ON-LINE CONTROL OF THE LIMBS DURING BIMANUAL REACHING IS INDEPENDENT WITH DIRECTLY- AND SYMBOLICALLY-CUED TARGET PERTURBATIONS

by

Jarrod Paul George Blinch

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

The Faculty of Graduate Studies

(Human Kinetics).

The University of British Columbia

(Vancouver)

December 2009

ABSTRACT

Using both hands at the same time is an important ability of the human action system. This is referred to as bimanual coordination, and complex cases of coordination are often tested to reveal its limitations. A common limitation is that the limbs cannot make independent movements but are drawn to follow the same spatial trajectories with similar temporal properties. These examples of bimanual interference are called spatial and temporal interference. Another type of interference is seen in the initiation of bimanual reaching movements. When a reaching movement is directly-cued by illuminating the targets, the reaction time is the same for symmetric or asymmetric movements. However, the reaction time is longer for asymmetric compared to symmetric movements if they are symbolically-cued. The leading hypothesis for this reaction time cost is that the increased processing demands on response selection for symbolically-cued asymmetric movements results in bimanual interference (Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001). In two experiments, we investigated the effect of this interference when it occurred as the result of a perturbation during a movement that required an on-line correction. We sought to determine if there was larger spatial interference in one limb when the other limb responded to a symbolically-cued on-line correction compared to a directly-cued correction. Participants made bimanual reaches to targets that were occasionally perturbed at movement onset. These perturbations required on-line corrections with one limb to the new target location. The new target location was indicated by illuminating the new target as a direct cue (experiments 1 and 2) or symbolically cueing the target with a colour change (experiment 1) or displaying the letter L or S (experiment 2). We found larger spatial interference for symbolically-cued on-line corrections compared to directly-cued corrections. Although there was greater interference with symbolic cues, the interference was small and transient with direct and symbolic cues. It was also subtle in comparison to spatial interference during preplanned bimanual reaches. Since a correction in one limb can be accomplished without a large or lasting effect on the other limb, we conclude that on-line control of the limbs during bimanual reaching is largely independent.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

To my Pappy, Roy Robinson.
I wish my future wife and children could have known you. I am honoured to know that so much of you lives on in me.

1 INTRODUCTION

Using both hands at the same time is an important ability of the human action system. This is referred to as bimanual coordination, and complex cases of coordination are often tested to reveal its limitations. These limitations are not always obvious in everyday tasks but they are important as "limitations in producing bimanual movements can illuminate the underlying functional architecture of the action system" (Diedrichsen, Grafton, Albert, Hazeltine, & Ivry, 2006, pp. 1729). A common limitation is that the limbs cannot make independent movements but are drawn to follow the same spatial trajectories with similar temporal properties. These examples of bimanual interference are called spatial interference and temporal interference. Another type of bimanual interference is seen in the initiation of bimanual reaching movements. When a bimanual reaching movement is cued directly by illuminating the targets, the reaction time is the same or similar for symmetric or asymmetric movements. However, the reaction time is longer for asymmetric compared to symmetric movements if they are cued symbolically. The leading hypothesis for this reaction time cost is that the increased processing demands on response selection for symbolically-cued asymmetric movements results in bimanual interference (Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003). We proposed to investigate the effect of this bimanual interference when it occurred as the result of a perturbation during the movement that required an on-line correction. The on-line correction may result in spatial and temporal interference. We asked: will there be larger spatial interference for a symbolically-cued on-line correction compared to a directly-cued correction? Next, we will begin to detail our experimental logic by reviewing foundational research on bimanual reaching movements.

1.1 Bimanual reaching

Kelso, Southard, and Goodman (1979) investigated how bimanual reaching movements are coordinated by the nervous system. One possibility is that there are "functional groupings of muscles that are constrained to act as a single unit," which is defined as a coordinative structure (Kelso, Southard, & Goodman, 1979, pp. 229). For unimanual movements, Fitts' Law describes the relationship between movement times and the amplitude and width of targets (Fitts, 1954).

Simply, movement times increase with larger movement amplitudes or smaller target widths. Kelso and colleagues were interested in comparing the movements times of each limb when one limb made a short movement to a big target (easy target) and the other limb made a long movement to a small target (difficult target), while being as quick and accurate as possible. Fitts' law states that the former movement time will be much faster than the latter. However, if the nervous system imposes a coordinative structure, a bimanual movement to an easy and difficult target may be synchronized. They found that bimanual movements had synchronous initiation and termination. Compared to unimanual movements, the movement time to the easy target increased to match the movement time to the difficult target. Peak velocity and peak acceleration were practically synchronized, even though the limbs moved at different speeds. Kelso and colleagues (1979) concluded that even disparate movements are constrained with an invariant temporal structure. This creates a coordinative structure where the two limbs act as a single unit and solves the problem of controlling multiple degrees of freedom in a bimanual task (Bernstein, 1967; Turvey, 1977).

