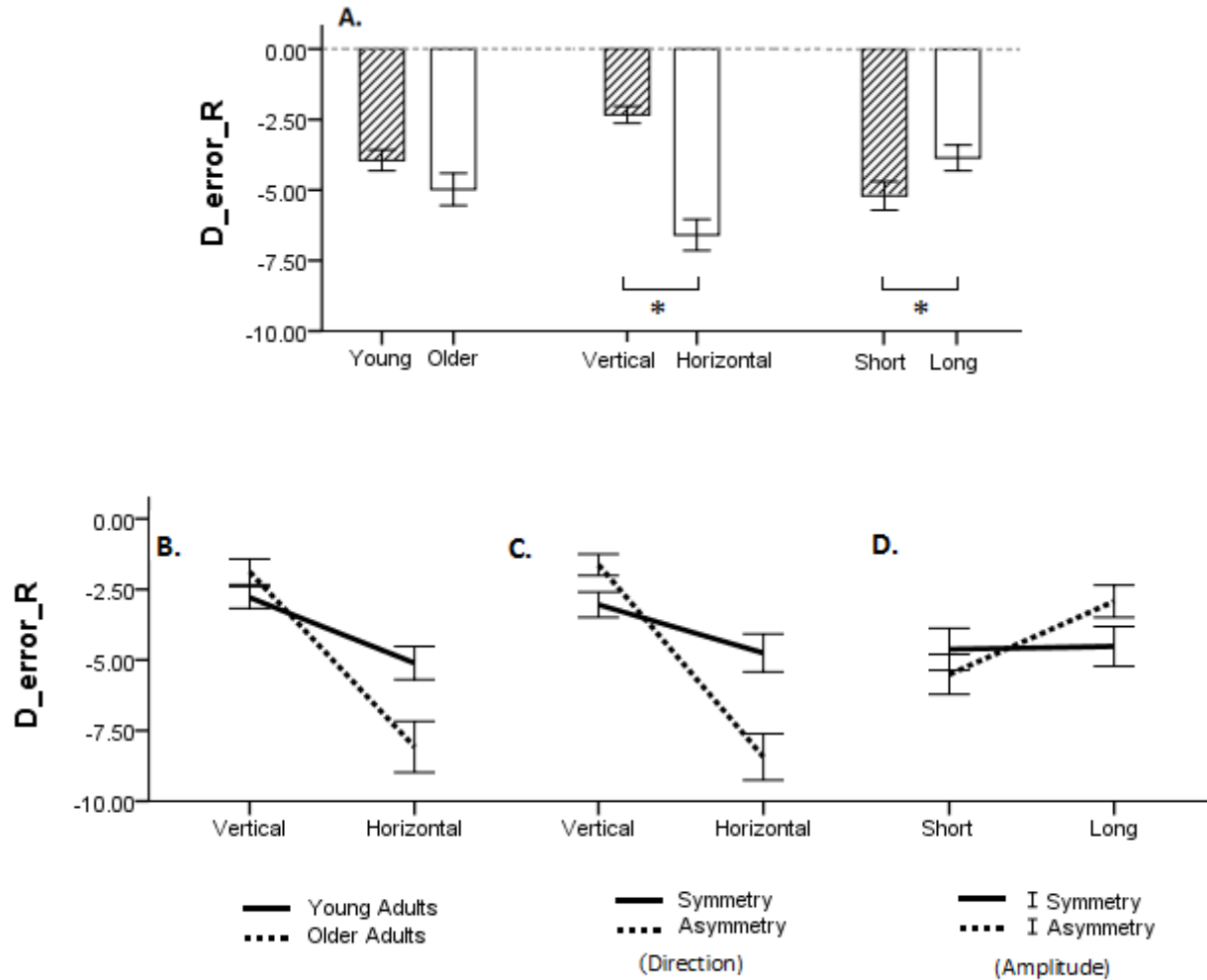


Figure 3.3. Panel A showed similar level of direction error in young and older groups. In accordance with findings of our previous study, larger D-error-R was found when the right hand drawing a horizontal line compared to when drawing a vertical line. On the other hand, the D-error-R was larger when drawing a short line compared to drawing a long line. Panel B showed that the D-error-R were similar between young and older adults when drawing a vertical line, while older adults had larger D-error-R than young adults when drawing a horizontal line, indicating age intensify the tendency of shifting the horizontal line. Panel C showed that the D-error-R were similar between symmetric and asymmetric direction when drawing a vertical line, while the D-error-R was larger in asymmetric direction than symmetric direction when drawing a horizontal line, indicating direction congruency alter the tendency of shifting the horizontal line. Panel D showed that the D-error-R were similar between different amplitude length when the amplitude congruency is symmetric, while larger D-error-R was found in short compared to long amplitude length when the amplitude congruency is asymmetric.

About interaction, Age-group did significantly interact with target direction ($F(1,224) = 10.634, p = .001, \eta^2 = .045$), and also the interactions between target direction*direction

congruency ($F(1,224) = 18.313, p < .001, \eta^2 = .076$) and target length*amplitude congruency ($F(1,224) = 4.267, p = .040, \eta^2 = .019$) proved to be significant, see Figure 3.3., panel B. In summary, age-group did interact with direction, which interaction was caused by an exacerbated tendency of older adults to draw horizontal lines more slanted.

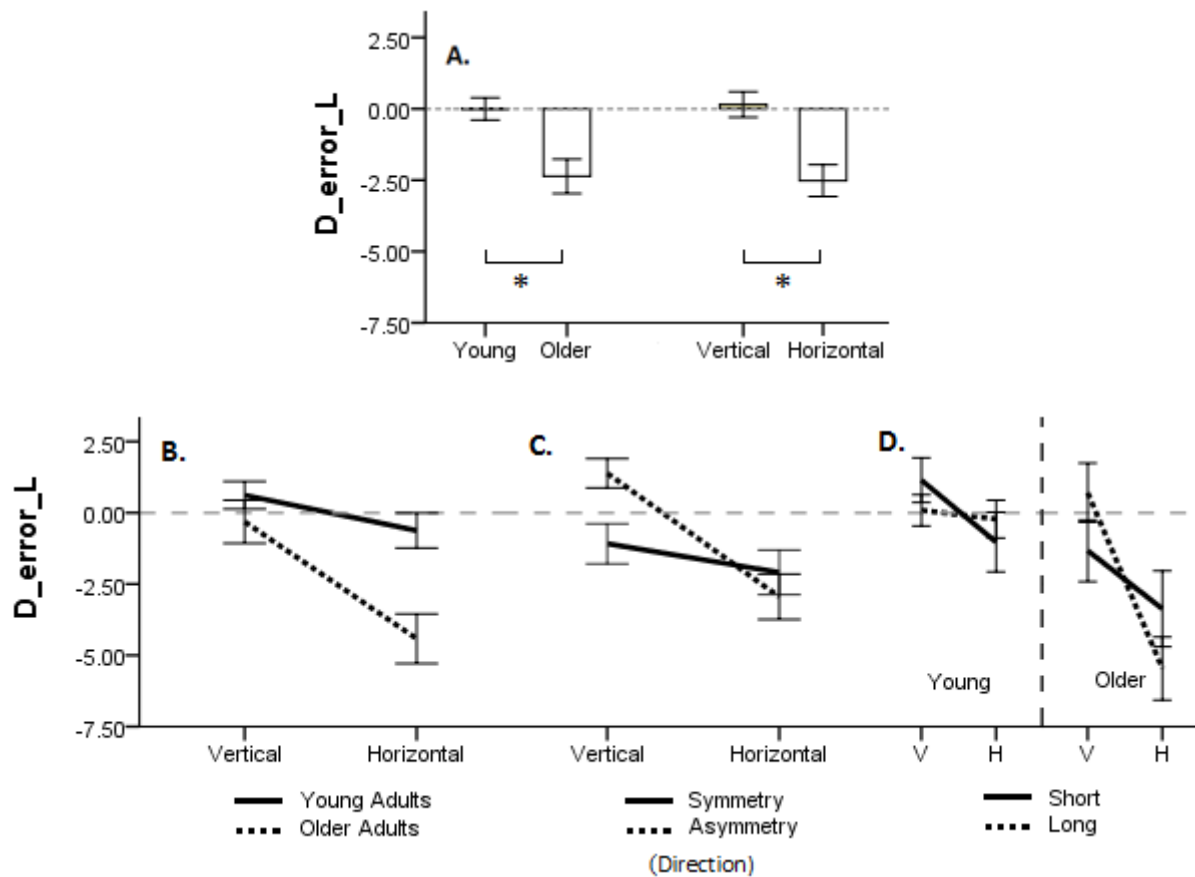


Figure 3.4. Panel A showed that older adults had larger D-error-L than young adults. In accordance with findings of our previous study, larger D-error-L was found when the left hand drawing a horizontal line compared to drawing a vertical line. Panel B showed that the D-error-L were similar between young and older adults when drawing a vertical line, while older adults had larger D-error-L than young adults when drawing a horizontal line, indicating again that age intensify the tendency of shifting the horizontal line. Panel C showed that the D-error-R were similar between vertical and horizontal when movement direction were symmetric, while the D-error-R were evidently differ between vertical and horizontal when movement direction were asymmetric. Panel D showed that, when the left hand needs to produce a long line, the D-error-R was close to zero in both vertical and horizontal conditions in young group, while the D-error-R was larger in horizontal than vertical in older group, indicating compound effect of amplitude length and orientation in older adults, but not young adults.

The direction error of the line drawn on the left with the left hand, D-error-L showed a significant main effect for age-group ($F(1,224) = 11.688, p = .001, \eta^2 = .050$) and target direction ($F(1,224) = 14.946, p < .001, \eta^2 = .063$), see Figure 3.4., panel A. Furthermore, significant interactions were found for age-group*target direction ($F(1,224) = 4.288, p = .040, \eta^2 = .019$; see Figure 3.4., panel B), target direction*direction congruency ($F(1,224) = 5.805, p = .017, \eta^2 = .025$; see Figure 3.4., panel C) and age-group*target direction*target length ($F(1,224) = 4.710, p = .031, \eta^2 = .021$; see Figure 3.4., panel D). In summary, an age-group effect was found for D-error-L, and similarly to the findings for D-error-R, D-error-L showed an age associated orientation effect in which the older adults showed an exacerbated tendency to move the drawn line more upward if the target line was oriented horizontal.

Discussion

The present study investigated the impact of advanced age on the spatial accuracy in bimanual coordination tasks. There were two major findings. The first finding was that advanced age reduces spatial accuracy of the movements made with the non-dominant hand, regardless whether movement amplitude or direction is specified. The second finding was that advanced age exacerbates the tendency of drawing horizontal lines with upward grade (directional control), while age had a limited impact on the tendency to overshoot short lines (amplitude control).

Age reduces spatial accuracy on the non-dominant side

When the two hands need to move simultaneously as required for performing a bimanual coordination task, the current study shows that older adults are able to maintain on the dominant side a similar level of spatial accuracy as young adults. However the spatial accuracy suffers on the non-dominant side in older adults when performing a bimanual coordination task. The results

seem to suggest that motor function on the dominant side remains relatively stable when aging, while motor function on the non-dominant side seems to decline with age. This difference in motor function between the dominant and non-dominant motor systems seems to be only supported if performance requires bimanual coordination, because several studies investigating aging effects of motor function in unimanual motor tasks have shown that the dominant hand's superiority reduces when getting older, which leads to motor function of the dominant and non-dominant limb to become more symmetric in older adults (Kalisch, Wilimzig, Kleibel, Tegenthoff, & Dinse, 2006; Przybyla, Haaland, Bagesteiro, & Sainburg, 2011). Further support for the reduced asymmetry of motor function in older adults comes from a study which showed that inter-limb transfer in older adults is more symmetric than inter-limb transfer in young adults (Wang, Przybyla, Wuebbenhorst, Haaland, & Sainburg, 2011). Based on the "hemispheric asymmetry reduction in older adults (HAROLD)" model, functional capabilities of the hemispheres decrease with age (Cabeza, 2002). According to this model older adults compensate for declines in brain functions by recruiting the hemispheres more bilaterally and increasing the hemispheric cooperation (Cabeza 2002; Cabeza, Anderson, Locantore, & McIntosh, 2002). In other words, if older adults were allowed to complete task with each hand separately, the accuracy of movements produced by the non-dominant hand should be as good as the movements produced by the dominant hand. To unite the findings of the current study and findings of previous studies, we suggest that an unimanual drawing task with amplitude and direction constraints is challenging for older adults, which require them to access extra attentional resources and/or recruit more neural areas than younger adults. Therefore, when the task becomes more complex due to the requirement to coordinate simultaneously the two hands to execute a drawing task with amplitude and direction constraints (such as in the current study),

the attention demands exceed those available to older adults resulting in deteriorated performance of the non-dominant hand due to a bias to use the dominant hand. In other words, older adults may (partially) decompose bimanual tasks into two unimanual tasks, and direct all necessary resources to the motor system on the dominant side in order to execute the movements on this side accurately. However, this allocation of attention resources comes at a price paid by the non-dominant motor system which receives the remaining resources which may not be sufficient. As a result, the spatial accuracy of lines drawn with the non-dominant hand declined in older adults as compared to young adults, while spatial accuracy of lines drawn with the dominant hand remained equal to the accuracy observed in line-drawings of young adults.

Differential effects of age on amplitude and direction

The control of amplitude differs from the control of direction in older adults which may differ from young adults. More specifically, the control of amplitude seems to be similar between young and older adults. Both age-groups did overshoot short lines no matter the amplitude requirements were congruent or incongruent. In contrast, the control of direction changed in older adults when performing the bimanual coordination task as compared to young adults. Young adults produce quite accurate movement directions when required to draw a vertical line, but they tend to draw horizontal lines with an upward angle. Similarly, older adults produced quite accurate movement directions as well when required to draw a vertical line, but the tendency to draw horizontal lines with an upward angle was exacerbated in older adults irrelevant if the horizontal line was drawn with the dominant or non-dominant hand.

Based on the representation model for bimanual coordination (Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003), our

previous study (see chapter2) proposed that, for discrete bimanual tasks with movement amplitude constraints, the movement system selects out of two possible movement length, the longer movement extent as a standard for the spatial code. However, for the shorter movements the motor system needs to derive spatial codes for the shorter movement from the longer movement standard. Therefore, shorter movements are more vulnerable to be influenced by longer movements when participants are informed that two possible movement amplitudes are included in the movement extent requirements. Similarly, the spatial code for horizontal movements may get derived from the spatial code for vertical movements, which are set as the standard for all movements. Thus horizontal movements become more vulnerable to be influenced by vertical movement requirements. It seems that the effects of the use of a standard spatial code for movement amplitude does not change in older adults, but the effects of using a standard spatial code for direction increases the effects on horizontal movements in older adults. In a study of Krakauer, Pine, Ghilardi and Ghez (2000), it was found that adapting to directional rotation is more challenging than adapting to a gain change of movement amplitude, indicating that directional adaption is more demanding than an amplitude adaption. Thus, it is prudent to assume that directional constraints in a bimanual coordination task places heavier demands on specialized neural structures, which resources of these neural structures may be limited in older adults. Thus, directional errors do increase in older adults when a horizontal direction is required and a vertical direction is a possibility in the requirements of the movements.

In summary, the present study showed that older adults were able to maintain a similar level of spatial accuracy on the dominant side as young adults, but they showed a reduced spatial accuracy on the non-dominant side, which is proposed to occur as result of the distribution of more attention resources to the movement on the dominant side. Furthermore, advanced age

demonstrated a clear effect on the control of movement direction in the bimanual coordination task, but the effect of age was limited for the control of movement amplitude. It is proposed that this pattern is probably caused by the higher demands necessary to have the motor system adapt to a directional constraint as compare to an adaptation to an amplitude constraint.

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CHAPTER 4: THE EFFECTS OF PARKINSON'S DISEASE ON SPATIAL ACCURACY IN BIMANUAL COORDINATION

Introduction

Bimanual coordination is the simultaneous movements of two hands. When two hands produce different actions, the stability and accuracy of the performance declines (Franz, Eliassen, Ivry, & Gazzaniga, 1996; Eliassen, Baynes, & Gazzaniga, 1999; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Semjen, 2002). Several studies have reported that individuals with Parkinson's disease (PD) show deficits in the control of bimanual movements (Johnson, Cunnington, Bradshaw, Philips, Lansek, & Rogers, 1998; Serrien, Steyvers, Debaere, Stelmach, & Swinnen, 2000; Swinnen, VanLangendonk, Verschueren, Peeters, Dom, & DeWeerdt, 1997; Van den Berg, Beek, Wagenaar & Van Gieringen, 2000). The common findings in these studies were that individuals with PD perform with more error and variability when producing asymmetric movement than healthy controls, and they have a strong tendency to revert from asymmetric to symmetric coordination patterns. Parkinson's disease is associated with basal ganglia dysfunction, which affects the complex basal ganglia-thalamic-neocortical loops including the supplementary motor area (SMA) and other cortical areas (Wu, Wang, Hallet, Li, & Chan, 2010). Considering that the SMA has been proposed as the critical cortical area for the control of bimanual coordination (Tanji, Okano, & Sato, 1988; Donchin, Gribova, Steinberg, Bergman, de Oliveira, & Vaadia, 2001; Sadato, Yonekura, Waki, Yamada, & Ishii, 1997; Lang, Oberg, Lindinger, Cheyne, & Deecke, 1990; de Oliveira, 2002), it should not be a surprise if individuals with deteriorated basal ganglia function, such as PD patients, demonstrate difficulties when performing bimanual coordination tasks. Additional support for this suggestion is a brain image study of Wu, Wang, Hallet, Li, & Chan (2010) revealed that Parkinson's disease resulted in

decreased connection between the putamen and SMA, which further resulted in difficulties of individuals with PD to produce bimanual movements.

The majority of research investigating the influence of Parkinson's disease on bimanual coordination focused on temporal coordination and examined performance of bimanual tasks in "in-phase", "anti-phase", and "multi-phase" coordinative patterns. Impaired bimanual coordination was observed in individuals with PD when they performed bimanual anti-phase or multi-phase movements. For example, Johnson, Cunnington, Bradshaw, Phillips, Iansek, and Rogers (1988) investigated performance on bimanual tasks by requiring participants to perform bimanual in-phase and anti-phase coordination patterns at fast (2Hz) and slow (1Hz) speeds, and with and without an external cue to pace the movements (i.e., a metronome). The results showed that individuals with PD are able to perform the in-phase movements with external fast and slow paced cues. However, when the external cues were withheld, they showed a loss of accuracy and stability, and if the task required an anti-phase coordination pattern they were unable to keep the anti-phase movement pattern no matter if the pace was externally cued at a high or low speed. In another study (Almeida, Wishart, & Lee, 2002), participants coordinated simultaneous displacements of two linear sliding devices toward and away from the midline of the body under three speeds with either an in-phase or anti-phase coordination pattern. This study found that individuals with PD are able to produce in-phase patterns, but that they were unable to produce anti-phase patterned movements. Moreover, movement freezing occurred in 8.1% of individuals with PD when they tried to perform the anti-phase bimanual movements, suggested a deteriorated ability in bimanual coordination due to dysfunction of the basal ganglia. Also the study of Ponsen, Daffertshofer, van den Heuvel, Wolters, Beek and Berendse (2006) showed support for the difficulty individuals with PD experience when drawing in anti-phase

coordination patterns. They used a paradigm in which participants had to draw two circles in an in-phase or anti-phase coordination pattern with high or low speeds. The results again showed that maintaining a constant phase relationship between the hands was more difficult for individuals with PD than controls when participants were required to follow an anti-phase coordination pattern.