In one part of a follow-up experiment, Kelso, Putnam, and Goodman (1983) examined if bimanual movements have spatial constraints as well as temporal constraints. They introduced an obstacle in the path of one limb to see if the trajectory of the other limb would also be modified. They found there was a compensatory effect on the trajectory of the limb without an obstacle for the majority of participants. The participants that avoided spatial interference tended to move their limbs more asynchronously, delaying the initiation of the second limb. The temporal aspects of the movements with the left and the right limbs were still synchronized, regardless of the compensatory strategy. From both experiments, they concluded that bimanual movements have a coordinative structure that entails common spatial and temporal properties.

Marteniuk and MacKenzie (1980; Marteniuk, MacKenzie, & Baba, 1984) tested the proposal of a coordinative structure for bimanual movements. Their methods were similar to Kelso and colleagues (1979) except that participants held styli and moved to targets that were 1 mm in diameter instead of moving their fingers to targets that were 3.6 or 7.2 cm wide. The target distances were 10 or 30 cm, with the bimanual symmetric movements coded as 10-10 or 30-30 and asymmetric movements as 10-30 or 30-10. They also included trials in which weight was added to either stylus or both styli and examined if the limbs remained synchronized. Two main differences were found from Kelso and colleagues (1979). First, when a weight was added to

one stylus, the unweighted stylus reached its target earlier than the weighted stylus. Second, the non-dominant limb significantly overshot the short target when the dominant limb moved to a long target (10-30 for right-handed participants), which they referred to as amplitude assimilation. Specifically, the non-dominant limb overshot the short target by 7.0 mm in the 10-30 condition compared to 2.3 mm in the 10-10 condition. There was a slight decrease in the length of the dominant limb moving to a long target, but it was not significant. In the 30-10 condition, there was a small, non-significant amount of amplitude assimilation in each limb.

Marteniuk and MacKenzie (1980) argued that the statistically significant difference in movement time in the weighted condition opposed Kelso and colleagues' (1979) hypothesis of a coordinative structure with time as an invariant feature of bimanual control. They also proposed a model of bimanual coordination based on the functional properties of the central nervous system where ipsilateral and contralateral motor commands may interfere with each other at three levels: "the relatively high levels [cortical] where these processes first originate [during information processing]; the brain stem level where movement commands converge; or, at the spinal level where contralateral and ipsilateral projections interact from both corticospinal and descending brain stem pathways" (pp. 193). Marteniuk and MacKenzie (1980) theorized that movement time asymmetry and amplitude assimilation resulted from command interference at the brain stem and spinal levels during movement execution. Interference was proportional to the intensity of activation in the contralateral movement, which explained why the increase in amplitude of the short movement was greater than the decrease in amplitude of the long movement.

Kelso and colleagues (1983) responded that the average difference in movement times measured by Marteniuk and MacKenzie (1980) was only 20 ms and may be the result of increased accuracy demands for targets that were 1 mm in diameter. They also suggested that amplitude assimilation could be a coordinative structure imposing common spatial properties, as seen when an obstacle is placed in the path of one limb (Kelso et al., 1983). Common to both of these approaches, there is interference during bimanual movements whether it is caused by the demands of the coordinative structure or the crosstalk of the movement commands. The concept of neural crosstalk assumes there are separate neural commands for the two limbs. When these commands differ, such as the case for a bimanual asymmetric movement, neural interference between these commands can occur. This interference, or crosstalk, can occur during movement

preparation and movement execution at many levels of the central nervous system (Swinnen & Wenderoth, 2004). A likely source of cortical crosstalk is the information processing required to produce the motor commands, which includes stimulus identification, response selection, and response programming. The neural crosstalk perspective will be the paradigm used in this thesis. Next, we will show how crosstalk can occur at cortical levels during information processing.

1.2 Cortical crosstalk

1.2.1 Response programming

Spijkers, Heuer, Kleinsorge, and van der Loo (1997) also examined short and long bimanual reaching movements that could be symmetrical or asymmetrical in choice reaction time conditions. Precuing the target amplitudes 0 to 1000 ms before the imperative stimulus altered the amount of time for preprogramming. This was done to examine interference during response programming. Their logic was that if there is interference during response programming for asymmetric movements, then reaction times for asymmetric movements should be longer than symmetric movements. When the precue occurs before the imperative stimulus, this interference occurs during preprogramming and has less influence on the reaction time. Thus, reaction times for symmetric and asymmetric movements should be equivalent when the precue is long enough to accommodate the interference caused by asymmetric movements.