In contrast to the temporal accuracy aspects of bimanual coordination, spatial accuracy aspects of bimanual coordination in PD affected individuals have received much less attention. It has been suggested that temporal and spatial interference in bimanual coordination tasks have a different origin (Heuer, 1993; Franz, Eliassen, Ivry, & Gazzaniga, 1996; for a review see Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004). Specifically, temporal interference in discrete bimanual coordination reflects our general limitation to represent complex temporal relationships, which probably arise from an internal timing system in the cerebellum, whereas temporal interference in continuous bimanual coordination arises from interactions between time-varying spatial representations on the cortical level (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Franz, Eliassen, Ivry, & Gazzaniga, 1996; Semjen, 2002; Spencer, Semjer, Yang, & Ivry, 2006). In contrast, spatial interference in bimanual coordination arises from the interaction or overlap between the two or more spatial representations which specify the spatial parameters (i.e., one spatial code for movement amplitude on the right side and another spatial code for the movement amplitude on the left side) (Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003). Our previous study, which investigated the impact of age on the spatial interference in a bimanual task, in which movement amplitude and direction was manipulated, showed that advanced age altered the control of movement direction, but the effect of age did not exacerbate the reductions in control of

movement direction when the task required a spatially incongruent movement pattern (see chapter3). The latter findings differ from findings of studies emphasizing temporal coordination, thus indicating that there is least partial disassociation between temporal and spatial control in bimanual coordination tasks.

The purpose of the study is to explore the influence of Parkinson's disease on spatial aspects of bimanual coordination tasks. To this end, we compared performance of individuals with PD and healthy older controls on a bimanual coordination task, in which we manipulated movement amplitude and direction.

Methods

Participants

Nineteen individuals with PD (64.44 ± 8.00 ; range from 45 to 79) were recruited from the Baton Rouge community in addition to 16 older adults (67.69 ± 6.89 ; range from 49 to 78) from study two. Three individuals with PD failed to finish the whole test, so their data were excluded from further analysis. All participants were asked to fill out a short health history questionnaire. 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). All older participants scored higher than 25 (out of a maximum of 30) on the Mini Mental State Exam (MMSE) (Folstein, Folstein, & McHugh, 1975). All individuals with PD were tested during the "on" phase of their medication cycle. The individuals with PD scored from 2 to 34 on the motor subscale of the Unified Parkinson's Disease Rating Scale (UPDRS) (Fahn & Elton, 1987). The detailed information (i.e. gender, age, score of UPDRS-III and duration of disease) of individuals with PD are presented in Table 4.1.. 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. 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.

Table 4.1. Information for participants with Parkinson's disease

Participant number	Gender	Age(years)	UPDRS-III	duration of disease (years)
1	M	67	27	12
2	F	66	18	1
3	M	62	21	3
4	F	58	7	6
5	M	64	14	7
6	M	79	11	2
7	M	70	12	3.5
8	F	59	19	6
9	M	45	22	0.5
10	M	70	13	7
11	M	66	20	9
12	F	72	34	25
13	M	54	17	8
14	F	61	8	1
15	F	69	2	5
16	F	69	11	5

Apparatus

The apparatus included a WACOM Intuos digitizer tablet (12x18 inches), two digital pens (WACOM GP-100), a 1 by 18 inch wooden stick, and two 20 inch monitors (monitor-1 and monitor-2). The tablet recorded the X- and Y-position of each pen with a sampling rate of 100Hz and spatial resolution of 0.001cm. The wooden stick was placed on the vertical midline of the tablet to restrain the movement area of each hand, so the two pens and hands could not touch each other or cross over into each other's working area. 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 visual information of the movement of the hands. The experimental procedures were programmed in MovAlyzeR (NeuroScript LLC, Tempe, Arizona, USA) running on a PC (Dell Dimension 8400).

The monitor-1 (which was the lower monitor) was placed approximately 80cm in front of the participants. Prior to the start of the go-stimulus, participants needed to study an example of the required movement directions and amplitudes shown on the lower monitor. After completion of the movements, monitor-2 (the upper monitor), which was placed right on top of the lower monitor, showed participants their actual movement trajectories (see Figure 2.1.).

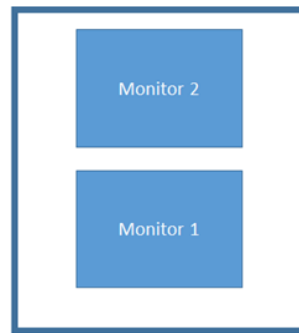


Figure 4.1. Monitors Configuration

Experimental design

The possible requirements for the movement amplitude for each hand were a short line (3cm) and a long line (6cm). Thus, there were four possible bimanual coordination tasks regarding the movement amplitudes: “Short-Short”, “Long-Long”, “Short-Long” and “Long-Short”.

Moreover, participants needed to draw two 3cm lines in the “Short-Short” condition, two 6cm lines in the “Long-Long” condition, a 3cm line with the left hand and a 6cm line with the right hand in the “Short-Long” condition, and a 6cm line with the left hand and a 3cm line with the right hand in the “Long-Short” condition. The target amplitude ratio between the right and the left line was 1 (3:3 or 6:6) for the “Short-Short” and “Long-Long” conditions, while the target amplitude ratio between the right and the left line was 2 (6:3) for the “Short-Long” condition and 1/2 (3:6) for the “Long-Short” condition (see Table 2.1.).

The possible requirements for movement direction for each hand were drawing a vertical line and a horizontal line. Thus, there were four possible movement direction targets for the

bimanual coordination task. They were both hands drew lines straight away from the body, i.e., vertical lines (“Vertical-Vertical”), both hands drew perpendicular lines to the body away from the center, i.e., horizontal lines (“Horizontal-Horizontal”), the left hand drew a perpendicular line to the body going left away from the center, i.e., horizontal line, while the right hand drew straight away from the body, i.e., vertical line (“Horizontal-Vertical”), and the left hand drew straight away from the body, i.e., vertical line, while the right hand drew a line perpendicular to the body going right away from the center, i.e., horizontal line (“Vertical-Horizontal”). Thus, the target angle between the two lines was 0° for the “Vertical-Vertical” condition, 180° for the “Horizontal-Horizontal” condition, and 90° for the “Horizontal-Vertical” and “Vertical-Horizontal” conditions (see Table 2.1.).

Table 2.1. Experimental design

Target directions Target amplitudes	Vertical-Vertical (target = 0°)	Horizontal-Horizontal (target = 180°)	Vertical- Horizontal (target = 90°)	Horizontal-Vertical (target = 90°)
Short-short (target = 1)	x	— — o	— x	— o
Long-long (target = 1)	o	— — x	— o	— x
Short-long (target = 2)	x	— — o	— x	— o
Long-short (target = 1/2)	o	— — x	— o	— x

The current study used a 4 (four target amplitudes)*4(four target directions) nested design (see Table 2.1.). The four target amplitudes were “Short-Short”, “Long-Long”, “Short-Long”, and “Long-Short”. The four target directions were “Vertical-Vertical”, “Horizontal-Horizontal”, “Horizontal-Vertical”, and “Vertical- Horizontal”. In the pilot study, we found that completing the 16 conditions would take about 60-70 minutes and participants reported to be fatigued after about 30-40 minutes, therefore to avoid fatigue to be introduced as a confounding

factor, the experimental design was adapted to limit fatigue to become a 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”) (see Table 2.1.).

Procedures

Participants sat comfortably in a chair in front of a table, where the tablet and monitors were placed on. Participants were instructed to hold one pen in each hand with their normal pen grip and they were allowed to rest their arms on the tablet. Each trial contained three parts: presentation of two lines showing the required movements, producing the bimanual coordination task, and receiving feedback. A trial started when two home positions were shown on the lower monitor. After participants placed the right pen in the right home position and placed the left pen in the left home position, the home positions disappeared and two lines showing the required movement trajectories was shown on the lower monitor. These lines, (one on the right one on the left side) showed the required movement directions and amplitudes. For instance, if the lines showed a 3cm vertical line on the left side and a 6cm 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 in the home position while the lines showing the required movement directions and amplitudes were presented. The presentation of the lines indicating the required bimanual task was shown for a random duration between 5 and 8 seconds, after which it disappeared with a loud beeping sound indicating 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). During execution of the bimanual task no visual on-line feedback was provided. Furthermore, participants were instructed to draw the lines at their comfortable speed, and to only lift the pens up from the digitizer tablet after they had finished the movements. After the participant finished the bimanual task, the upper monitor 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 grey lines) to the required target movements (i.e., the black lines), and to note any differences between their executed movements and the target movements. The experimenter also provided knowledge of results verbally, by stressing the differences between the lines, e.g., “the right line is too short relative to the left line” and “the angular difference between two lines is too small”. This verbally given knowledge of results together with the visual presentation of the result in comparison to the required movements was provided to help participants to improve their performance on the next trial.

A practice session was provided before the experimental session started. First, the experimenter explained the procedures to the participants and asked participants to practice to draw 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 her/him 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 8 trials in each condition. Participants completed all 8 trials of one condition before moving on to the next condition. The sequence of experimental conditions was randomized for every participant. If a trial was deemed invalid, the participant needed to redo the trial. A trial was deemed to be invalid when any of the following requirements were not met:

- Participant drew visually curved instead of straight lines.
- Participant did not wait for the go-signal to start the bimanual movement task.
- Participants started the movement after about 2 seconds or more (i.e., the participant did not follow the direction to immediately start after the go-signal).
- After movement initiation the participant paused with one or both hands before the bimanual movement task was completed.
- The participant moved only one hand, i.e., they did not move the hands simultaneously.
- The participant did not make a complete stop before the participant lifted one or both pens of the digitizer tablet.

Measurements and statistical analysis

First the movement data were low-pass filtered at 7 Hz with a 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. To estimate spatial accuracy for each hand four dependent variables were calculated; two for each hand. The first two dependent variables estimated amplitude error for each hand. The dependent variable for amplitude error for the line on the right (i.e., produced with the right hand) is A-error-R, which is calculated by the formula:

$$\frac{[actual_amplitude(R) - target_amplitude(R)]}{target_amplitude(R)}$$
. Positive A-error-R would indicate prolonged movement

amplitudes produced with the right hand, while negative A-error-R would suggest shortened movement amplitudes produced with the right hand. Similarly to the estimation of amplitude error of the produced lines with the right hand, the amplitude error for the line on the left (i.e., produced with the left hand) is A-error-L, which is determined by using the formula:

$$\frac{[actual_amplitude(L) - target_amplitude(L)]}{target_amplitude(L)}$$

Positive A-error-L would indicate prolonged movement amplitudes produced with the left hand, while negative A-error-L would imply shortened movement amplitudes produced with the left hand. The other two variables used to assess spatial accuracy estimated the directional accuracy of the movements of each hand. The movement direction was defined as the stroke angle (at peak velocity) in relation to the straight line between the centers of the starting position and the target circle. The D_error_R was determined by the angle between the target line and the line produced on the right by the right hand. Positive D_error_R would indicate that the right hand moved away from the center of the body, while a negative D_error_R would imply that the right hand moved toward the center of the body (see Figure 2.2.). Similarly, D_error_L was determined by the angle between the target line and the line drawn on the left with the left hand. Positive D_error_L would indicate that the left hand moved away from the center of the body, while negative D_error_L would suggest that the left hand moved toward the center of the body (see Figure 2.2.).

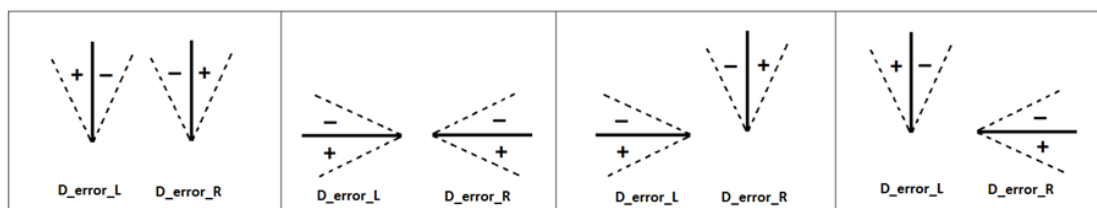


Figure 2.2. Interpretations for signs in D_error_R and D_error_L

The study focused on the effects group, and how the manipulations of target amplitude, target direction, and the spatial congruency of the required movements of both hands (i.e.,

amplitude congruency and direction congruency) would affect each of the dependent variable. Therefore, the independent factors used were: group, (i.e., older adults and individuals with PD), target length (short and long), amplitude congruency (symmetric and asymmetric amplitude), target direction (vertical and horizontal), and direction congruency (symmetric and asymmetric direction). Therefore, the dependent variables were separately entered in a five factors (i.e., group, target length, amplitude congruency, target direction, direction congruency) analysis of variance (ANOVA). If an interaction proved to be significant, bonferroni corrected post-hoc analyses were applied to identify the locus of the significant interaction.

Results

We investigated the effects of Parkinson's disease on spatial coordination in bimanual movements. To estimate the accuracy of spatial coordination in the bimanual movement tasks, two sets of two dependent variables were analyzed, each focused on a different aspect of spatial accuracy (i.e., amplitude and directional accuracy). Therefore, to investigate the influence of Parkinson's disease on spatial coordination, the results section is divided in two separate sections, i.e., one focused on amplitude and one focused on direction.

Analysis of amplitude accuracy

The amplitude error of the line drawn with the right hand, A-error-R showed a significant main effect for target length ($F(1,224) = 43.539, p < .001, \eta^2 = .163$) and target direction ($F(1,224) = 31.954, p < .001, \eta^2 = .125$), but the factor of age-group did not reach significance ($F(1,224) = 1.314, p = .253, \eta^2 = .006$; see Figure 4.1., panel A). The interactions of target length*amplitude congruency*target direction* direction congruency showed significance ($F(1,224) = 9.666, p = .002, \eta^2 = .041$), see Figure 4.1., panel B. No other interactions reached statistical significance.

In summary, these results suggest that there is no main group effect or a group associated effect when using the dominant (right) hand. Both older adults and individuals with PD overshoot the short line and they overshoot the vertical lines.

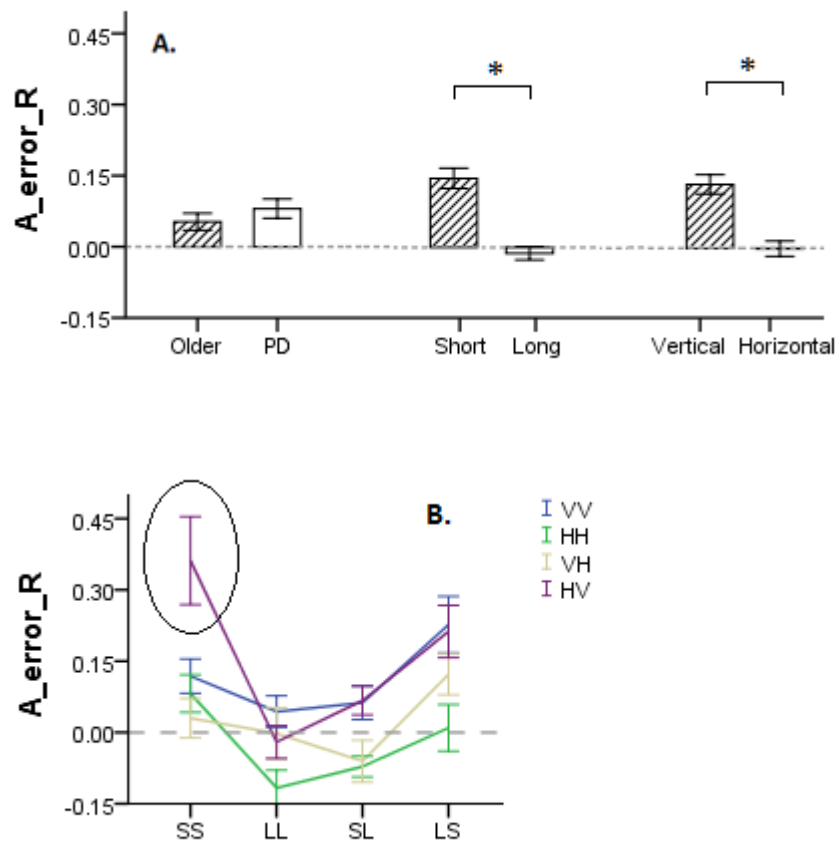


Figure 4.1. Panel A showed similar level of amplitude error on the right side in older and PD groups. In accordance with findings of our previous study, larger A-error-R was found when the right hand drawing a short line compared to drawing a long line, showing the dominant hand overshoot the short line. Moreover, larger A-error-R was found when the right hand drawing a vertical line compared to drawing a horizontal line, showing the dominant hand overshoot the vertical line. Panel B showed that when the right hand need to draw a short vertical line (**Short-Short** and **Horizontal-vertical**), while the left hand need to draw a short horizontal line (**Short-Short** and **Horizontal-vertical**), the A-error-R was evidently larger than in other coordinative conditions.

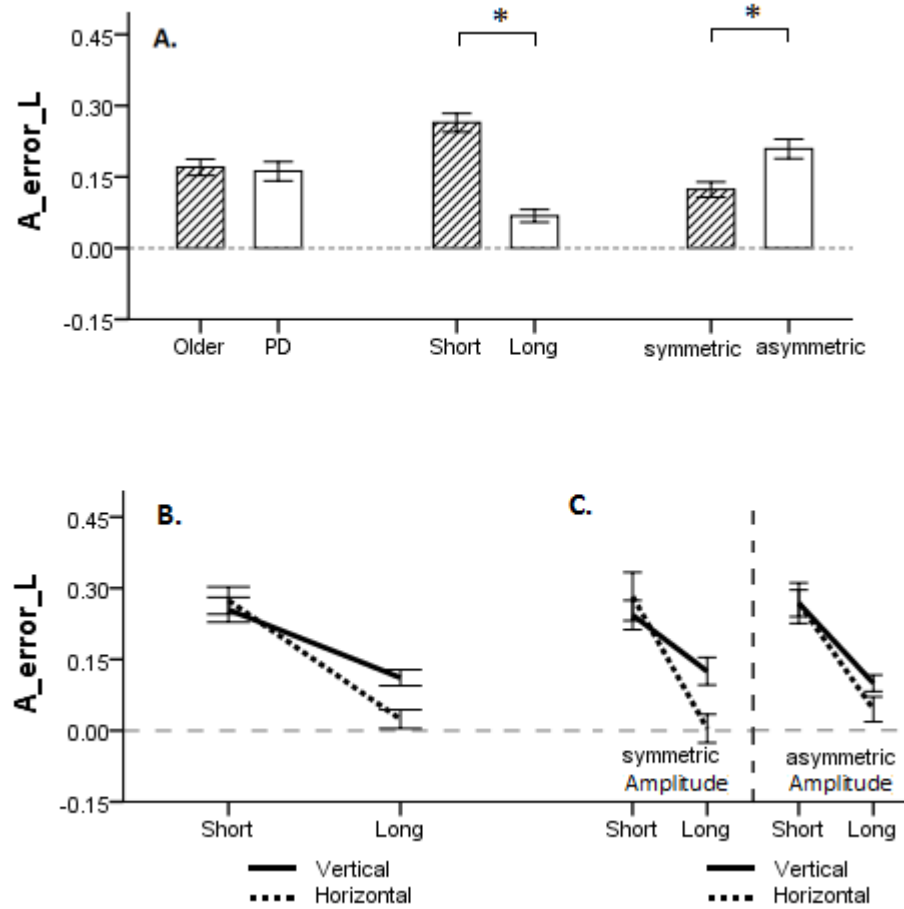


Figure 4.2. Panel A showed similar level of amplitude error on the right side in older and PD groups. Larger A-error-L was found when the left hand drawing a short line compared to when drawing a long line. Larger A-error-L was also found under directional asymmetric condition compared to when under directional symmetric condition. Panel B showed that the smallest A-error-L was found when the left hand draws a long horizontal line. Panel C further demonstrated that the smallest A-error-L was found when the left hand draws a long horizontal line while the right hand draws a long line at the same time.