The precue was the German word for "short" or "long" for each limb. Spijkers and colleagues (1997) found that when the precue was coincident with the imperative stimulus, the reaction times for asymmetric movements were longer than symmetric movements, with a difference of 174 ms. As predicted, the reaction time cost for asymmetric movements diminished as the precue interval increased but was still significant at the longest precue interval of 750 ms (Figure 1.1 left). The precue was altered to be more movement-compatible in a second experiment by displaying a short or long horizontal bar for each limb. The reaction time cost with a 0 ms precue was reduced to 57 ms, but it had the same trend as the less compatible precue and was no longer significant with a 1000 ms precue (Figure 1.1 right). Since the reaction time cost only existed when the time for movement preparation was limited, they reasoned that this type of

4

interference occurs at a cortical level during response programming. Amplitude assimilation was also seen, but it was less influenced by the precue interval than the reaction time cost. It was hypothesized that amplitude assimilation occurs at low-levels (brain stem, spinal) during movement execution.
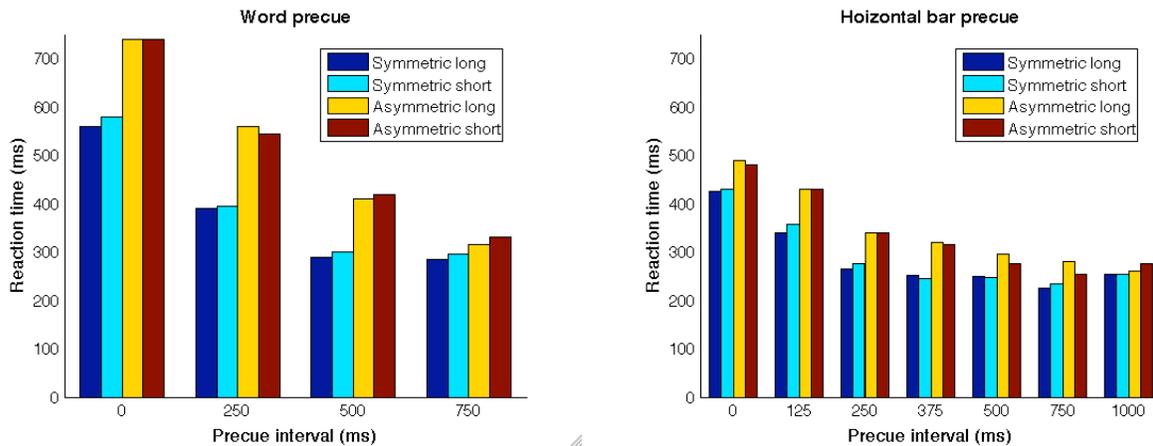
Figure 1.1. Reaction time by precue interval for the word precue (left) and the more movement-compatible horizontal bar precue (right). In both cases, the reaction time for asymmetric movements (yellow and red) compared to symmetric movements (blue and cyan) was still significant at a precue interval of 750 ms. Based on data from Spijkers and colleagues (1997).

1.2.2 Stimulus identification or response selection

It is possible that the reaction time cost for asymmetric movements is the result of interference during response programming. However, since preprogramming influences all three stages of information processing, the interference could occur during any stage or any combination of stages. Diedrichsen, Hazeltine, Kennerley, and Ivry (2001) reasoned that the symbolic precues used by Spijkers and colleagues (1997) placed high processing demands on response selection that are atypical for goal-directed actions. Symbolically-cued movements, like displaying the words "short" and "long", require more processing during response selection to translate the cue into a movement goal than a directly-cued movement in which the target is visually specified (Goodman & Kelso, 1980). The reaction time cost could be the result of increased processing during response selection for different symbolic cues in asymmetric conditions that requires more processing as symmetric conditions with identical cues. They tested the hypothesis that the reaction time cost is the result of interference during stimulus identification or response selection that can be abolished by cuing the movements directly. Independent of the type of cue (direct or symbolic), the same response programming was required. Therefore, if the reaction time cost

5

was eliminated by directly cuing the movements, then the interference would appear to occur during stimulus identification or response selection and neither response programming nor movement execution.