The amplitude error of the line drawn with the left hand, A-error-L, showed a significant main effect for target length ($F(1,224) = 69.632, p < .001, \eta^2 = .237$) and direction congruency ($F(1,224) = 13.219, p < .001, \eta^2 = .056$), but the factor of age-group did not reach significance ($F(1,224) = 0.123, p = .726, \eta^2 = .001$; see Figure 4.2.). Furthermore, significant interactions were found for target length*target direction ($F(1,224) = 5.153, p = .024, \eta^2 = .022$; see Figure 4.2., panel B) and target length*target direction* direction congruency ($F(1,224) = 3.939, p = .048$,

$\eta^2=.017$; see Figure 4.2., panel C). No other interactions reached statistical significance. In summary, these results suggest that there is no main group effect or a group associated effect when using the dominant (right) hand. Both older adults and individuals with PD overshoot the short line and they overshoot the directional asymmetric lines.

Analysis of direction accuracy

The direction error of the line drawn on the right with the right hand, D-error-R, showed a significant main effect for group ($F(1,224)=5.709, p=.018, \eta^2=.025$) and target direction ($F(1,224)=68.355, p<.001, \eta^2=.234$), Figure 4.3., panel A. The interactions between target direction and direction congruency (target direction*direction congruency) proved to be significant ($F(1,224)=12.709, p<.001, \eta^2=.054$), see Figure 4.3., panel B. In summary, a group effect was found for D-error-R, but there is no group associated effect when using the dominant (right) hand. Both older adults and individuals with PD shift the horizontal line upwards, especially when the directional coordination between hands is asymmetric.

The direction error of the line drawn on the left with the left hand, D-error-L showed a significant main effect for target direction ($F(1,224)=25.235, p<.001, \eta^2=.101$), but the factor of age-group did not reach significance ($F(1,224)=0.734, p=0.734, \eta^2=.003$; see Figure 4.4., panel A). Furthermore, significant interactions were found for target direction*direction congruency ($F(1,224)=11.540, p=.001, \eta^2=.049$; see Figure 4.4., panel B) and age-group*target direction* direction congruency*target length*amplitude congruency ($F(1,224)=5.062, p=.025, \eta^2=.022$; see Figure 4.4., panel C). In summary, these results suggest that there is no main group effect. Both older adults and individuals with PD shift the horizontal line upwards.

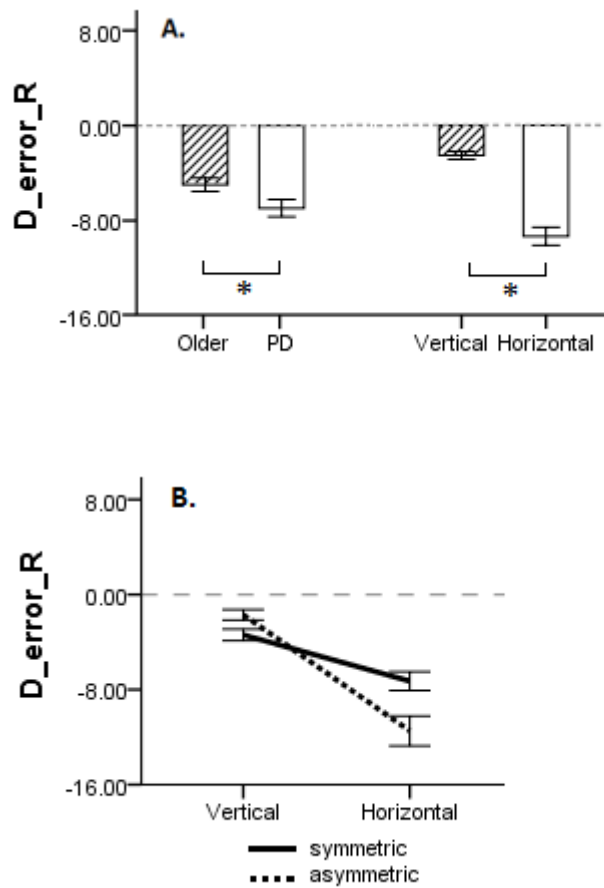


Figure 4.3. Panel A showed larger direction error on the right side PD group than older groups. In accordance with findings of our previous study, larger D-error-R was found when the right hand drawing a horizontal line compared to when drawing a vertical line. Panel B showed that the D-error-R were similar between symmetric and asymmetric direction when drawing a vertical line, while the D-error-R was larger in asymmetric direction than symmetric direction when drawing a horizontal line, indicating direction congruency alter the tendency of shifting the horizontal line.

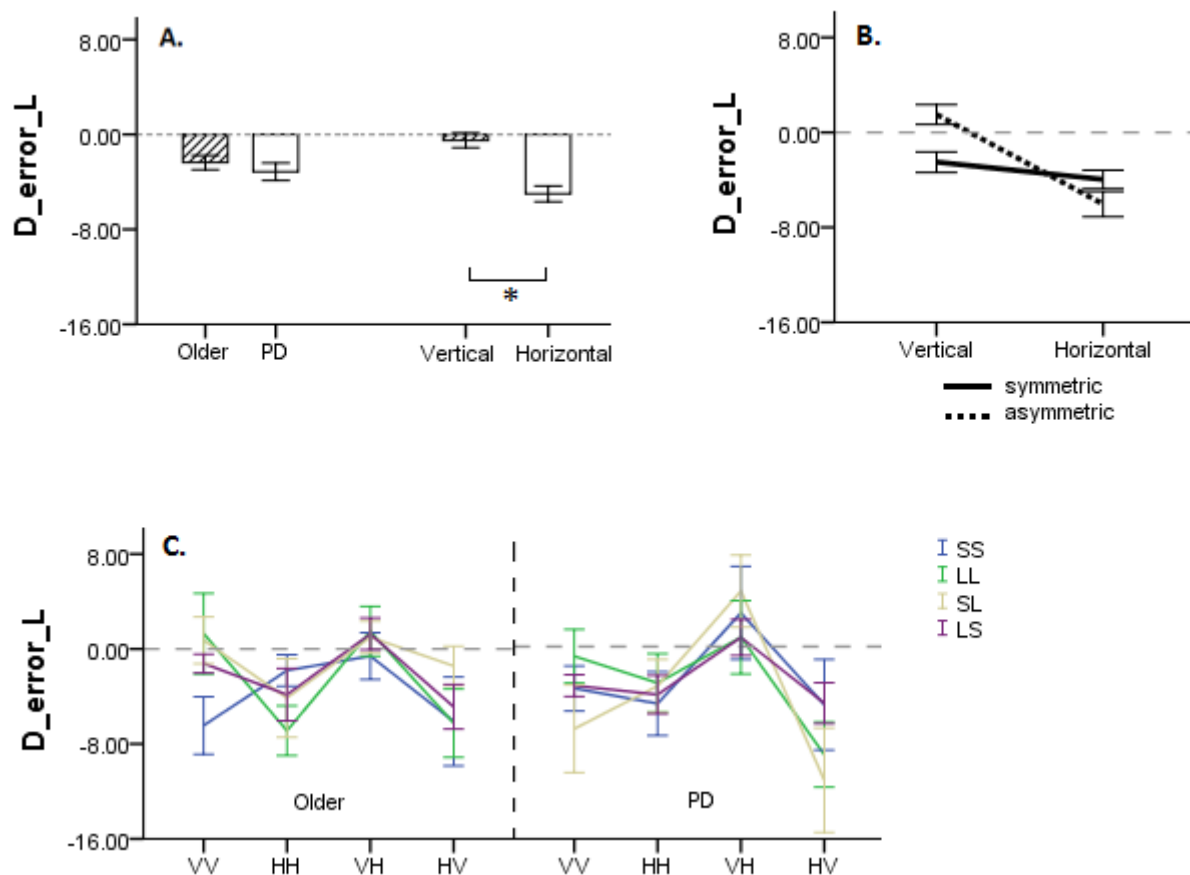


Figure 4.4. Panel A showed similar level of directional error on the left side in older and PD groups. In accordance with findings of our previous study, larger D-error-L was found when the left hand drawing a horizontal line compared to drawing a vertical line. Panel B showed the D-error-L were similar between vertical and horizontal when movement direction were symmetric, while the D-error-R were evidently differ between vertical and horizontal when movement direction were asymmetric.

Discussion

The present study investigated the impact of Parkinson's disease on the spatial accuracy in bimanual coordination tasks. In accordance with our previous study (see chapter3), the present study found that both groups (individuals with Parkinson's disease and older controls) overshoot short lines no matter the amplitude requirements were congruent or incongruent. The results also showed that shifting the horizontal line upward is a general tendency for individuals with Parkinson's disease and older controls when bimanual coordination is required. More

importantly, it was shown that individuals with Parkinson's disease are able to maintain a similar level of spatial accuracy as older controls, except directional accuracy of the line drawn with the dominant hand, which showed in individuals with Parkinson's disease a decline of about two degrees. Furthermore, the spatial control for bimanual movement seems to be similar between young and older adults because none of the interactions with group reached statistical significance. Taken together, the present study demonstrated that Parkinson's disease has a very limited influence in addition to effects as result of age on spatial accuracy in bimanual coordination tasks.

Obvious impairments of Parkinson's disease patients in bimanual coordination have been consistently reported in previous studies movements (Johnson, Cunnington, Bradshaw, Philips, Lansek, & Rogers, 1998; Serrien, Steyvers, Debaere, Stelmach, & Swinnen, 2000; Swinnen, VanLangendonk, Verschueren, Peeters, Dom, & DeWeerd, 1997; Van den Berg, Beek, Wagenaar, & Van Gieringen, 2000). The study of Posen, Daffertshofer, van den Heuvel, Wolters, Beek and Berendse (2006) even reported the occurrence of bimanual coordination dysfunction in early Parkinson's disease patients, i.e., individuals with disease durations of no more than 2 years. The majority of studies which observed impaired bimanual coordination in individuals with Parkinson's disease focused on temporal aspects of the coordination and examined performance of bimanual tasks in "in-phase", "anti-phase", and "multi-phase" coordinative patterns. In contrast to the multiple studies investigating temporal aspects of bimanual coordination in Parkinson's disease patients, the current study showed only very limited impairments in the spatial aspects of bimanual coordination in these individuals. However, some evidence has been shown that individuals with Parkinson's disease perform bimanual movements with minimal impairments. For example, the study of Stelmach and

Worringham (1988) reported intact bimanual performance in individuals with Parkinson's disease. In their study, the participants were instructed to make lateral arm movements away from the midline as rapidly as possible to the target(s) indicated by illuminations of the LEDs. The targets were located either at 10.5cm or 20cm away from the home position, therefore in this study the spatial features (i.e., movement amplitude) of the bimanual coordination task were manipulated instead of temporal features. The experiment tested unimanual and bimanual movements. An unimanual movement was required when only one LED was illuminated, while a bimanual movement was required when two LEDs were illuminated. In this study, the reaction time (RT) and movement time (MT) for each hand in each task were recorded as the dependent variables. The results showed that RT of the bimanual movements increased as compared to the unimanual movements similarly for individuals with PD and controls. Moreover, individuals with PD needed a similar amount of additional time as controls to execute bimanual movements when compared to the unimanual movements. In another study (Tresilian, Stelmach, & Adler, 1997) a reach-to-grasp task in which the accuracy demands were manipulated was used. Individuals with Parkinson's disease and older control either completed the task with one hand (unimanual movement) or with both hands (bimanual movement). Similar to the previous findings of Stelmach and Worringham (1988), this study (Tresilian, Stelmach, & Adler 1997) found that older controls and individuals with Parkinson's disease showed similar performance impairments in bimanual movements when these movements were compared to unimanual movements. Moreover, the performance declines due to increased accuracy requirements were also similar between the older controls and individuals with Parkinson's disease. These conflicting findings with other studies investigating bimanual coordination seem to suggest that the influence of Parkinson's disease on the performance of bimanual coordination is task-

dependent: Parkinson's disease affects the temporal control of bimanual movements, while it has a very limited influence on the spatial control of bimanual coordination.

Parkinson's disease is associated with basal ganglia dysfunction. Therefore, the many observations in previous studies that individuals with PD demonstrate difficulties when performing bimanual coordination tasks indicate that the basal ganglia is involved in the control of bimanual movements. However, the findings of the present study along with the two studies of Stelmach and colleagues (Stelmach & Worringham, 1988; Tresilian, Stelmach, & Adler, 1997) suggest that although the basal ganglia may be important for temporal control in bimanual coordination, spatial control of bimanual coordination seem to be less dependent on basal ganglia functioning. The notion that the basal ganglia play important role in temporal control, but not spatial control is also supported by the the study of Cunnington, Iansek, Bradshaw and Phillips (1995), which reported that, the basal ganglia and supplementray motor area (SMA) play important role in temporal organization of sequential movements, but not programming of specific movements (i.e. spatial parameters of movement control) (Cunnington, Iansek, Bradshaw, & Phillips, 1995). Eventhoug bimaual movements and unimanual sequential movements are under different controlling mechanisms, and the basal ganglia and SMA may not play the same roles in those two types of motor tasks (Donchin, Gribova, Steinberg, Bergman, de Oliveira, Vaadia, 2001), the relatively limited influence of Parkinson's diseas on spatial control obsereved in bimaual movements and sequential movements did indicate the distinctive roles of basal ganglia in temporal and spatial control. Based on the cognitive representation model of bimanual coordination, spatial coordination in bimanual movements highly relies on the cognitive representation of the task and the corpus callsoum to share the goal representations between two hemispheres (Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004). Our

previous study (see chapter3) showed effects of aging on spatial accuracy on the non-dominant side, and control of movement direction in bimanual coordination. The age-related difficulties in spatial control of bimanual coordination is hypothesized to be associated with increased requirements of attention resources and/or declined function of the corpus callosum in older adults. The present study found that Parkinson's disease has a very limited influence in addition to effects as result of age on spatial accuracy in bimanual coordination tasks, indicating that Parkinson's disease does not further exacerbate the factors (such as increased requirements of attention resources and/or declined function of the corpus callosum) which are hypothetically associated with declined spatial control of bimanual coordination. In other words, disorders of the basal ganglia caused by Parkinson's disease do not affect the spatial representations or the communications between the two hemispheres regarding the spatial representations.

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CHAPTER 5: DISCUSSION

Key results

Spatial coordination of bimanual movements is important when performing daily activities. Whereas, older adults and individuals with Parkinson's disease commonly show difficulties in temporally coordinating the hands in bimanual coordination tasks, the effects of aging and Parkinson's disease on the quality of spatial coordination between the hands are unclear. Spatial control includes the control of movement amplitude and movement direction, therefore, in **Chapter 2** the relationship between direction and amplitude in a bimanual coordination task was examined by analyzing parameters representing the quality of spatial aspects of coordination between the hands and parameters signifying accuracy of direction and amplitude for each hand separately. **Chapter 3** investigated the impact of old age on spatial control in a bimanual coordination task when the movement amplitude and direction are specified. **Chapter 4** compared performance of individuals with PD and healthy older controls on the same bimanual coordination task utilized in Chapter 2 and Chapter 3, in which we manipulated movement amplitude and movement direction. The following discussion will recap the key results from these studies.

In healthy young adults, the amplitude of movements produced with the hand drawing short lines were more vulnerable to the influence of movements produced with the hand drawing long lines, while movement direction of the dominant hand was more affected by the direction of the non-dominant hand. Moreover, directional requirements regulate the interference between the hands on movement amplitude, and amplitude requirements only influence the dominant hand on movement direction. Older adults were able to maintain a similar level of spatial accuracy on the dominant side as young adults, but they showed reduced spatial accuracy when using the non-

dominant hand. Furthermore, advanced age altered the control of movement direction in the bimanual coordination task, but not the control of movement amplitude. Individuals with Parkinson's disease and older adults showed similar levels of spatial accuracy, except for the directional accuracy of the lines drawn with the dominant hand; these lines showed angles with the target direction were increased about two degree in the PD group as compared to older control group. In summary, the quality of spatial coordination declined only in part in older adults, and the decline in the quality of spatial coordination was not exacerbated in individuals with PD.

The following sections will discuss the combined major results from chapter 2 to 4. Furthermore, it will discuss the limitations of the present work and it will end with suggestions for the directions of future research.

Discussion of the key results

In healthy young adults, there was a general tendency of overshooting short lines when performed as part of a bimanual task in which longer and shorter amplitude constraints are specified, which suggests that the movement system selects the longer movement extent as a standard for the spatial codes for both the long and short movement amplitudes, i.e., the spatial code for the shorter movement extent seems to be derived from the selected longer standard. The selection of the standard and thus the control of amplitude seemed to be similar between young and older adults (i.e. both age-groups overshoot short lines to a similar extent) (see Figure 5.1. panel A and B). Therefore, the effects of the use of a longer standard spatial code for movement amplitude did not change in older adults. Young adults produce more accurate movement directions when drawing vertical lines, while the dominant hand tends to draw horizontal lines with an upward angle (i.e away from the body). The results indicate that, compared to the

dominant hand, the non-dominant hand is more proficient in direction control. Moreover, the spatial code for horizontal movements may get derived from the spatial code for vertical movements, which seems to be set as the standard for both movement directions. Similar to young adults, older adults produce accurate movement direction when drawing vertical lines. However, the tendency of drawing horizontal lines with an upward angle was exacerbated in older adults regardless which hand (dominant or non-dominant) produced the horizontal line (see Figure 5.1. panel C and D). In summary, older age alter the control of direction in bimanual movements. As directional adaptation is more demanding than amplitude adaptation (Krakauer, Pine, Ghilardi & Ghez, 2000), it is possible that directional constraints in a bimanual coordination task places a heavier demand on specialized neural structures, which resources of these neural structures may be limited in older adults.

Older adults maintained on the dominant side a similar level of spatial accuracy (i.e., the accuracy of amplitude and direction) as young adults, while the spatial accuracy on the non-dominant side declined in older adults (see Figure 5.2.). These results indicate that, when performance requires bimanual coordination, motor function on the dominant side remains relatively stable with age, while motor function on the non-dominant side declines with age. Bimanual tasks in which movement amplitude and direction are manipulated require older adults to access extra attention resources, which may strain the system since the functional capabilities are assumed to decrease with older age (Cabeza, 2002). When the attention demands exceed those available to older adults, older adults direct all necessary resources to the motor system on the dominant side in order to execute the movements on this side accurately, while the remaining resources are directed to the non-dominant side. Thus, spatial accuracy declines on the non-

dominant side when the remaining resources are not sufficient to accurately control movements on the non-dominant side.

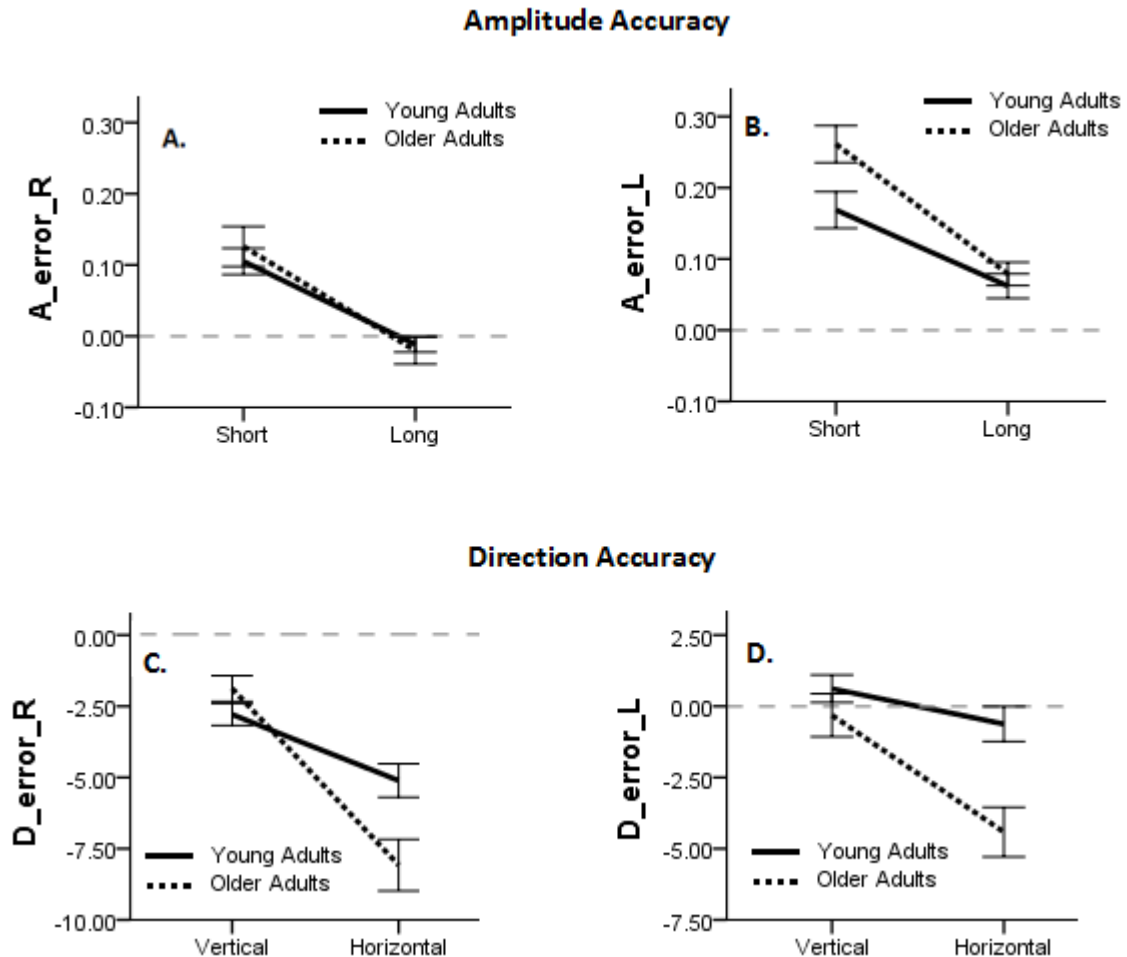


Figure 5.1. Panel A showed the A-error-R were similar between young and older adults in condition of short and condition of long. Panel B showed the A-error-L were similar between young and older adults in condition of short and condition of long. Panel C showed the D-error-R were similar between young and older adults when movement direction were vertical, while the D-error-R were evidently larger in older adults when movement direction were horizontal. Panel D showed the D-error-L were similar between young and older adults when movement direction were vertical, while the D-error-L were evidently larger in older adults when movement direction were horizontal.

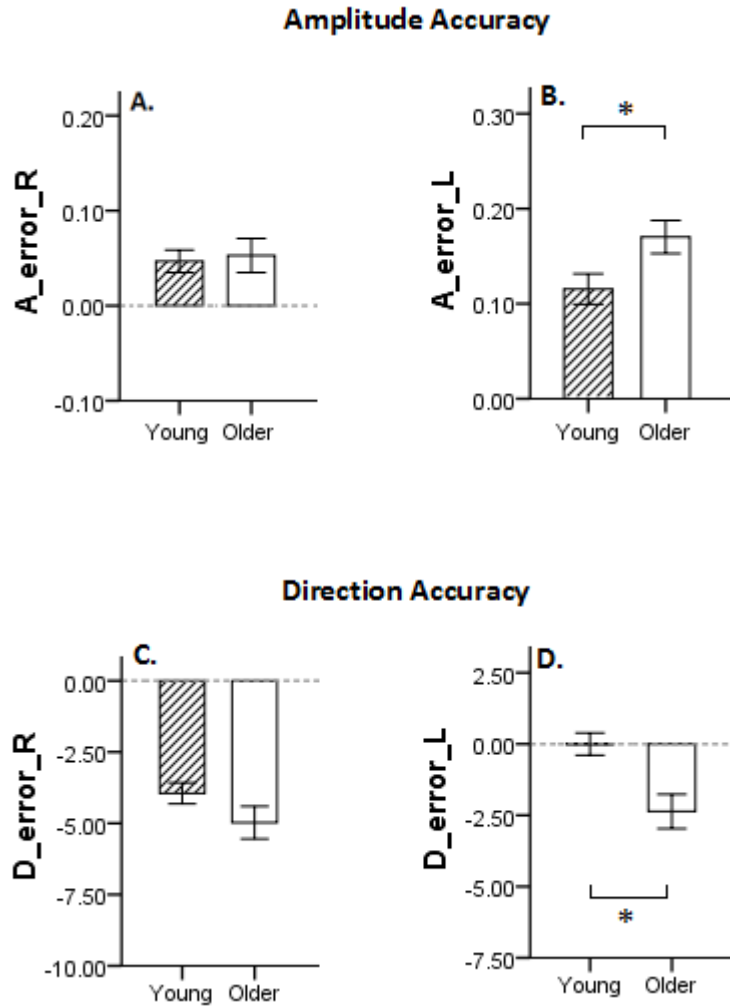


Figure 5.2. Panel A showed the A-error-R were similar between young and older adults. Panel B showed the A-error-L were significantly larger in older adults. Panel C showed the D-error-R were similar between young and older. Panel D showed the D-error-L were evidently larger in older adults.

Both older adults and individuals with PD overshoot short lines. More importantly, the extent of overshooting in conditions requiring to draw short lines were similar between the two groups, indicating that Parkinson's disease does not exacerbate the tendency to overshoot the short lines (see Figure 5.3. panel A and B). Therefore, the effects of the use of standard spatial code for movement amplitude did not change due to Parkinson's disease. Older adults and individuals with PD drew horizontal lines with an upward angle. Parkinson's disease does not

exacerbate the tendency of shifting the horizontal lines (see Figure 5.3. panel C and D).

Furthermore, Individuals with PD maintained a similar level of spatial accuracy as healthy older controls. However, the directional accuracy of lines drawn with the dominant hand showed a small decline of about two degrees in individuals with Parkinson's disease (see Figure 5.4.).

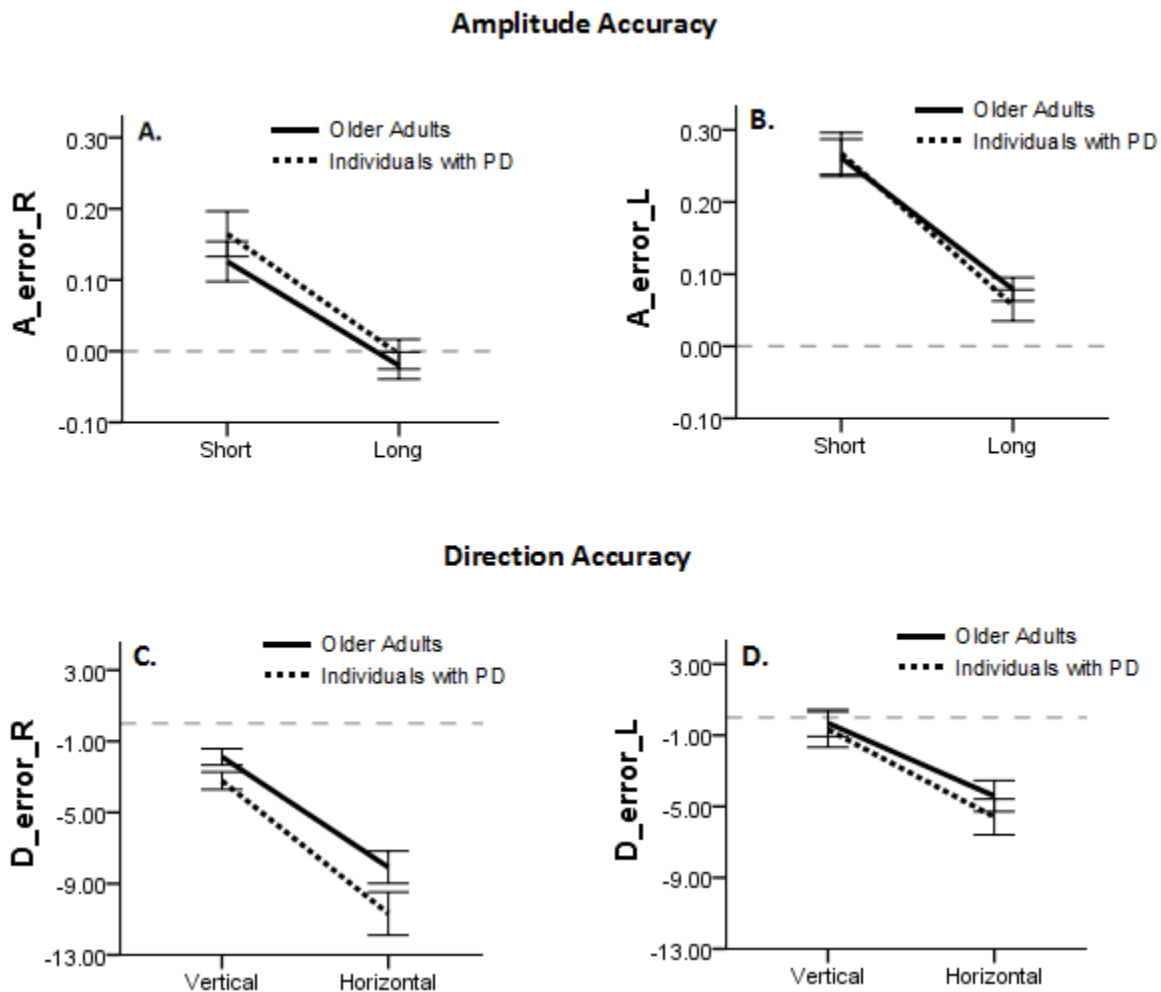


Figure 5.3. Panel A showed the A-error-R were similar between older adults and individuals with PD in condition of short and condition of long. Panel B showed the A-error-L were similar between older adults and individuals with PD in condition of short and condition of long. Panel C showed the D-error-R were similar between older adults and individuals with PD in condition of vertical and condition of horizontal. Panel D showed the D-error-L were similar between older adults and individuals with PD in condition of vertical and condition of horizontal.

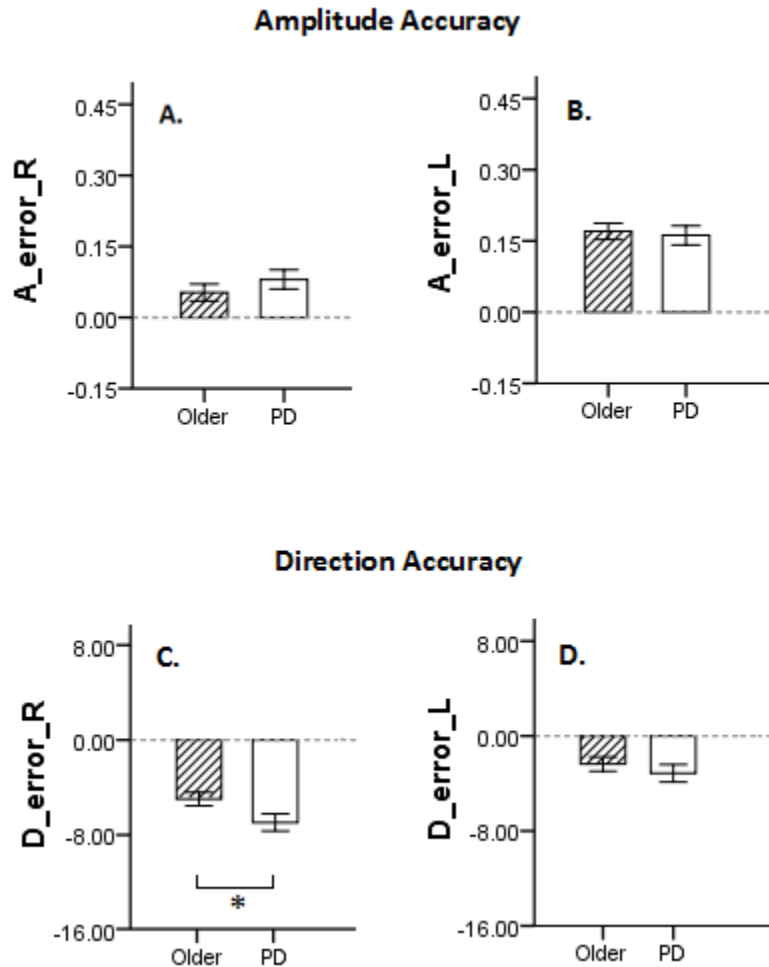


Figure 5.4. Panel A showed the A-error-R were similar between older adults and individuals with PD. Panel B showed the A-error-L were similar between older adults and individuals with PD. Panel C showed the D-error-R were larger in individuals with PD. Panel D showed the D-error-L were similar between older adults and individuals with PD.

Obvious impairments of Parkinson's disease patients in bimanual coordination have been consistently observed in studies that focused on temporal aspects of the coordination (Johnson, Cunningham, Bradshaw, Philips, Lansek, & Rogers, 1998; Serrien, Steyvers, Debaere, Stelmach, & Swinnen, 2000; Swinnen, VanLangendonk, Verschueren, Peeters, Dom, & DeWeerd, 1997; Van den Berg, Beek, Wagenaar, & Van Gieringen, 2000), while studies focused on spatial aspects have shown that individuals with Parkinson's disease are able to perform these tasks with

similar level of impairments as older adults (Tresilian, Stelmach, & Adler, 1997; Stelmach & Worringham, 1988). The present study also found that Parkinson's disease has a very limited influence on spatial accuracy in bimanual coordination tasks, in addition to already shown aging effects. It seems that the influence of Parkinson's disease on the performance of bimanual coordination is task-aspect dependent: Parkinson's disease affects the temporal control of bimanual movements, while it has a very limited influence on the spatial control of these activities, indicating the divergent role of basal ganglia for the control of temporal and spatial aspects (Donchin, Gribova, Steinberg, Bergman, de Oliveira, Vaadia, 2001).

Young adults, older adults and individuals with PD all showed a tendency to overshoot short lines in bimanual coordination tasks when there are different conditions and two movement amplitudes requirements are possible (see Figure 5.5. panel A and B). These results indicate that the movement system selects the longer movement extent as a standard for the spatial code guiding both the long and short movement amplitudes regardless of one's age, or if the individual is suffering from PD. When the conditions in a bimanual coordination task include vertical and horizontal lines as possible direction requirements, young adults, older adults and individuals with PD all produce more accurately the vertical lines as compared to the horizontal ones. All groups draw the horizontal lines with an upward angle (i.e., away from the body). The discrepancy in accuracy between the movement direction performance for all groups indicate that, regardless of one's age, or if one is suffering from PD, the spatial code for horizontal movements may get derived from the spatial code for vertical movements, which seems to be set as the standard for both movement directions (see Figure 5.5. panel C and D). However, older adults and individuals with PD did exacerbate the tendency to draw the horizontal lines with an upward angle regardless which hand was used (i.e., dominant or non-dominant) for the

production of the horizontal line (see Figure 5.5. panel C and D). Thus, the effects of the use of the vertical standard spatial code for the movement direction did not change with older age or Parkinson's disease, but the capability of using the standard spatial code of the vertical line to produce movements in other directions (i.e. a horizontal line) becomes more rigid with older age and Parkinson's disease, resulting more directional error towards the vertical standard in older adults and individuals with PD.

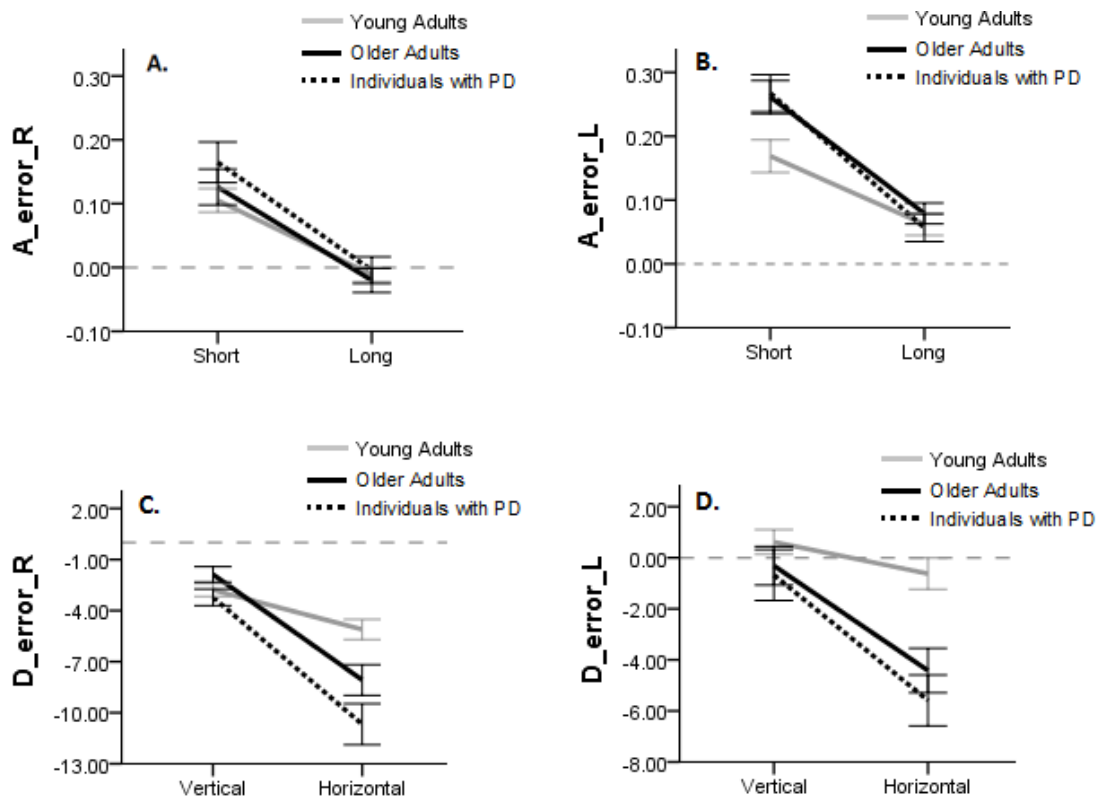


Figure 5.5. Panel A showed the A-error-R were similar between young adults, older adults and individuals with PD. Panel B showed the A-error-L were similar between young adults, older adults and individuals with PD in condition of long, while the A-error-L was smaller in young adults in condition of short. Panel C showed the D-error-R were similar between older adults and individuals with PD in condition of vertical, while the D-error-R were different between three groups in condition of horizontal. Panel D showed the D-error-L were similar between young adults, older adults and individuals with PD in condition of vertical, while the D-error-L was smaller in young adults in condition of horizontal.