To test their hypothesis, symmetric and asymmetric reaching movements were made to short and long targets. The participants were instructed to move as quickly and accurately as possible to the targets specified by the direct or symbolic movement-cues that also served as the imperative stimulus. The symbolic cues were the letters S and L for the short and long targets, and the targets were illuminated as direct cues. A reaction time cost of 55 ms for symbolically-cued asymmetric movements replicated Spijkers and colleagues (1997) (Figure 1.2 left). There was no difference in reaction time for symmetric or asymmetric movements that were directly cued (Figure 1.2 left). This supported their hypothesis that the bimanual interference occurred during stimulus identification or response selection and not response programming.
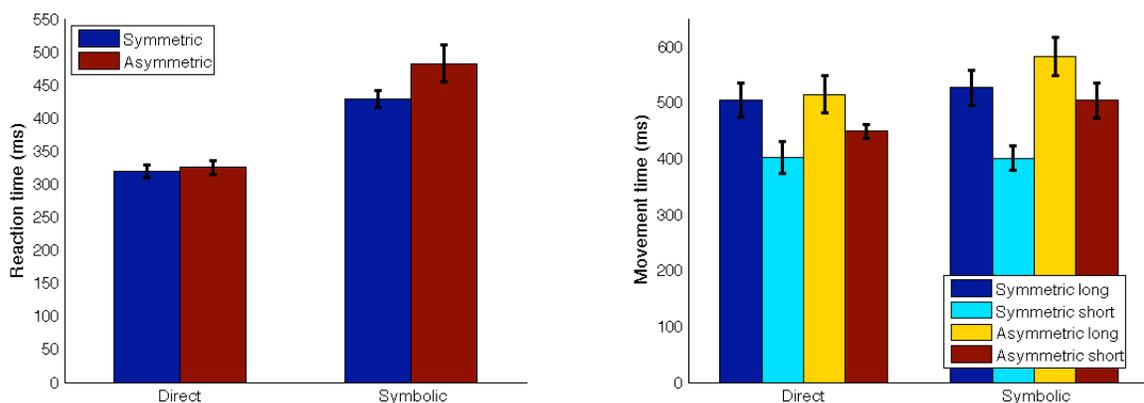
Figure 1.2. Reaction times (left) and movement times (right) in symbolic and direct conditions. Error bars are plus or minus one standard error. Based on data from Diedrichsen and colleagues (2001).

The movement times also yielded some interesting results (Figure 1.2 right). With direct cues, asymmetric movements had movement times closer to symmetric long movements than symmetric short movements. It is has been shown (Kelso, Putnam, & Goodman, 1983; Kelso, Southard, & Goodman, 1979; Marteniuk & MacKenzie, 1980, Marteniuk, MacKenzie, & Baba 1984) that the movement time of the short movement accommodates to the movement time of the long movement so the movements can begin and end simultaneously. However, in the study by Diedrichsen and colleagues (2001), the asymmetric movements had an even larger increase in movement times in the symbolic compared to direct conditions, and the movement time of a long movement paired with a short movement was even longer than a symmetric long movement.

6

This suggests the larger accommodation effects in symbolically-cued asymmetric movements may also be contributed to by the bimanual interference that results in the reaction time cost. This cost is eliminated with a 1000 ms precue, so it is possible this interference also affects the movement time when the precue is coincident with the imperative stimulus. In different terms, the stimulus identification or response selection of symbolically-cued asymmetric movement produces interference that can be measured during movement preparation and movement execution. This has been shown in the measures of reaction time and movement time, respectively. We will return to the possibility that this interference may also appear in the trajectory of the movement.

1.2.3 Response selection

A follow-up experiment investigated if the reaction time cost is the result of interference during stimulus identification or response selection (Diedrichsen et al., 2003). The hypothesis was that the reaction time cost for asymmetric movements might be the result of translating two different symbolic cues into movements. Translating the same cue twice for a symmetric movement may result in a time-savings (Hazeltine, Diedrichsen, Kennerley, & Ivry, 2003). If the reaction time cost is the result of increased processing to identify or translate two cues into movements, then it should be seen regardless of the type of movement required, symmetric or asymmetric. Using the same or different colour cues that required either symmetric or asymmetric movements tested this. Identical reaction time costs of 185 ms were found when different symbolic cues required symmetric or asymmetric movements. This supported the earlier hypothesis that bimanual interference can result from stimulus identification or response selection. To compare the roles of identification and selection they manipulated the demands on these stages in a series of experiments. They found the reaction time cost was independent of the demands on stimulus identification and dependent on the demands on response selection. This supported the hypothesis that bimanual interference occurred during response selection, and not stimulus identification. They argued that interference during selection results from a competition between the cue-to-target rules for each limb when the symbolic cues are different.

1.3 Spatial coupling of movement trajectories

The type of cues used to specify the targets of bimanual reaching movements can result in bimanual interference. This interference is expressed as a reaction time cost when each limb is cued with two different cues instead of identical cues (Spijkers et al, 1997; Diedrichsen et al., 2001). The reaction time cost is found regardless of if the two different cues require symmetric or asymmetric movements (Diedrichsen et al., 2003). Interestingly, illuminating the targets as direct cues eliminates the reaction time cost (Diedrichsen et al., 2001). The hypothesis is that the increased processing demands on response selection for the cue-to-target translations with symbolic cues compared to direct cues results in bimanual interference (Diedrichsen et al., 2001; Diedrichsen et al., 2003; Hazeltine et al., 2003). However, response selection can also occur during a movement as part of on-line control processes. How would the bimanual interference be expressed if it occurred during on-line control; would it result in the spatial interference of the movement trajectories?