Advanced age demonstrated that the control of movement direction is affected in the bimanual coordination tasks, but the effect of age on the control of movement amplitude is very limited. It is proposed that this pattern of effects of age on spatial control is probably caused by the higher demands necessary to have the motor system adapt to a directional constraint as compare to an adaptation to an amplitude constraint. Furthermore, Parkinson's disease seems to not to influence spatial accuracy in bimanual coordination tasks beyond the effects of aging in general; thus, this may indicate that basal ganglia may not play a critical role in control of spatial aspects of bimanual coordinated movements.

Limitations

The dissertation contained several methodological limitations that may affect generalization of findings.

The first primary limitation is sample bias. The research used the data of the young subjects in chapter 2 to compare to the data of the older adults in chapter 3, and the data of the older adults of chapter 3 where used to compare to the data of the individuals with PD in chapter 4. This may limit generalization of the results. Recruiting a set of new young adults for comparisons in chapter 3 would reduce the effects of recruitment bias, and could also be used to establish more support for the findings for spatial coordination in bimanual movements of young adults. Recruiting a new group of older adults for comparison in chapter 4 could also be used to establish more support for the findings observed in chapter 3 for performance of older adults. Another issue related to sample bias is that the analyzed data of individuals with PD were limited yo those who were able to hold a pen in a normal pen grip and complete all 8 variations of the bimanual coordination task, which may limit generalization of results to the entire PD population. In other words, one may wonder whether the conclusion that Parkinson's disease has

a very limited influence on the spatial control of bimanual coordination can be generalized to the entire PD population, such as those who have difficulty holding pen in a normal pen grip and/or producing bimanual tasks as applied in the present dissertation.

A second limitation of this dissertation was the nested design, which resulted in having half of the subjects completing 8 conditions and the other half of the subjects completing the remaining 8 conditions. The nested design was applied to avoid fatigue. Thus participants were only performing half of the coordinative conditions making condition a between group, instead of within group, factor. Suggestions for future studies include reducing the number of trials in each condition, or asking participants to come back the second day to complete the second half of conditions to avoid the influence of between group factor.

Another limitation of this dissertation was that it only included relatively simple coordination patterns (i.e., an amplitude ratio of 1:1, 1:2, and 2:1; a directional relationship of 180°, 0°, and 90°) without a movement speed requirement stressing the temporal aspects of the coordination task. One may wonder whether the effects of older age and Parkinson's disease on spatial coordination change when the difficulty of coordination pattern increases or when all participants have to meet certain temporal criteria.

Regardless of study limitations, the research identified informative outcomes. Overall, being older affects the spatial coordination in bimanual movements of relatively simple coordination patterns. In addition, Parkinson's disease does not exacerbate the influence of older age on the spatial coordination in bimanual movements for the given task.

Future directions

Spatial coordination of bimanual movements is important for daily activities. The present research found that being older affects the spatial coordination in bimanual movements, but Parkinson's disease does not exacerbate the effects beyond the influence of older age in regard to spatial coordination aspects of relatively simple bimanual movement tasks. Based on the findings and limitations listed above, several directions of future research are warranted.

Studies have reported that older adults (Lee, Wishart, & Murdoch, 2002; Serrien, Swinnen, & Stelmach, 2000; Swinnen, Verschueren, Bogaerts, Dounskaia, Lee, Stelmach, & Serrien, 1998) and individuals with Parkinson's disease show deficits in the control of bimanual movements (Johnson, Cunnington, Bradshaw, Philips, Lansek, & Rogers, 1998; Serrien, Steyvers, Debaere, Stelmach, & Swinnen, 2000; Swinnen, VanLangendonk, Verschueren, Peeters, Dom, & DeWeerd, 1997; Van den Berg, Beek, Wagenaar & Van Gieringen, 2000), especially when high movement speeds are required. The present study in this dissertation did not include a movement speed requirement. All participants were allowed to produce bimanual movements at their comfortable speed. The present research found that having Parkinson's disease had a very limited influence in addition to effects of age on spatial accuracy in the given bimanual coordination tasks. Constraining movement speed by training participants to produce bimanual movements within a certain speed range would offer insight to see if stressing the motor system would result in effects on spatial coordination accuracy as result of older age and/or Parkinson's disease.

The findings in chapter 2 of the present research are based on an experimental design with relatively simple coordination patterns (i.e., amplitude ratios of 1:1, 1:2, and 2:1; directional relationship of 180°, 0°, and 90°). Studies that focused on temporal aspects of coordination in

bimanual movement tasks have shown that the production of complex phase (i.e. multi-phase) relationships between the two hands are less stable and accurate than performance of anti-phase or in-phase relationships (Franz, Eliassen, Ivry, & Gazzaniga, 1996; Eliassen, Baynes, & Gazzaniga, 1999; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Semjen, 2002). Therefore, it would be interesting to examine if and how the findings in chapter 2 of the present research would change when the difficulty of coordination pattern increases by including amplitude ratios of 1:3 and 2:3, in addition to the used 1:2 and 1:1 relationships, and/or directional relationships of 45° and 60° , in addition to the used 0° , 90° , and 180° relationships. The present research proposed that the movement system selects the longer movement extent as a standard for the spatial codes when the conditions include longer and shorter movement amplitudes, while the spatial code for the shorter movement extent was hypothesized to be derived from the selected standard. The present research also proposed that the spatial code for horizontal movements may get derived from the spatial code for vertical movements, which latter direction was hypothesized to be the standard for the movements. Application of complex amplitude ratio and/or directional relationships would offer greater insights to the use of vertical direction and longer movement standards.

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APPENDIX A – IRB APPROVAL FORM

ACTION ON PROTOCOL APPROVAL REQUEST



Institutional Review Board
Dr. Robert Mathews, Chair
130 David Boyd Hall
Baton Rouge, LA 70803
P: 225.578.8537
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irb@lsu.edu | lsu.edu/irb

TO: Arand Van Gemmerl
Kinesiology

FROM: Robert C. Mathews
Chair, Institutional Review Board

DATE: October 3, 2013

RE: IRB# 3406

TITLE: The effects of Parkinson's disease on bimanual coordination

New Protocol/Modification/Continuation: Modification

Brief Modification Description: Adding Katelyn Thibodeaux and Kristina Hickey as Co-PI's

Review type: Full ☐ Expedited ☒ **Review date:** 10/3/2013

Risk Factor: Minimal ☒ Uncertain ☐ Greater Than Minimal ☐

Approved ☒ **Disapproved** ☐

Approval Date: 10/3/2013 **Approval Expiration Date:** 8/20/2014

Re-review frequency: (annual, unless otherwise stated)

Number of subjects approved: 200

Protocol Matches Scope of Work in Grant proposal: (If applicable) ☐

By: Robert C. Mathews, Chairman *Robert C. Mathews*

PRINCIPAL INVESTIGATOR: PLEASE READ THE FOLLOWING –
Continuing approval is **CONDITIONAL** on:

1. Adherence to the approved protocol, familiarity with, and adherence to the ethical standards of the Belmont Report, and LSU's Assurance of Compliance with DHHS regulations for the protection of human subjects*.
2. Prior approval of a change in protocol, including revision of the consent documents or an increase in the number of subjects over that approved.
3. Obtaining renewed approval (or submittal of a termination report), prior to the approval expiration date, upon request by the IRB office (irrespective of when the project actually begins); notification of project termination.
4. Retention of documentation of informed consent and study records for at least 3 years after the study ends.
5. Continuing attention to the physical and psychological well-being and informed consent of the individual participants including notification of new information that might affect consent.
6. A prompt report to the IRB of any adverse event affecting a participant potentially arising from the study.
7. Notification of the IRB of a serious compliance failure.
8. **SPECIAL NOTE:**

*All investigators and support staff have access to copies of the Belmont Report, LSU's Assurance with DHHS, DHHS (45 CFR 46) and FDA regulations governing use of human subjects, and other relevant documents in print in this office or on our World Wide Web site at <http://www.lsu.edu/irb>

APPENDIX B – REVIEW OF RELEVANT LITERATURE

**THE EFFECTS OF PARKINSON’S DISEASE ON BIMANUAL COORDINATION:
THE ROLE OF BASAL GANGLIA IN THE SYNERGISTIC COUPLING OF TWO
HANDS**

A General Exam

Submitted to the Graduate Faculty of the

Louisiana State University and

Agricultural and Mechanical College

In partial fulfillment of the

Requirements for the degree of

Doctor of Philosophy

In

The School of Kinesiology

by

Zhujun Pan

B.E., Southwest Jiaotong University, 2005

M.Ed., Capital Institute of Physical Education, 2009

April, 2013

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BIMANUAL COORDINATION

Definition of Bimanual Coordination

Bimanual coordination, or interlimb coordination, is defined as the simultaneous movement of both hands. In our daily life, many of movements require some degree of interactive coordination between the hands. In general, there can be distinguished two types of bimanual coordination. The first type is symmetric bimanual coordination involving mirror or isomorphic actions of the two hands, such as clapping with the hands, pulling a large box, rowing a boat, pushing a wheelchair forward, etc. The second type is asymmetric bimanual coordination, which requires different actions for each hand, such as sewing, opening a bottle, driving a car, playing guitar, typing, eating with fork and knife, buttoning a shirt, cutting paper with scissors, tying shoelaces, etc. Tasks applied in laboratory settings which investigate bimanual coordination are usually quite different from everyday bimanual tasks. For example, continuous motor tasks, like rhythmic bimanual circle and/or line drawing tasks, and discrete motor tasks, like button pressing and/or reaching to targets, are popular in bimanual coordination research. Scientific observations usually report that tasks involving symmetrical movements of the two hands are more stable and accurate than tasks involving asymmetric movements, and these studies often show that a spontaneous shift occurs from an asymmetric towards a symmetric movement pattern, especially when bimanual tasks are required to be performed in high speed. In some studies, the tendency of synergistic coupling of the two hands is referred to as “preferred patterns of coordination” from the perspective that symmetric bimanual coordination is the default state of neural control. It has also been called “coordination constraints/interferences/coupling” which stems from the view that people’s ability to perform different movements with the two hands simultaneously is limited (Swinnen et al. 2001).

Behavioral Features of Bimanual Coordination

The spatial and temporal couplings in bimanual coordination are normally discussed separately because it is proposed that they result from distinguishing sources in the hierarchy of control (Heuer 1993). This view is supported by many studies. For example, in a study by Verschueren, et al. (1998), it was reported that tendon vibration of the dominant limb affects the temporal, but not the spatial control characteristics of the other limb's movement (Verschueren et al. 1998a). Another study with split-brain patients observed that temporal coupling remained the same as control participants; while spatial coupling almost vanished (Franz et al. 1996). Spatial constraint is defined as the tendency of the two hands to produce movements with similar amplitude, movements in a mirror direction and/or comparable shapes. For example, when required to move simultaneously with different amplitudes, the movement length of two limbs tends to become similar to each other (Marteniuk et al. 1984; Sherwood 1994). The influence of movement of one hand on the other hand can also be observed when two hands are required to in different direction (Swinnen et al. 1998; Swinnen et al. 2001) or when one hand drew a line and other hand drew a circle simultaneously (Franz et al. 1991). On the other hand, the temporal constraint in bimanual coordination is the tendency of both hands to move within a similar time frame. For example, two hands tends to initiate and end movements at the same time even though the amplitude of one hand is longer/shorter than the other hand (Kelso et al. 1979). In rhythmic movements, complex ratio (3:2) is more difficult to produce than simple ratio (1:1) (Summers et al. 1993), and tends to slip to the simpler ratio's when the movement speed is increased (Peper et al. 1995). Moreover, movement stability was reported to be lower for complex-phase movements compared to in-phase and anti-phase movements (Zanone and Kelso 1992).

Even though in experimental studies the synergistic coupling in bimanual coordination seems very difficult to dissociate, our daily tasks show that this coordination constraint can be overcome. Driving cars, tying shoelaces, playing guitar, playing piano, and serving a tennis ball are examples of our ability to perform asymmetric bimanual coordination in daily life. In fact, it has been reported in experimental studies as well that when certain external aids are provided one can overcome the coordination constraint. A study has found that application of directly visual cues (target light illuminates) reduced reaction time of an asymmetric (different amplitude for each hand) bimanual movement to the level of symmetric (same amplitude for both hands) bimanual movements (Diedrichsen et al. 2001). In another study, it was reported that performance of drawing movements with orthogonal orientations improved when visual representation was altered, so movements were displayed as being parallel motions instead of orthogonal motions (Bogaerts et al. 2003). Furthermore, complex ratios in bimanual coordination have been shown that they can be achieved when the visual feedback is altered to a simple 1:1 ratio (Mechsner et al. 2001) or when the polyrhythm is interpreted into one temporal structure made by the interleave of the two hands (Summers et al. 1993). Cyclical bimanual tasks with complex phases can be simplified by switching attention from movement trajectories to anchor points in the form of a metronome beat and/or a haptic contact (Swinnen et al. 1997a; Kelso et al. 2001). The ability of individuals to overcome the coordination constraints in everyday life and in laboratory settings demonstrates the flexibility and adaptability of human's movement control and learning. It also provides a good perspective to understand mechanisms responsible for bimanual coordination.

Importance of Bimanual Coordination

Bimanual coordination is gaining increasing attention. Bimanual coordination is a good paradigm of multitasking (Hazeltine et al. 2003; Pashler 1994); therefore bimanual coordination studies help to understand how the central nervous system integrates distributed neural assemblies to coordinate multiple-tasks. Bimanual tasks also provide ideal platform to unravel the influence of aging, neurological pathologies on hemispheric lateralization and interaction. Studies of bimanual coordination are not simply of academic interest, they play also an important role in the clinical practice. For example, it is very difficult to train the paretic limb of stroke survivors. However, based on the synergistic coupling nature of bimanual coordination, movements performed in bimanual context may help to functionally improve the paretic limb of stroke patients. Moreover, performances in bimanual coordination may also be used as diagnostic criteria for movement disorders. For example, researchers found that particularly bimanual coordination tasks involving anti-phase movements at high frequencies may be used for the early diagnosis of Parkinson's disease (Ponsen et al. 2006).

MECHANISMS BEHIND BIMANUAL COORDINATION

The majority of studies of bimanual coordination have emphasized spatial and temporal constraints as they affect asymmetric coordination. The principle that governs coordination can be identified through analyzing the causes of these constraints. A variety of models have been developed with different explanations for behavior as result of bimanual coordination, but there is a general agreement that the coordination constraints originate from either muscular, sensory, or cognitive constraint, or an interaction between two or more of these constraints in our movement control.

Homologous Muscles Activities

Simultaneous activation of homologous muscles of the two limbs was observed in neurophysiologic studies. In 1942, Davis found that when one limb performs a movement, electromyography (EMG) activity occurred for the quiescent contralateral limb. Relatively recently, researchers have shown more evidence for the simultaneous activation hypothesis, when they showed in a transcranial magnetic stimulation (TMS) experiment, that during unimanual movements, the motor cortex of the moving limb modulates the excitability of the motor pathways of the contralateral hand (Carson et al. 2005). However, the view of homologous muscle activity is not unequivocally supported. It is known that when the forearms pronate, wrist flexion/extension is more stable when the movements are symmetric. These symmetric movements involve homologous muscle activity, as well as symmetric movement directions of two hands. To distinguish the role of homologous muscle activity and symmetric movement directions in coupling of bimanual movements, Baldissera et al. (1982, 1991) dissociated these two factors by asking participants to have the palm of one hand face down, while the other hand was held face up in the start position (Baldissera et al. 1982; Baldissera et al. 1991). The results showed that performance is more stable when the two hands move in the same direction, even though in this condition the muscle activities are different for the two hands because one wrist is flexing while the wrist on the other hand is extending. Therefore, homologous muscle activity may not be the prominent factor for the occurrence of synergistic coupling in bimanual coordination. Another study, a group of upper limb amputees with vivid phantom limb were asked to draw a straight line with the intact arm and draw a straight line or in a circle with the phantom arm. The results showed that performance of the intact limb was negatively affected in the asymmetric coordination condition, which suggests, again, that our preference of symmetric

bimanual coordination does not critically depends on the processes related to activation patterns of homologous muscles (Franz and Ramachandran 1998).

Proprioception

What is the role of proprioception in bimanual movements? To answer this question, Verschueren, et al. (1998) designed an experiment, in which blindfolded participants drew mirror circles with two hands simultaneously. In some trials, the proprioception of the dominant arm was distorted by the application of tendon vibration on the biceps and/or anterior deltoid muscles of the dominant arm. The results show that distorted proprioceptive information of one arm has minimal effects on the spatial movement pattern of the other arm. On the other hand, the temporal coupling of the two arms was disturbed by the distortion of proprioception caused by the tendon vibration. Therefore, it was concluded that proprioception plays a role in bimanual coordination; at least it has some contribution to the temporal coupling of bimanual movements (Verschueren et al. 1998b). However, this view was not supported by a study involving patients who had minimal deficits of the motor signals, while they had a severe loss in sensory input from the arms. Spencer, Ivry, Cattaert, & Semjen (2005) examined the coupling of these patients in symmetric and asymmetric bimanual circle drawing tasks. The results showed that patients without proprioception maintained strong coupling in bimanual movements. They showed more interference in the asymmetric coordination compared to the symmetric coordination. These results underscore that the proprioception may not be a critical factor for the occurrence of interference in bimanual coordination (Spencer et al. 2005).

Cognitive Representation

Generalized Motor Program, Cross-talk Model and Cognitive Representation

Besides homologous muscles and proprioception, early studies for bimanual coordination also favor limitations in movement programming and execution as factors of interferences in bimanual movements. From the perspective of movement programming, it was proposed that, even though each limb needs to produce different movements, only one common motor program is required for task that requires bimanual coordination. Therefore, the basic concept of generalized motor program (GMP) is able to be applied to bimanual coordination in the way that one generalized program controls both limbs. However, as the program is partly for the right hand and partly for the left hand, the interferences between limbs occurs (Schmidt et al. 1979). On the other hand, the view of movement execution (or crosstalk model) proposes that there are independent motor plans in each hemisphere for each limb. The interferences occur in bimanual movements because of the intermanual crosstalk during the execution of two motor programs. Specifically, each limb is mainly controlled by the motor program in the contralateral hemisphere, but this motor program is partly disturbed by the motor program in the ipsilateral hemisphere (Marteniuk and MacKenzie, 1981) (Marteniuk and Mackenzie 1981). De Oliveira (2002) proposed a hierarchical model which combined the GMP and the crosstalk models. In the hierarchical model, a common GMP is first created at a high level. This motor program can then be interpreted or adjusted to meet specific task requirements of each arm at a lower level, which is called “the hand-specific realization of the GMP”. The hierarchical model explained to a certain extent why, in asymmetric bimanual coordination, the movement of each limb is partly similar as well as partly different from each other (de Oliveira 2002).

A body of recent research evidences point to the critical role of cognitive representation in constraint in bimanual coordination ((Ivry et al., 2004). In other words, how the task goals are conceptualized has more influence on the pattern of bimanual movements than other factors like

the muscles, proprioception, the motor program and the execution of motor program. For example, the study of Mechsner, Kerzel, Knoblich, Prinz (2001) revealed that, for asymmetric bimanual movements, the coupling of two limbs can be successfully dissociated if participants' perception of the tasks were altered. This and many other studies suggested that interferences in bimanual coordination are highly sensitive to how action goals are perceived, which is the basis of movement representation (Mechsner et al. 2001; Oliveira and Ivry 2008; Kennerley et al. 2002; Diedrichsen et al. 2006).

The Cognitive Representation of Spatial Coupling

To examine the role of cognitive representation in spatial coupling of bimanual coordination, Diedrichsen, Hazeltine, Kennerley, and Ivry (2001) designed a bimanual task which was performed in symbolic and spatial/direct cueing conditions. In these experiments, participants were required to make two reaching movements with the right and the left hand simultaneously with long or short amplitude. The coordination condition was defined as symmetric when the two hands both reached to a target with long or short amplitude and it was defined as asymmetric when one hand had to reach to a target with long and the other hand had to reach to a target with short amplitude. Two types of cueing were applied to each coordination condition to see whether the differences between symmetric and asymmetric bimanual coordination change when perception of the tasks be altered. In the symbolic cueing condition, the letter "S" was used to instruct the hand to move with short amplitude and the letter "L" was used to instruct the hand to reach with long amplitude. In the spatial cueing condition, the target location for each hand was highlighted directly. For example, if the participant's right hand needed to reach with short amplitude, and the left hand needed to reach with long amplitude, the target with the short distance was highlighted on the right side, while the target with long distance was highlighted on

the left side. The results showed that, when the movements were symbolically cued, the reaction time was much longer in the asymmetric coordination condition compared to the symmetric coordination condition. However, when the movements were directly cued the cost of reaction time in asymmetric coordination was substantially reduced, so that the reaction time in asymmetric condition became comparable to the symmetric condition. These results support the cognitive view of bimanual coordination, because the effects on the coordination pattern of two limbs, or at least on the movement preparation stage, were affected by how the action goal was perceived and further represented (Diedrichsen et al. 2001). To further investigate whether the interference of bimanual coordination is altered when the representation of task is changed, Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen (2004) conducted an experiment which required participants to draw simultaneously three side squares in a shape of U and/or C (rotated by 90 degrees with respect to the U) with two hands (symmetric movement), or one hand drawing the U and the other hand drawing the C (asymmetric movement). In the symbolic cueing condition, the shapes of U and C were presented on a monitor in front of participants. In the spatial/directly cueing condition, instead of presenting the whole shape, four specified target locations were provided one by one, thus participants only needed to move to the target showing on the monitor. Strong spatial interference occurred in both the symbolic and spatial cueing condition; that is each shape skew to the side when both hands produced the U or C. However, the reaction time cost in the asymmetric coordination task was dramatically reduced when the task was spatially cued compared to the symbolically cued condition. The results supported the view that the cost of reaction time in asymmetrical bimanual coordination is mainly spend on translating symbolic cues into different movement responses for each hand. It is further proposed that cognitive representations (induced by cueing conditions in the experiments above) of the action goals play

a critical role in the occurrence of spatial interference in bimanual coordination. More specifically, when direct cues are used, the actions are represented as movements to endpoint locations one by one; while when symbolical cues are used, the actions are represented as two distinct movement trajectories for each hand (Diedrichsen et al. 2001; Diedrichsen et al. 2006). Based on the representation view, spatial coupling commonly observed in research may be due to the fact that most studies applied symbolic cues for bimanual tasks. Moreover, the spatial coupling of two hands can be dissociated when appropriate external aids are provided (Kennerley et al. 2002). The spatial uncoupling produced by the manipulation of task goals provides additional evidence supporting the view that action representation is critical for the occurrence of interference in bimanual coordination.

As discussed above, the spatial interference of bimanual coordination is attributed to the representation of bimanual task. The next question is how exactly the spatial interferences happen and what is the neurological basis for the representation view. Study of Franz, Eliassen, Ivry, & Gazzaniga (1996) have talked about involvement of the corpus callosum in the occurrence of spatial coupling in bimanual coordination. Split-brain patients who underwent resection of the corpus callosum were included in a study in which the researchers tried to determine the role of the corpus callosum in bimanual coordination. The communication between the two cerebral hemispheres was largely limited due to the resection of the corpus callosum. Participants were instructed to draw three sides of a box in the shape of U and/or C simultaneously. The required shape of each hand was shown on the side of its visual field. For example, if the task required the right hand to draw U and the left hand to draw C, the shape of U was presented in the right visual field, and the C was presented in the left visual field. In the symmetric coordination condition, both hands drew the U or C simultaneously, while one hand

drew the U and the other hand drew the C in the asymmetric coordination condition. For controls, spatial assimilation effects were commonly observed indicating strong spatial coupling in the asymmetric conditions. However, the results for split-brain patients were very different from the controls. The taxing spatial couplings, observed in the controls, was almost fully absent in the split-brain patients: the patients dissociated spatial movements of two arms with ease as if they were performing a movement with symmetric coordination. The spatial uncoupling of split-brain patients evidenced that the spatial interference between the two limbs are closely related to the interaction between the two cerebral hemispheres through the corpus callosum (Franz et al. 1996). It is also worth noting that, even though the spatial coupling was diminished, split-brain patients maintained consistent temporal coupling in asymmetric coordination tasks. This result implied that, unlike the spatial coupling, temporal coupling in bimanual coordination has a different origin, which may not depend on hemispheric interaction via the corpus callosum.

The study of the split brain patients pointed out that hemispheric interaction through the corpus callosum is a key factor for spatial coupling in bimanual coordination. Answers for the questions of why spatial interference occurs in symbolic cueing conditions, but is reduced in direct cueing conditions may shed light on our understanding of how the hemispheric interaction through the corpus callosum leads to spatial coupling in bimanual movements. One explanation for the representation view was proposed by Ivry et al. (2004). These researchers stated that the direct cueing movements linked to representation of location-based codes, which may be processed through the dorsal visual stream across occipital-parietal cortex. The dorsal stream is essential for visually guided actions by automatically directing the hand to move towards the visual target (Cohen and Andersen 2002). When bimanual coordination is directly cued, movements of each hand are controlled independently by the dorsal visual stream of its

contralateral hemisphere in a pattern that is similar with unimanual control (Ivry et al., 2004). Thus, presentation of target locations does allow two hands to produce spatially incongruent movements simultaneously. On the other hand, the symbolical cueing movements are related to the representation of movement trajectories, which may require involvement of the ventral visual pathways besides the dorsal visual stream. The ventral visual stream plays an important role in stimuli identification, and mapping abstract symbols onto movement trajectories. In other words, when the task is symbolically cued, the ventral visual stream needs to be activated to identify the symbol and further represent movement trajectories based on the abstract symbols. Considering the lateralization of the ventral visual stream and the role of the corpus callosum in spatial coupling based on the split brain patients study (Franz et al. 1996), it was proposed that trajectory representation is mainly produced by the ventral stream in the left hemisphere and transmitted to the right hemisphere through callosal connections. In the condition of asymmetric bimanual coordination, two different representations need to be produced: one representation for the movement trajectory should be sent to one hand, while another representation for a different movement trajectory should be sent to the other hand. As the two representations originate from one site, inevitably, there will be more or less overlap between the two representations, which will lead to the occurrence of spatial coupling (Ivry et al., 2004). The pathway of inferior parietal cortex may be an important factor for symbolically cued movements because it meets to the two major features: highly active when the task represented complex object properties (Johnson et al. 2002) and very left-hemisphere dominant ((Frey et al. 2005). Researchers are still uncertain what the neural locus is of bimanual coordination, but the view that cortical pathways in the left hemisphere play prominent roles in the spatial coupling during bimanual coordination tasks has been supported by studies using functional imaging methods. The study of Diedrichsen et al.

(2006) found that, symbolical cued movements induced greater activation of multiple regions (the intraparietal sulcus, the inferior parietal, pre-motor, and the inferior frontal cortices) which were all located in the left hemisphere. This finding suggests that the left hemisphere is highly involved in tasks requiring the representation of movement trajectories, like bimanual movements that are symbolically cued (Frey et al. 2005; Diedrichsen et al. 2006).

In summary, spatial coupling in bimanual coordination relies highly on the cognitive representation of the task. Symbolically cued movements induce more lateral (left-dominant) cortical activation, and rely on the corpus callosum to share goal representations with the other hemisphere. The overlaps in representations result in the spatial coupling in bimanual movements. On the other hand, spatially/directly cued movements lead to more bilateral cortical activity. The lack of callosal connections and/or representational overlap allows the two hands to spatially uncouple in the spatially cued conditions (Diedrichsen et al. 2006). Figure 1 demonstrates a model for spatial interference of bimanual coordination. This model is based on a review of the paper of Ivry et al (2004).

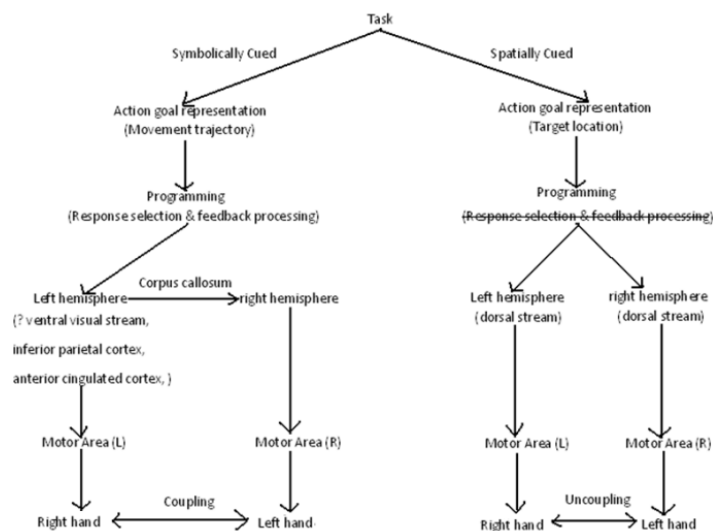


Figure1. A model for spatial interference of bimanual coordination

The Cognitive Representation of Temporal Coupling

Temporal coupling of bimanual coordination is the tendency of both hands to move within the similar time frame. A “coupled oscillators model” was developed to explain the temporal constraints (Haken et al. 1985). In this model, two limbs are depicted as coupled oscillators with interactions to each other. Each limb may have its own preferred movement frequency, but the interactions keep the frequency of the two limbs the same. For rhythmic bimanual movements, certain phase relationships (like in-phase or anti-phase states) of two limbs serve as attractors; the applied relative phase serves as order parameter and movement frequency/speed serves as control parameter whose changes could make the order parameter unstable and therefore shift from one attractor to another. For example, Yamanishi et al (1980) found that performance of complex-phase movements were less stable compared to in-phase or anti-phase movement. There is also a tendency of shifting from complex-phase movements to the in-phase or anti-phase movement, especially when movement frequency increased from low to high (Yamanishi et al. 1980). Some researchers argued that the temporal constraints in bimanual coordination may not result from interaction of two limbs as stated by the coupled oscillators model. They suggested that the temporal constraints represent our general limitation in producing complex temporal relationship. This view is supported if temporal constraints are not unique to bimanual movement, but if they are similar to the temporal constraints that can be found in unimanual movements. Semjen and Ivry (2001) replicated the Yamanishi et al.’s study (1980) with all task procedures being completed using unimanual movement control instead the bimanual movement control. The results showed that temporal constraints are very similar between unimanual and bimanual conditions: no matter if the tasks were completed by one hand (finger) or two hands (fingers), there was always a tendency of shifting from complex-phases to simpler phases. In

other words, the temporal constraints of bimanual coordination (and unimanual movement) resulted in the limited ability to perform complex temporal relationships, but not the coupled oscillatory interaction of the two limbs (Semjen and Ivry 2001). Temporal representation is closely associated to the term “event structure”, which is defined as the fundamental unit for the timing component in movement control (Wimmers et al. 1992). It is assumed that in-phase movements only need one representation of the “event structure”; while the timing structure of an anti-phase movement need to be represented by two common events, and complex-phase movements need even more common events. For example, during cycles of wrist flexion and extension movements (when external aids are not provided), most in-phase movements (or symmetric coordinated movements) are conceptualized within one common event, the reflection onset, for each cycle; while the temporal goal of anti-phase movements (or asymmetric coordinated movements) normally involve two events, the reflection onset of each hand, for each cycle. In this condition, the anti-phase movements are less stable and more difficult to produce than in-phase movements, because more timing events are involved, which may challenge individual’s limited ability to represent complex temporal relationships (Semjen 2002). The idea that anti-phase movements require more complex event structures than in-phase movements are supported by the study of Spencer, Semjen, Yang & Ivry (2006). To this end, wrist flexion and extension movement cycles were recorded. In the in-phase condition, both hands performed the flexion or extension movement in unison; while in the anti-phase condition, one hand flexed at the same time the other hand extended. To show the conceptualization of the event structure, participants were required to say the word of “Ba” repeatedly during their movement, which was assumed to be temporally coupled with temporally salient events of movement. The results showed that, for in-phase movement, one “Ba” was vocalized per cycle on 61% of the trials and

the productions of “Ba” were around the onset of reflection. However, in the anti-phase condition, people say two “Ba” for every trial: one around the maximum wrist-flexion, and another one around maximum wrist-extension. These results clearly supported that the event structure is more complex for anti-phase than in-phase movement. The movement accuracy and stability decrease when complex event structure is involved (Spencer et al. 2006).

Wrist flexion and extension cycles discussed above and any other forms of tapping movements can be conceptualized as a string of series of discrete events. These types of movement normally involve some discontinuations (e.g. a short pause) before the onset of flexion in the cycling wrist flexion and extension. It is assumed that an internal timer, which may be located in the cerebellum, is used to achieve certain intervals for each cycle of movement (Ivry and Richardson 2002). Researchers found that the “event structure” principle derived from tapping movements has problems to be applied to other types of movements (e.g. continuous circle drawing). For example, temporal variability in tapping and circle drawing are reported not correlated (Robertson et al. 1999; Zelaznik et al. 2002). From the perspective of movement classification, tapping is normally conceptualized as discontinues movements, while circle drawing is more likely to be represented as continues movements. The temporal goal of discontinues movements are to separate each successive event, whereas the goal of continues movements are to connect each successive event (Ivry and Richardson 2002; Kennerley et al. 2002). Therefore, the principle of “event structure” and internal timer is no longer necessary for continues movements. Instead, the target intervals of continues movement are achieved through an “emergent” pattern by optimizing other movement parameters (Zelaznik et al. 2002). The idea that there are two distinct temporal representation patterns for continues movements and discontinues movements was supported by the study of Spencer et al. (2003). In this study,

cerebellar patients performed a repetitive bimanual tapping task and a circle drawing task. The results showed that patients exhibited increased temporal variability for the discontinuous movement of tapping, while they were unimpaired for continuous movements, i.e., the circle drawing task. These results do not only support the dissociation of temporal representations between discontinuous and continuous movements, they are also consistent with the idea that the internal timer in the cerebellum is not necessary for timing of continuous movements (Spencer et al. 2003). Studies involving split brain patients provided further support for the temporal dissociation between discontinuous and continuous movements. In a study with callosotomy patients, a bimanual circle drawing task was performed in a symmetric and an asymmetric condition. Patients' spatial coupling was found diminished compared to strong spatial coupling of controls. Moreover, it was found that patients' temporal coupling was largely decreased as well (Kennerley et al. 2002). The observed temporal dissociation in split brain patients in this study seems in conflict with results of many studies, which reported that split-brain patients maintain strong temporal coupling (Franz et al. 1996; Ivry and Hazeltine 1999; Tuller and Kelso 1989). However, detailed analysis revealed that study of Kennerly et al. (2002) applied continuous circle drawing movements, while other studies applied either discrete or discontinuous movements; i.e, a three sides squares drawing task was adopted by Franz et al(1996), a repetitive tapping task was applied by Ivry and Hazeltine(1999), and a rhythmic tapping task was used by Tuller and Keldo(1989). Therefore, it can be concluded that the temporal coupling of discontinuous movement is maintained in split brain patients, possibly because the event structure is located in the cerebellum. On the other hand, the temporal coupling of continuous movements are diminished in split brain patients, because the temporal representation attached to the spatial representation is shared by the two hemispheres through the corpus callosum. This idea is

supported by a follow-up experiment of study of Kennerley et al. (2002), which examined split brain patients' temporal coupling in continuous and discrete tapping conditions. The results showed strong temporal coupling of patients in discrete tapping conditions. However, in the continuous tapping conditions, temporally uncoupled movements were commonly observed in the callosotomy patients, which was similar as the observations made in bimanual circle drawing tasks performed by these patients (Kennerley et al. 2002).

In summary, temporal representations of discontinuous movements embodied in event structure arise from the cerebellum. On the other hand, the temporal coupling of continuous movements is dependent on other movement parameters (e.g. the abstract spatial goals for these actions). Figure 2 demonstrates a model for temporal interference of bimanual coordination. This model is based on a review of the paper of Ivry et al (2004).