Spatial interference of movement trajectories has been shown in bimanual reaching movements (Kelso, Putnam, & Goodman, 1983; Kelso, Southard, & Goodman, 1979; Marteniuk & MacKenzie, 1980, Marteniuk, MacKenzie, & Baba 1984; Swinnen, Walter, & Shapiro, 1988) as well as continuous bimanual movements (Franz, 1997; Franz, Eliassen, Ivry, & Gazzaniga, 1996). For example, when attempting to continuously draw lines with one limb and circles with the other, both shapes end up looking like ovals (Franz, 1997). Spatial interference results in this egocentric symmetry, which can be visualized as mirrored movements about the midsagittal plane. If one limb moves to the left, then spatial interference pulls the other limb to the right to maintain the egocentric symmetry. The opposite is allocentric symmetry, which is when the limbs move in the same direction in external space; if one limb moves to the left, then the other limb also moves to the left. Spatial interference has been suppressed in continuous movements with the use of salient (Lissajous) feedback that displays the relationship between the limbs (Swinnen, Verschueren, Bogaerts, Dounskaia, Lee, Stelmach, & Serrien, 1998) and haptic tracking (Rosenbaum, Dawson, & Challis, 2006). It is possible that these manipulations altered the movements from being cued symbolically to directly. How would spatial interference compare in bimanual reaching movements with directly- or symbolically-cued target perturbations?

The reaching movements with spatial interference that have been investigated are all movements that are planned in advance of movement execution (Kelso, Putnam, & Goodman, 1983; Kelso, Southard, & Goodman, 1979; Marteniuk & MacKenzie, 1980, Marteniuk, MacKenzie, & Baba 1984; Swinnen, Walter, & Shapiro, 1988). For example, the obstacle used by Kelso and colleagues (1983) was visible before the start of the trial, so bimanual movements that avoided the obstacle could be preplanned. The limb with the obstacle had a higher trajectory than control trials. Spatial interference was seen in the majority of participants as higher trajectories in the limb without the obstacle. Another example of spatial interference in preplanned bimanual reaching movements is the experiment by Swinnen, Walter, and Shapiro (1988). Participants made simultaneous elbow flexion movements from far targets to close targets with egocentric symmetry, but the right limb had to make a double reversal action in the middle of the movement. Spatial interference was seen as a concomitant double reversal in the left limb that was most evident in the acceleration profile. The required acceleration profile of the left limb should have one positive and negative peak. Instead, it resembled the acceleration profile of the right limb and had two positive and negative peaks. In contrast, we proposed to examine spatial coupling caused by on-line control. Response selection (and more broadly, information processing) occurs during preplanning and on-line control, but there is behavioural and neurophysiological evidence that shows a distinction between these processes (Glover, 2004; Milner & Goodale, 2008).

1.3.1 On-line control of bimanual reaches

We asked the following research question: will there be larger spatial interference in the unperturbed limb when the perturbed limb responds to a symbolically-cued on-line correction compared to a directly-cued correction? Having a target change locations or change colour at movement initiation will compare directly- and symbolically-cued on-line control. On-line control will be required to adjust to wherever the target jumped (direct) or to translate the colour change into a new target location and perform an adjustment (symbolic). There should be a difference in the time required to respond to the target perturbation, with directly-cued perturbations beginning sooner (more automatic) than symbolically-cued ones (more voluntary) (Diedrichsen et al., 2001). By automatic, we mean that target jumps can sometimes elicit

corrections contrary to task instructions (automatic capture) (Pisella, Gréa, Tilikete, Vighetto, Desmurget, Rode, Boisson, Rossetti, 2000) or corrections when the participant is unaware of the target displacement (Goodale, Pelisson, & Prablanc, 1986). We are interested if symbolically-cued on-line corrections will have larger spatial coupling than directly-cued corrections.

To our knowledge, directly and symbolically-cued on-line corrections have not been compared. The effect of directly-cued corrections on the movement trajectories has been examined (Diedrichsen, Nambisan, Kennerley, & Ivry, 2004; Mason, 2008). In the experiment by Diedrichsen and colleagues (2004), participants made bimanual reaching movements to targets that were 2.4 cm in diameter and 23 cm in front of the starting position. The targets appeared as the imperative stimulus and the goal of the movement was to be as accurate as possible and to have a movement time below 450 ms. The forward positions of the limbs were displayed in real-time, but lateral deviations were not shown; feedback of the spatial accuracy was given after each trial. Unimanual movements with and without a target jump and bimanual movements without a target jump were included as control conditions. In the experimental bimanual trials, one or both targets jumped to the left or right at movement initiation. This required on-line control of the limbs (the perturbed limbs) to adjust to the directly-cued target perturbation. When one target jump occurred, the mean trajectory of the other limb (the unperturbed limb) was compared to control for spatial interference.