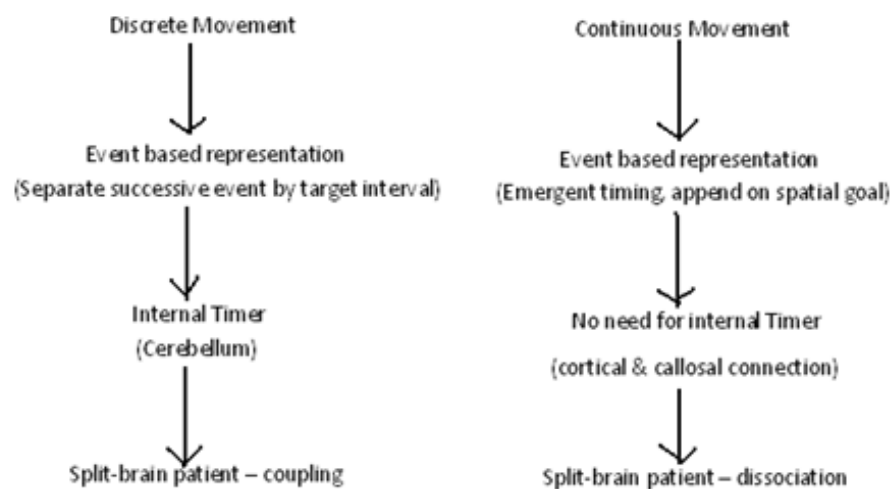


Figure2. A model for temporal interference of bimanual coordination

THE NEUROLOGICAL BASIS OF BIMANUAL COORDINATION

From the view of cognitive representations, there are two essential factors for the occurrence of (spatial) interferences in bimanual coordination. One is the interacting medium allowing two hemispheres to share/transfer representations of tasks, and the other one is the locus or pathways creating these representations.

Interhemispheric Interaction

The corpus callosum has long been suggested as the major bridge for the interaction between the hemispheres in bimanual coordination. This notion has been supported by studies showing how corpus callosum lesions lead to dramatic reduction of spatial and temporal coupling for certain bimanual coordination tasks. In the study of Franz, Ivry, & Gazzaniga(1996), split-brain patients with eliminated interhemispheric communication were asked to simultaneously produce congruent or incongruent three side squares with the two hands. The results showed that, in contrast to controls, the patients performed similarly in symmetric and asymmetric conditions, which means that spatial coupling vanished if interhemispheric interaction through the Corpus Callosum is absent. In other words, an intact Corpus Callosum is necessary for occurrence of spatial coupling in bimanual coordination tasks, especially when no spatial cues are provided. In the study of Kennerly et al. (2002), split-brain patients performed discrete and continuous tapping tasks respectively. The results showed that patients were able to produce temporally uncoupled movements frequently when the task required performance of a continuous pattern, indicating role of the corpus callosum in temporal coupling of bimanually coordinated continuous movements, which, as discussed above, may be related to the spatial coupling of the bimanual coordination. Studies with split brain patients reported dramatic reductions in spatial coupling, and decreases temporal coupling in continuous movements (Eliassen et al. 1999; Franz

et al. 1996; Tuller and Kelso 1989; Kennerley et al. 2002; Semjen et al. 1995). The study of Eliassen et al. (1999) showed that the posterior region of corpus callosum is a major contributor to spatial coupling in bimanual coordination tasks. This study included patients that underwent two successive surgeries. The first operation resects the anterior region of the corpus callosum. After which the patients performed the three sides square bimanual task in an asymmetric coordination condition before and after the first resection. No spatial uncoupling was found in those periods, indicating that the anterior corpus callosum does not contribute to the interference observed in bimanual coordination tasks. The second operation resects the rest, so the posterior region of corpus callosum. After the second surgery the patients started to show spatial uncoupling when performing the bimanual task, indicating the critical role of the posterior corpus callosum for interference in bimanual coordination tasks. Beside the important role in coupling in bimanual coordination tasks, the Corpus Callosum was also reported to be a fundamental structure in acquiring a novel bimanual skill (Sisti et al. 2012; Franz et al. 2000).

Addition to the high level of hemispheric interaction through the corpus callosum, there are also lower level interactions between two limbs occurring in the way of projecting efferent excitability to the other limb besides the limb ought to be projected. Those low level interactions are related to motor irradiation. The coupling of bimanual coordination could be categorized as a type of motor irradiation. Therefore, they may play some minor role in the interference of bimanual coordination. The low level interactions include the uncrossed corticofugal fibers, branched bilateral corticomotoneuronal projection, and segmental networks (Carson 2005). Uncrossed corticofugal fibers are also called the ipsilateral corticospinal pathway. They are the fibers that fail to cross at the pyramidal decussation, which is thought to be 10% to 15% of fibers of the corticospinal projections. The study of Kagerer, Summers, and Semjen

(2003) found that participants who produced high variability in asymmetric bimanual coordination also evoked large ipsilateral motor potentials by transcranial magnetic stimulation (TMS), indicating the involvement of ipsilateral pathways in coupling of bimanual coordination by simultaneously activating ipsilateral muscles (Kagerer et al. 2003). However, studies with more direct evidence supporting this hypothesis are needed to verify the role of uncrossed corticofugal fibers in bimanual coordination. Branch bilateral corticomotorneuronal projection is the branching pattern of the last-order synaptic inputs to the motoneurons. In patients with mirror movements, activities in last-order branched fibers have been obtained to mediate homologous muscles of limbs. This and other related observations were used to propose that the branch bilateral corticomotorneuronal projection may be partly responsible for the composition of synergistic muscle activities, and even interference in bimanual coordination (Farmer et al. 1990). However, as proposed by Carson (2005), activities in last-order branched fibers have mainly been obtained in pathological, but not in normal limb function. Therefore, the role of branch bilateral corticomotorneuronal projection is still under debate. Another low level interaction occur in the segmental networks, in which afferent feedback of the intended motoroutput of a single limb is transmitted to motor pathway of the other limb, and therefore an unintended motor output is projected to muscles of this limb. The study of Meyer, Roricht, Von Einsiedel, Kruggel and Weindl (1995) reported that patients with radiographical abnormalities of the corpus callosum maintained the ability of evoking motor potentials of one hand by strongly contracting muscles in the other hand, which support that some interactions may occur at the segmental level. In other words, the segmental networks may play a role in the coupling in bimanual coordination because motor irradiation was found to be maintained in patients with agenesis of the corpus callosum (Meyer et al. 1995).

Candidate locus

From the perspective of neurological function, interference in bimanual coordination is suggested relating to information transmission from one to the other hemisphere via the corpus callosum as well as bilateral irradiation of efferent excitability through lower level of neural interactions. The next question in this chapter is, what are the potential loci producing the representations for bimanual tasks. We want to clarify in advance that we are not attempting to find a static neurological locus for the functions of bimanual coordination because it is highly possible that brain function for bimanual coordination involve distributed network with interaction of multiple areas and levels rather than be assigned to a single locus. In fact, in the following chapters, several candidate loci will be discussed individually as potential neural assemblies involving in control of bimanual coordination of the network. The candidates favored by related studies include cortical areas of supplementary motor area (SMA) and the cingulate motor area (CMA), and sub-cortical structures of the cerebellum and the basal ganglia (BG).

The supplementary motor area (SMA):

The SMA is known as the motor area mainly responsible for controlling sequential movements, movement preparation, movement organization and controlling internally guided movements. Considering its functions in movement control, it is not surprising that the SMA has also long been proposed as the critical cortical area for bimanual coordination which is normally under internal guide, with high requirements of movement sequence, preparation and organization. Some evidences supporting the role of the SMA in bimanual coordination come from the studies revealed distinct neural function of the SMA in both bimanual and unimanual movement. In the study of Tanji, Okano & Sato (1988), neuronal activity in the cortical motor areas of pre-central,

pre-motor and SMA were recorded when monkeys performing ipsilateral, contralateral and bilateral digit movements. One of the observations was that 28% of SMA neurons are exclusively in relation to the movement of bilateral key press, indicating the special role of the SMA in bimanual movement (Tanji et al. 1988). To compare the movement-evoked potentials (mEP) in unimanual and bimanual movement, Donchin, Gribova, Steinberg, Oliveira and Vaadia (2001) recorded the local field potentials (LFP) in the SMA of monkeys when they performing unimanual and bimanual movements. Greater size of the mEP in SMA was found for bimanual movement compared to unimanual movement, indicating unimanual and bimanual movement are represented differently in SMA. In other words, the SMA plays a special role in bimanual coordination that cannot be explained through its role in unimanual movement (Donchin et al. 2001). Furthermore, the neuroanatomical study of Rouiller, Babalian, Kazennikov, Moret, Yu and Wiesendanger (1994) found that, compared to MI, a more dense bilateral callosal projection of hand representation was found between the SMA in two hemispheres. This observation implies that the SMA is a bilaterally organized system, which, as proposed by researchers above, should have important contribution to bimanual coordination (Rouiller et al. 1994).

Besides the special role for bimanual coordination in general, some studies reported that the SMA is particularly responsible for asymmetric bimanual movements which resulted in higher levels of activation in the SMA compared to symmetric movement. For example, the study of Sadatoki, Yonekura, Waki, Yamada & Ishii (1997) instructed participants to produce right only, left only, bimanual mirror (symmetric coordination) and bimanual parallel (asymmetric coordination) finger movements under measures of regional cerebral blood flow (rCBF) and positron emission tomography (PET). The results showed that activations of the SMA were significantly higher for asymmetric bimanual movement than symmetric bimanual movement or

unimanual movements, supporting the function of the SMA for bimanual coordination, especially for the asymmetric bimanual movements (Sadato et al. 1997). Increased SMA activation was observed for temporally asymmetric movement as well. For example, the study of Lang, Obrig, Lindinger, Cheyne and Deecke (1990) found large activation of the SMA area when musicians were instructed to tap in bimanual rhythm of 3:2 as compared with synchrony rhythm of 2:2, indicating the role of the SMA for temporally asymmetric bimanual movements (Lang et al. 1990). Therefore, it is reasonable to conclude that the SMA plays a vital role for controlling of bimanual movements, especially when the coordination of two hands is asymmetric.

The cingulate motor area (CMA)

The CMA is situated very close to the SMA. Therefore, before discussion of studies about the CMA and bimanual coordination, it is important to know that activations or lesions of the CMA may partly involve the SMA, and damage and neural activities of the SMA may partly include the CMA as well.

Study of Stephan, Binkofski, Halsband, Dohle, Wunderlich, Schnitzler, Tass, Posse, Herzog, Sturm, Zilles, Seitz and Freund (1999) found that one patient who had lesion of the CMA maintained the ability of performing unimanual movement, but had difficulty to produce simultaneously bimanual movement. To further testify the role of the CMA for bimanual coordination, the same bimanual tasks were applied to healthy participants. Strong activations of the cingulated and ventral SMA were observed when healthy participants performing bimanual movements. Thus, results from both patients and healthy participants support that the CMA does has certain contribution for mediating bimanual movements (Stephan et al. 1999). The view that

the CMA is assemble of the neural network for bimanual coordination is also supported by a primate study of Kermadi, Liu and Rouiller (2000), which found high proportion (56%) of bimanual neurons in the CMA supporting again that the CMA is a component of the cortical areas participating in controlling bimanual coordination (Kermadi et al. 2000). Study of Ullen, Forssberg and Ehrsson (2002) investigated the involvement of neural areas for bimanual coordination under different temporal relationships. The functional magnetic resonance imaging (fMRI) results showed that the CMA is highly participated in controlling of the in-phase bimanual coordination, while extensive activations of the SMA was observed for anti-phase bimanual coordination. Therefore, it was concluded that the CMA is responsible for integrating simple (symmetric) bimanual movement, and the SMA is essential for bimanual movements with complex temporal coordination (Ullen et al. 2003). However, the study of Diedrichsen, Grafton, Albert, Hazeltine and Ivry (2006) claimed that the CMA may contribute to asymmetric bimanual coordination as well. In the study, participants performed symmetric or asymmetric bimanual reaching movements under symbolic or spatial cues respectively. Asymmetric coordination under symbolic cues is associated with conflict of goal selection between two hands, while asymmetric coordination under spatial cues is associated with conflict of movement planning and execution between two hands. The fMRI results showed that the CMA plays a role in the goal-selection conflict because the increased activations of the CMA were observed when two hands produced asymmetric movement with symbolic cues (Diedrichsen et al. 2006).

The cerebellum

The functions of subcortical motor areas for bimanual coordination are currently under intense investigation. The role of the cerebellum in movement coordination has long been recognized (Holmes 1939). Some of recent studies about the cerebellum and movement coordination are

interested in utilizing brain imaging techniques to investigate specific function of the cerebellum for bimanual coordination. In the fMRI study of Debaere, Wenderoth, Sunaert, Hecke and Swinnen (2004), participants were instructed to perform cyclical movements under different spatiotemporal complexities and different movement frequencies. Even though, the imaging work showed that the task features of spatiotemporal complexity and frequency were under distinguished functional subcircuits, a strong correlation was observed between activations of the cerebellum and the interaction of frequency and spatiotemporal complexity of bimanual movements. This association implies that the cerebellum is one of the principal regions represent for the control of bimanual coordination (Debaere et al. 2004). The study of Tracy, Faro, Mohammed, Pinus, Madi and Laskas (2001) applied the tasks for clinical test of limb ataxia with palm pronated then supinated. The imaging results showed that neural activations of the anterior medial and posterior cerebellum were uniquely elicited by the bimanual movement. Thus, it was proposed that the cerebellum is part of the network for mediation of bimanual movements, especially when complex integrations of limbs are required (Tracy et al. 2001). The view that the cerebellum is a part of the distributed neural network for bimanual coordination is also supported by many studies included cerebellar patients, who normally showed clear deficits in bimanual coordination. As discussed in the cognitive representation model for temporal coupling of bimanual coordination above, the temporal interferences of discontinues bimanual movements like finger tapping were disturbed in cerebellar patients (Semjen et al. 1995; Kennerley et al. 2002), indicating that the cerebellum plays an important role in temporal components of bimanual movements, at least for discontinuous bimanual movements. Another study with cerebellar patients observed that, in a visuomotor tracing task with bimanual coordination, the initiation of eye movement as well as arm movement were both delayed for patients with mild

cerebellar dysfunction, supporting again the critical function of the cerebellum for controlling visuomotor bimanual tasks (Brown et al. 1993). In the study of Wiesendanger and Serrien (2004), chronic cerebellar patients were instructed to perform a bimanual-drawer task. Compared to controls, the patients encounter problems to initiate movements with bimanual synchronization, implying the cerebellum involves in bimanual coordination (Wiesendanger and Serrien 2004). The role of the cerebellum in bimanual coordination should be taken in caution, because, as stated by Oliveira (2002), it is still not clear that movement deficits occurred for cerebellar patients (like patients in studies discussed above) are specific for bimanual movements or are results of general deficits of motor coordination in this population. The neural basis of bimanual coordination is sketched as below.

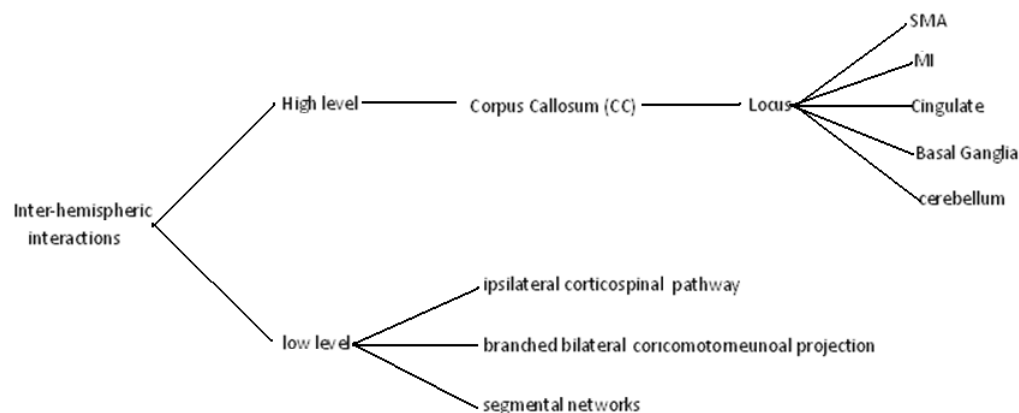


Figure3. Neurological basis of bimanual coordination

Potential role of the basal ganglia in bimanual coordination

The Basal Ganglia is a subcortical collection of nuclei with components of caudate nucleus, substantia nigra, putamen, and globus pallidus buried within the cerebral hemispheres.

Information processed in the Basal Ganglia project to several cortico-subcortical circuits. The major role of Basal Ganglia are sequencing movements, planning movement, initialing and

timing of movements, the designation of specific muscles for a motor task, the execution of automatic, and over learned motor programs. The basal ganglia are not a traditional candidate for the function of bimanual coordination because direct evidences are rare to support that synchronization of bimanual coordination or other motor irradiations are mediated by the basal ganglia. However, the clinical observations that population with basal ganglia lesions like patients with Parkinson's disease (PD) or Huntington's disease have deficits in controlling bimanual movements still make researchers curious about the role of the basal ganglia in bimanual coordination. For example, individual with PD were reported having problem to produce asymmetric movement, and have extremely strong tendency to shift from asymmetric to symmetric coordination (Johnson et al. 1998; Serrien et al. 2000; Swinnen et al. 1997b; van den Berg et al. 2000; de Oliveira 2002). Besides studies with Parkinson's disease, some non-patients brain imaging studies also revealed the role of the basal ganglia in bimanual coordination. For example, neural activations of the basal ganglia were observed during performing of bimanual movements (Kraft et al. 2007; Rao et al. 1997; Debaere et al. 2003). We first discuss studies involving individual with PD and bimanual movements.

Effects of Parkinson's disease on bimanual coordination

PD is a neurodegenerative disease: the neurotransmitter transmitter of dopamine produced by substantia nigra in the basal ganglia gradually degenerates and dies, result in decreased neural information sending into the basal ganglia, unbalanced neural facilitation and inhibition interaction, and reduced interactions with motor cortex. The cardinal motor signs and symptoms of PD include the characteristic clinical picture of resting tremor, rigidity, akinesia (reduced amplitude of movement), bradykinesia (reduced speed of movement) and impairment of postural reflexes. Considering the dysfunction of the basal ganglia and related movement disorders,

individual with PD provide good samples to study the role of the basal ganglia in bimanual coordination by demonstrating possible deficits during control of bimanual movements. However, we should use caution when trying to attribute movement deficits of individual with PD to the basal ganglia because disorder of the basal ganglia may affect the complex basal ganglia-thalamic-neocortical loops. In other words, movement deficits of individual with PD in bimanual coordination may result from dysfunction of the whole loop including SMA and other cortical areas rather than the basal ganglia alone. In addition to discussion of movement deficits of individual with PD in many bimanual tasks, the following chapters will also investigate how the disordered basal ganglia affect specific dimensions of bimanual movements through the perspective of the cognitive representation model of bimanual coordination.

When two hands perform the same movement task simultaneously, individual with PD do not necessary have profound movement deficits compared to controls. The study of Stelmach and Worringham (1988) tried to answer three questions. The first question is does individual with PD experience more movement latencies slower speeds for bimanual as compared to unimanual movements. The second question is can individual with PD keep a consistent temporal linkage between hands. The third question is does individual with PD and controls differ with respect to the asynchrony of movement onset and termination in bimanual tasks. To answer those questions, the participants were instructed to move the index finger(s) as rapidly as possible to the target(s) indicated by illuminations of the LEDs. Unimanual movement was required when only one LED was illuminated, while bimanual movements were required when two LEDs were illuminated. The reaction time (RT) and movement time (MT) for each hand in each task were recorded as the dependent variables. The results showed that RT of bimanual movement increased similarly for individual with PD and controls compared with unimanual

movement. Moreover, the similar additional time of MT was need for individual with PD and controls to execute the bimanual movement. These results indicated that individual with PD are not slower than controls in the planning and execution of bimanual movement, and the compensation mechanism was quite unaffected in individual with PD (Stelmach and Worringham 1988). The similar results have been observed in another study, during which individual with PD and controls draw fixed triangles with the dominant hand and squeeze a rubber bulb with the non-dominant hand simultaneously. The results showed that the squeezing frequency and drawing velocity are similar between individual with PD and controls, indicating that, for both groups, timing of the dominant hand determined the squeezing frequency of the non-dominant hand. Moreover, both groups adapted the timing in the same way, indicating that individual with PD maintained the ability of generating common temporal representations for both hands (Horstink et al. 1990). Now, we attempt to analyze the task applied and the results of those studies through the direction of the cognitive representation model discussed above. The tasks of fixed triangles drawing and rubber bulb squeezing are both discontinuous movements with clear pause between movement segments. The tasks of moving finger to target are discrete movement. Based on the cognitive representation view, timing of discontinuous movement is represented in form of “event structure”. As the “event structure” mainly arises from the cerebellum, which is normally unimpaired in individual with PD, it is not surprising that individual with PD were still able to generalize time-program as controls did in the study. In other words, individual with PD with dysfunctional basal ganglia have relatively unaffected temporal function in discrete movement of bimanual coordination because temporal representation for discrete bimanual tasks are mainly origin from the cerebellum.

Individual with PD normally encounter problems to simultaneously produce different movements with two hands, which require capability of attention sharing and shifting. In the study of Horstink, Berger, van Spaendonck, van den Bercken & Cools (1990), individual with PD and controls were instructed to drawing fixed triangles with the dominant hand and squeezing a rubber bulb with the non-dominant hand simultaneously. The task of drawing fixed triangles is strongly determined by external cue because participants only need to connect fixed dots to draw the triangles. The task of squeezing a rubber bulb is almost entirely depends on internal control because no spatial, ratio or force cues were provided for this task. The variables of squeezing amplitude, squeezing frequency and drawing velocity were recorded. The study found the squeezing amplitude was significantly reduced in individual with PD, even though the spatial performance of triangles did not change. These results indicated that there are two separated spatial representations for each hand. The result can be explained from the perspective that individual with PD has a diminished capacity to shift attention from drawing to squeezing as proposed by this study. Indeed, reduced capability of “shift aptitude” of individual with PD has been observed as early as 1984 in the study of Cools, Van den Bercken, Horstink, Sparndonck and Berger (1984). The study found that individual with PD needed more trials to detecting changing of criterion and produced less response when movement sequences changes (Cools et al. 1984). Those results indicated an association between dysfunctional basal ganglia of individual with PD and diminished ability of shifting attention. On the other hand, the result can also be explained from the perspective of the cognitive representation model of bimanual coordination. For the task of triangles drawing in this study, the movement amplitudes are directly cued because fixed dots were provided as movement targets, while no external cue was provided for the task of rubber bulb squeezing. Based on the cognitive representation view,

spatial representation of directly cued movement will not be affected by representation of the other hand's task, so task of bulb squeezing has very limited influence on the amplitude of triangles drawing. On other hand, spatial representation of movement without external cue can be easily affected by representation of the other task, so the amplitude of bulb squeezing was disturbed by the task of triangles drawing. It seems that controls' attention abilities are able to handle the overlapping between two representations (specifically, the influence of triangles drawing's representation on task of bulb squeezing), but individual with PD cannot. Therefore amplitude of rubber bulb squeezing of individual with PD reduced. In the study of Horstink, Berger, van Spaendonck, van den Bercken & Cools (1990), it was concluded that the disturbance of bimanual coordination of individual with PD is caused by their insufficient shift of attention from triangle drawing to bulb squeezing. We can also make another conclusion that this study supported the cognitive representation view of bimanual coordination: for discontinues movements, temporal coupling between two hands are associated with the cerebellum, therefore individual with PD with disordered basal ganglia maintain the temporal interferences like healthy participants. The spatial representation of movement without external cue is affected by spatial representation of the other task. Dysfunctional basal ganglia limit patient's ability of handling the overlaps of two representations, thus their spatial performance suffer. In fact, it seems that the ability of shifting attention is also the ability of handling overlapping of two simultaneous task representations.

To examine the role of the basal ganglia in bimanual coordination, Johnson, Cunnington, Bradshaw, Phillips, Iansek and Rogers (1988) instructed individual with PD and controls to perform in-phase and anti-phase bimanual movements in fast (2Hz) or slow (1Hz) speed, and with or without an external (metronome) cue to pace the movements. Movements

were performed with handles on a pair of manual cranks. The subjects were instructed to produce continuous, smooth movements for a period of 20s for each trial. The dependent variables included variation in coordination pattern (the SD of the difference between the right and the left hands), accuracy in coordination pattern (mean absolute difference between the two hands), variation in velocity and accuracy of velocity. The results showed that individual with PD are able to perform the in-phase movements, only with less accuracy and stability in the absence of external cues (Bradshaw et al. 1988). This result supported the critical role of the basal ganglia in internally generated movements. The results also showed that individual with PD were not able to produce the anti-phase movement at either high or low speed. First of all, it is worth noting the task applied in the study is relatively difficult because even healthy controls cannot maintain the anti-phase movement at the fast speed, even though they were largely able to produce it at slow speed. Secondly, the task applied is a circle drawing like task which should be categorized as continuous movement. Based on the cognitive representation model, temporal representation of continuous movement is attached to other parameters like the spatial component of the movements. In this study, the temporal component could be attached to the parameter of movement direction: the directions are the same for in-phase movement, while are opposite to each other for anti-phase movements. Therefore, inability of individual with PD to produce anti-phase movement actually implied their limited capability of producing movements in different directions, which may be because of overlapping of representations of two directions. In other words, it was evident again that intact basal ganglia are necessary to handle overlapping of different spatial representations. The similar results were found in the study of Almeida, Wishart & Lee (2002). In the study, participants coordinated simultaneous displacement of the two linear sliding devices toward and away from the midline of the body. Participants were instructed move

continuously (without stopping) within each 20s trials. There were in-phase and anti-phase under three speeds. The study found that individual with PD is able to produce in-phase but not the anti-phase movements. Moreover, movement freezing was occurred at a ratio of 8.1% for individual with PD when they try to perform anti-phase bimanual movements. It was claimed that the difficulties observed in anti-phase coordination for individual with PD is due to deteriorated ability of dysfunctional basal ganglia to inhibit the tendency toward limb synchronization or the in-phase coordination (Almeida et al. 2002). However, the results can also be explained through the cognitive representation model. As the experiment emphasizes continuous movement without stops, the temporal representations for movements of two hands are attached to the spatial components of directions. The lesion of the basal ganglia limited ability of individual with PD to handle two spatial representations with overlapping to each other. Therefore individual with PD failed to produce anti-phase movements.

Individual with PD do not only have problems to produce anti-phase movements, they also have a spontaneous tendency of shifting movement pattern from anti-phase to in-phase movements, even though they are required to produce anti-phase movements. In study of Ponsen, Daffertshofer, van den Heuvel, Wolters, Beek & Berendse (2006), participants performed in-phase and anti-phase bimanual circular drawing movements at an auditory paced frequency with high or low speed. The goal for participants is to follow the pacing signal and produce phase relation as instructed. The dependent variables were percentage of unsuccessful trials and pattern switching. The results showed that anti-phase movements were more changeling than in-phase movements for both individual with PD and controls. During anti-phase movements, maintaining a constant phase relationship between hands was more difficult for individual with PD than controls. Spontaneous pattern switching from anti-phase to in-phase movements occurred more

often for individual with PD relative to controls (Ponsen et al. 2006). Those results consistent with finding of study of Johnson, Cunnington, Bradshaw, Phillips, Iansek and Rogers (1988) discussed above, which also found that, during the anti-phase movement, the external cue made individual with PD tending to perform the in-phase movement instead of the required anti-phase movement. Indeed, many studies found that individual with PD have difficulty in performing bimanual movements; especially when asymmetric movements (like anti-phase movements) need to be produced. The pattern shifting of individual with PD are also observed in other studies (Serrien et al. 2000; Byblow et al. 2002; Swinnen et al. 1997b). Indeed, many studies have demonstrated that, for individual with PD, anti-phase movements tend to become unstable and to make way for in-phase movements. Study of Cohen (1979) found individual with PD spontaneously drift from anti-phase (produce flexion of one hand and extension of the other hand) to in-phase (both hand perform flexion or extension) movement (Cohen 1970). Study of Verschueren, Swinnen, Dom and De Weerd (1997) also reported that individual with PD drifted from anti-phase (continuous bimanual flexion-extension movement with a 90° phase difference between the arms) to in-phase interlimb movement when the external cue was withdrawn (Swinnen et al. 1997b). Johnson, Cunnington, Bradshaw, Phillips, Iansek and Rogers (1998) argued that the spontaneous drift to in-phase bimanual movement may relate to the negative influence of the dysfunctional basal ganglia to the SMA. Some studies reported that damage of the SMA lead to the tendency of revert to mirror-symmetrical movement, when the requisite movement is mirror asymmetrical (Brinkman 1981; Chan and Ross 1988). As the SMA receives thalamocortical input from the basal ganglia, it is possible that disorder basal ganglia lead to some degree of dysfunction of SMA or the basal ganglia-thalamic-SMA loop, which then result in mirror movement observed in the study. This point of view is supported by results of

functional imaging studies which showed that, for individual with PD, activation of the SMA is impaired during bimanual movements (Jahanshahi et al. 1995).

Non-patients brain imaging studies

Studies related to effects of individual with PD on bimanual coordination indicate that disorder of the basal ganglia decreases people's already limited ability of handling overlaps of multiple spatial representations, especially when no external cues are provided. Individual with PD largely maintain temporal performance for discrete or discontinuous movements, indicating that the basal ganglia are not an important part producing the representations of event structures for bimanual movements. Here we focus on non-patients brain imaging studies investigating role of the basal ganglia in bimanual coordination.

Study of Kraft et al (2007) found large signal differences of the basal ganglia between (parallel minus Rest) task than the (mirror minus Test) tasks. The signal changes were mainly observed in the putamen, indicating its special role for asymmetric bimanual movements. During the initiation phase of movement, greater putaminal activity was observed in the asymmetric (parallel) task compared to the symmetric (mirror) task. The different responses in the putamen between symmetric and asymmetric tasks were not observed in the later phases of the bimanual movement. Combining these results with the key contribution of the basal ganglia in movement initiation, it is possible that the basal ganglia play a special role in the initiation phase of bimanual movements. The basal ganglia are also critical neural component for internally generated bimanual movements, while they can be bypassed when bimanual movements are externally generated (i.e. under instruction of external cues). This notion is supported by study of Rao and colleagues (1997), which found putaminal activity was only observed in self-paced

finger tapping condition, not in the externally paced tapping condition. In the study of Debaere, Wenderoth, Sunaert, Van Hecke, and Swinnen (2003), participants performed bimanual movements of wrists flexion and extension. In the internally generated condition, participants performed bimanual movements without visual information (eyes closed), while in the externally guided condition, visual feedback of coordination was provided online when participants producing the movements. The results showed increased putaminal and globus pallidus activities when produce internally generated out-of-phase bimanual wrist movements, whereas basal activities are very limited when the bimanual wrist movements were externally generated. Those observations are in consistent with observations in bimanual studies with individual with PD, which normally report movement deficits of individual with PD in spatially asymmetric coordination when no external cues are provided. The role of the basal ganglia in bimanual coordination is also supported by non-human studies. A primate study trained monkeys a bimanual task of opening drawer with their left hand while grasping a food morsel with the right hand. Single unit recordings of the caudate, putamen and globus pallidus were performed when the monkeys performing the bimanual pull and grasp task. The results support a role for basal ganglia in bimanual coordination by showing that, during the bimanual trials, about 1/3 recorded units exhibited discharge patterns reflecting a bimanual synergy.

METHOD

Participants

The study plans to recruit 60 participants from three populations: twenty young healthy adults from Louisiana State University student body on the Baton Rouge campus, 20 healthy older adults and 20 individuals with PD from the Baton Rouge community. All participants need to be

right hand dominant, which is defined by having a laterality quotient of 0.5 or higher in the Edinburgh Handedness Inventory (Oldfield 1971). All participants will fill out a short health history questionnaire and the older participants and individuals with PD will be tested on the mini mental state examination (Folstein et al. 1975). Anyone who scored below 25 on the MMSE, indicated to have a history of neurological problems (besides the Parkinson's disease), had current vision and/or hearing problems, and/or were unable to use a pen due to a dexterity problem, will be excluded from further participation.

Young adults between the ages of 18 and 30 years and older adults and individuals with PD between the ages of 60-80 will be recruited. The older adults will be matched on age and gender to the individuals with PD. Older adults and individuals with PD should be able to continuously move their forearms for at least couple minutes when their elbows are rest on table. The year of onset of the disease, affected side, UPDRS and H&Y scales, and medication will be recorded for each individual with PD.

Procedures

The main purpose of the study is to examine the role of the basal ganglia in bimanual coordination within the frame of the cognitive representation model. This purpose can be accomplished by answering following series of questions: Can individual with PD produce stable and accurate symmetric bimanual movements? Are their performances different from those of young and older controls? Can individual with PD produce stable and accurate asymmetric bimanual movements? How are their performances in producing asymmetric bimanual movements compared with young and older adults? To answer this series of questions, the study plans to make all participants produce bimanual symmetric and asymmetric coordinated movements respectively. The second series of questions are about whether people's

performances of bimanual movements change with different types of tasks and whether performance changes of individual with PD follow the same pattern as that of young and/or older controls. A continuous and a discrete bimanual task will be separately applied in this study to answer the series of questions above. The third series of questions: What is the role of external cues for performance of bimanual symmetric and asymmetric movements? Do external cues help individual with PD more than young and/or older controls? To answer this series of questions, an external cue will be provided. Movement performances with and without cues will be compared to test whether cues aid disassociation of two limbs in asymmetric coordinated movements. Besides answers for these three series of questions, the study also focuses on possible compounding effects. For example, does an external cue facilitate bimanual movement in general or is more helpful for discrete than continuous motor task? Are individual with PD able to produce symmetric bimanual movement for discrete tasks as well as continuous tasks? The study will have two experiments: one with continuous motor task and one with discrete task. There will be a 3*2*2 design for each experiment with three populations (young controls, older controls and individual with PD), two conditions of coordination (symmetric and asymmetric coordination), and two cueing conditions (with and without external cues).

Participants sit in a chair in front of a 50×30cm monitor. A WACOM Intuos3 12×19 digitizer tablets will be placed between participants and the monitor. There will be a strip of 2cm wide wood stick placed on the center of the tablet to separate working space of two hands. The tablet records the X- and Y-position of the tip of two electronic pens (WACOM ZP-130) with sampling rate of 200Hz and spatial resolution of 0.0005cm. The experimental procedures are setup in MovAlyzeR (NeuroScript LLC, Tempe, Arizona, USA) running on a PC (Dell XPS 720). Participants are instructed to hold pen in normal pen grip and mainly use their wrist and

fingers to manipulate the pen while resting their arms above the tablet. Their arms will be covered so that no visual information about arm movements can be obtained. The task of discrete movement is drawing three side squares with two hands simultaneously. In the symmetric coordination condition, participants are instructed to draw simultaneously three side squares in a shape of U and/or C (rotated by 90 degrees with respect to the U) with two hands, while in the asymmetric coordination condition, participants need to use one hand drawing the U and the other hand drawing the C. In the cueing condition, four specified target locations are provided one by one, thus participants only needed to move to the target showing on the monitor. In the non-cueing condition, instead of presenting the four targets, shapes of U and C are presented on a monitor in front of participants. The task of continuous movement is drawing circles with two hands simultaneously. In the symmetric coordination condition, participants are instructed to draw in-phase circles, while in the asymmetric coordination condition, participants need to draw anti-phase circles. An auditory metronome beat was provided in the cueing condition, but not the non-cueing condition. The diameters of square and circle will be around 2cm and a fixed speed will be picked.

Participants will be allowed to practice sufficiently for each condition, so that none of the conditions is novel for them. During practice, online feedback about movement amplitude and speed will be provided to participants to help them obtain the required movement amplitude and speed. The required movement amplitude and speed, which should be comfortable for all groups, will be picked and practiced before the formal experiments. Participants will be required to try to maintain the required amplitude and speed during the test. The visual feedback of the cues and the on-line trajectory of the tip of the pen will be shown in real-time on the monitor. In experiment with discrete movement, each group of participants needs to perform 10 trials for

each condition, so 40 trials of discrete movements in total. In experiment with continuous movement, each group of participants needs to produce continuous movements for 10 seconds in every condition and repeat it for 4 times. The order of conditions will be randomized for participants.

Measures and Proposed analysis

The study will focus on the following parameters of bimanual coordination. The duration of movement preparation, this could be measured through reaction time which is the duration between the visual signal of “go” to onset of movement which is defined as the moment the pen tip hit the tablet. The ability of producing bimanual movements under required amplitude and speed, those could be obtained through means of movement time and movement amplitude. The ability of producing stable movement patterns is of interest as well. The standard deviations of movement time and movement amplitude are able to show information about stability of movement. The accuracy of drawing lines could be measured by the means and standard deviations of distance from the farthest right to the farthest left point. The coordination between two arms can be measured through the means and standard deviations of relative phase.

All data collected using the pen and digitizer tablet will be processed with a custom program developed in Matlab (Mathworks Inc., Natick, Massachusetts, USA). The position signals will be dual pass filtered with a Butterworth 4th order filter with a cutoff frequency of 7 Hz. The onsets and offsets of pen tip movements will be estimated by a fixed criterion of 5% of the peak in the absolute velocity profile. For each experiment, three-way ANOVAs will be applied with groups (young adults, older adults and individual with PD), conditions of

coordination (symmetric and asymmetric coordination) and cueing conditions (with and without external cues).

HYPOTHESIZED RESULTS

In general, I hypothesize that the basal ganglia are components of the neural loop for controlling of bimanual movements. The roles of the basal ganglia are particularly important when asymmetric bimanual coordination is required and no external cue is provided. It is possible that the basal ganglia are critical for handling overlaps of different representations for different movement of each hand. This may be closely associated with the limitation of shifting attention observed in individual with PD. Based on a review of the literature; I propose that individual with PD are able to produce symmetric bimanual movements, but that they will perform with less stability and accuracy than the control groups. Considering that the asymmetric bimanual task applied in the study is not very difficult, I hypothesize that individual with PD may be capable to produce part of the anti-phase movement, but that the coordination may not be stable. This means that the bimanual coordinated movements should show large standard deviations of relative phase. Furthermore, low drawing accuracy is also expected for asymmetric movement of individuals with PD. About comparison of continuous and discrete bimanual movements, and the comparison of movements with and without cues, I am particularly interest in their interactions. Based on the representation model, external cues may reduce temporal interferences of bimanual movement if the task is a continuous motor task. Therefore, I hypothesize that external cues are more helpful for continuous than discrete task. The effects of external cues should be especially profound for individual with PD due to their reduced ability of handling overlaps of multiple representations.

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