Diedrichsen and colleagues (2004) found that movements were as accurate in all of the target jump conditions as the control conditions. The average onset of adjustment to a target jump was 175 ms and also did not differ in unimanual or bimanual (one or both targets jumped) conditions. This showed that participants could perform on-line corrections to two target jumps as proficiently as one target jump in bimanual or unimanual conditions. When only one target jump occurred in a bimanual movement, there was small, transient spatial interference in the unperturbed limb that was statistically significant. The mean magnitude of the interference at peak lateral velocity was 2.1 ± 1.4 mm (mean ± standard deviation); it was corrected within 100 ms, and did not impact the endpoint accuracy of the movement. Interestingly, the interference was in the same direction as the correction for the target jump (see Diedrichsen et al., 2004 Figure 3B). This is the opposite of egocentric symmetry and is referred to as allocentric symmetry. They concluded that directly-cued on-line corrections can occur independently for

the two limbs with only small, transient spatial coupling. The allocentric interference may be the result of the reliance on the posterior parietal cortex for directly-cued on-line corrections.

Diedrichsen and colleagues (2004) showed small, transient bimanual interference for directly-cued on-line corrections. The interference was small in comparison to the size of the reaction time cost for symbolically-cued movements (Diedrichsen et al., 2001; Spijkers et al., 1997) or the magnitude of spatial coupling in preplanned bimanual reaches (Kelso, Putnam, & Goodman, 1983; Kelso, Southard, & Goodman, 1979; Marteniuk & MacKenzie, 1980, Marteniuk, MacKenzie, & Baba 1984; Swinnen, Walter, & Shapiro, 1988). To address our question, we required a comparison between directly and symbolically-cued on-line corrections.

In summary, high processing demands on response selection have been shown to result in bimanual interference (Diedrichsen et al., 2001; Diedrichsen et al., 2003; Hazeltine et al., 2003). We tested if increased processing demands on response selection for symbolically-cued on-line corrections compared to directly-cued corrections resulted in spatial coupling, a form of bimanual interference. Diedrichsen and colleagues (2004) found small, transient interference with directly-cued online corrections, so we expected to replicate this amount of interference in direct conditions and to find larger interference in symbolic conditions. Based on the results of a pilot study (Appendix A), we advanced the methods used by Diedrichsen and colleagues (2004) to allow a comparison of bimanual interference with directly and symbolically-cued on-line corrections.

11

2 EXPERIMENT ONE

2.1 Methods

2.1.1 Participants

The participants were 11 students from the University of British Columbia. The University of British Columbia Office of Research Services approved this study. All participants had normal or corrected-to-normal vision and were right handed based on self-report measures of the Edinburgh Handedness Inventory (Oldfield, 1971), with a laterality quotient greater than .60.

2.1.2 Task and apparatus

Bimanual reaching movements were made on a horizontal surface with forward movements in the transverse plane. The dimensions of the stimulus display are shown in Figure 2.1. This was displayed on the horizontal surface by placing a monitor above the surface and a half-silver mirror midway between the two. Vision of the limbs was available at the start of every trial to orient the participant, but it was removed during movements to prevent vision-based on-line corrections.
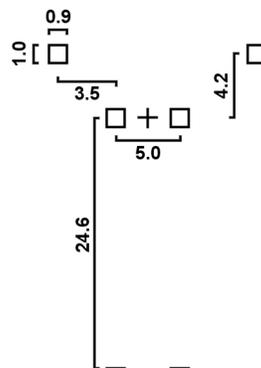
Figure 2.1. Dimensions of the stimulus display in the mid configuration. All dimensions are in centimeters.

The participant was instructed to maintain fixation on the cross, begin the movement when ready, and be as accurate as possible with a goal movement time of 500 ms ± 50 ms. The movements were made with digitization pens with infrared emitting diodes near the tip of each pen. These were used to record the spatial location of the pens and the status of the tips (up or down) at 500 Hz with an Optotrak imaging system (Optotrak 3020, Waterloo, Ontario) for two seconds beginning with the target presentation.

There were three bimanual reaching conditions: Control, Direct, and Symbolic. Feedback of the movement endpoint was displayed on the movement surface for only the Control condition (Figure 2.2 d2). The Direct and Symbolic conditions had target perturbations at movement onset, measured by when both pens were lifted off the aiming surface. The participant was instructed to begin an on-line correction as quickly as possible to any target perturbation and to be as accurately as possible. In the Direct condition, the initial target for one limb may jump to the posterior target placeholder (Figure 2.2 e1). The initial target for one limb may change colour in the Symbolic condition (Figure 2.2 f1). The target might change colour to blue, and the participant was taught the association between the change in colour and the target placeholders. At the end of trials with colour changes, the target placeholders were filled with their respective colour to remind the participant of the colour-to-target association (Figure 2.2 f2).

In all conditions, the locations of the target placeholders and fixation were randomized between three configurations (near, mid, far). The stimulus display in Figure 2.1 is the mid configuration where the distance from the starting positions to the two closest target placeholders (the initial target placeholders) was 24.6 cm. All the target placeholders and the fixation were moved 1 cm closer to the starting positions in the near configuration so that the distance from the starting positions to the initial target placeholders was 23.6 cm. The far configuration had the opposite adjustment, so the distance from the starting positions to the initial target placeholders was 25.6 cm. This was done to prevent increasingly open-loop movements in the control trials and for the limb without a target perturbation in direct and symbolic trials as the experiment progressed. Target perturbations always occurred in the mid configuration.
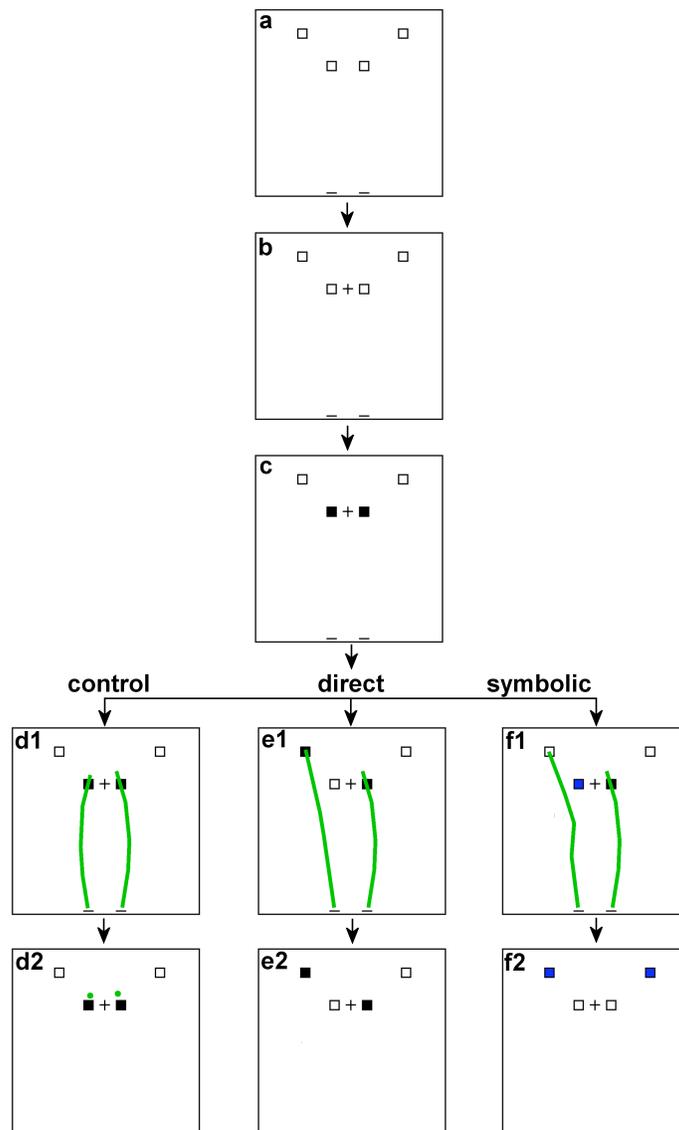
Figure 2.2. Stimulus progression. The limbs were moved into the starting positions (a), the fixation point appeared (b), and then the targets for the left and right limbs appeared (c). In the Control condition, the participant reached to the targets (d1) and feedback of their end positions was displayed at the end of the trial (d2). In the above example of a direct target perturbation, the target for the left limb jumped to the posterior target placeholder at movement initiation and an on-line correction was made to the new target (e1). No feedback was given at the end of direct trials (e2). In the above example of a symbolic target perturbation, the left target changed colours to blue (f1), which required an on-line correction with the left limb to the posterior target placeholder. The colour to target placeholder association was shown at the end of symbolic trials (f2).

2.1.3 Design

The experiment was divided into three sections: practice, direct, and symbolic (Table 2.1). The experiment began with 21 practice trials in control conditions to familiarize the participant with the procedure and to achieve a movement time of 500 ms ± 50 ms. The order of the Direct and

Symbolic sections was counterbalance. These sections consisted of 108 trials, with a
randomization of two-thirds control trials and one-third target perturbations, with an equal
number of the two types of perturbations (left limb long, right limb long).

Table 2.1. The experimental design.

Practice	Direct	Symbolic
	72 control	72 control
	18 x 2 perturbation	18 x 2 perturbation
21 control	**Symbolic**	**Direct**
	72 control	72 control
	18 x 2 perturbation	18 x 2 perturbation

2.1.4 Data analysis

The analyses were restricted to movements in the transverse plane. Raw trajectory data were
low-pass filtered with a dual pass fourth order Butterworth filter at a cut-off frequency of 10 Hz.
The data were then differentiated with a central finite-difference method to calculate velocity in
the forward and lateral directions. Temporal averages were used to calculate mean displacement
and velocity trajectories for each participant. This included mean trajectories for the control
limbs and the limbs that made the correction (the perturbed limbs) and the limbs that did not
make a correction (the unperturbed limbs) in Direct and Symbolic conditions.

Individual trials were excluded from analyses if they met any of the five exclusion criteria. First,
either Optotrak marker was missing for longer than 10 ms (5 frames at 500 Hz). Missing
markers in shorter intervals were estimated with linear interpolation. Second, either movement
began after the two-second recording interval of the Optotrak, or third, either movement finished
after the recording window. Fourth, the endpoint of either limb in the forward direction was
further than 25 mm from the centre of the target placeholder. This distance was selected, as it
was approximately half the distance between the control and the perturbed target placeholders.
Fifth, the absolute difference in the time from the initial target presentation to the pen-up of each
limb (the reaction time asynchrony) was larger than 25 ms. Trials with asynchronous reaction
times were determined on-line and recycled to the end of the section to prevent decreasing the
number of trials in each condition. This criterion was included to prevent the possibility of

reducing the spatial interference by delaying the initiation of the second limb (Kelso, Putnam, & Goodman, 1983).

Movement times were measured from the pen-up to the pen-down of each limb. The onset of adjustment to a target perturbation was measured by comparing the mean velocity of the perturbed limb to control, and this was done separately for each limb. An adjustment occurred if the perturbed trajectory went outside of two standard deviations from the control trajectory. This was traced back to when the two trajectories converged to determine the onset of adjustment, which was the time from movement onset (second pen-up) to when the trajectories diverged.

Constant error and variable error were calculated from the movement endpoint to the centre of the target placeholder in the forwards and lateral directions. If there is spatial interference that lasts until the end of the movement, then the unperturbed limbs may be less accurate or less consistent than controls. Spatial interference might occur in the forward direct, the lateral direction, or both directions. In the forward direction, spatial interference should pull the unperturbed limb in the same direction as the perturbed limb, which is further than control. The unperturbed limb should overshoot regardless of if the interference occurs in an allocentric or an egocentric reference frame, but the reference frame will impact the lateral interference. Allocentric interference will pull the unperturbed limb in the same lateral direction as the perturbed limb, so towards the midline. The unperturbed limb will move away from the midline, in the opposite lateral direction as the perturbed limb, if the interference occurs in egocentric coordinates.

Spatial interference in the unperturbed limbs may be transient, correcting itself before the end of the movement and not changing the reach accuracy or consistency. We therefore compared the unperturbed displacement trajectories to controls across the entire movement. We calculated the temporal average of these two reach types for each participant (and each cue and each limb), and then compared these averages across participants. The mean forward and lateral positions of the unperturbed limbs were compared to controls every 20 ms after movement onset to determine if the unperturbed limb was affected by spatial interference from the on-line correction of the perturbed limb. As with constant and variable error, spatial interference should pull the unperturbed limb further than control in the forward direction. In the lateral direction, the

unperturbed limb could be pulled in either direction depending on if the interference occurred in allocentric or egocentric coordinates.

Data were analysed with analysis of variances (ANOVAs) to determine statistically significant results (p < .05). All factors in the ANOVAs had repeated measures. The Huynh-Feldt correction was applied whenever the Mauchly's test of sphericity was statistically significant (p < .10). Significant main effects with more than two levels were further analysed by pairwise comparisons using the Sidak adjustment for multiple comparisons. Significant interactions were analysed with simple main effects and, if necessary, pairwise comparisons using the Sidak adjustment. Main effects and interactions that are not reported, did not reach significance (p > .05).

2.2 Results and discussion

The number of trials excluded for each participant is shown in Table 2.2. The most common reason for exclusion was reaction time asynchrony, but these trials were recycled to the end of the block to prevent decreasing the number of trials in each condition.

Table 2.2. The number of excluded trials for each participant and for each exclusion criterion.

Participant	Missing Markers	Asynchronous Reaction Time	Slow Movement Initiation	Slow Movement Termination	Poor Accuracy
1	0	5	0	0	4
2	2	69	0	0	6
3	1	4	2	0	0
4	0	12	0	4	6
5	0	8	0	0	1
6	1	56	0	17	4
7	1	49	0	0	24
8	36	8	0	4	9
9	0	3	0	1	6
10	4	12	1	0	5
11	1	37	0	4	5
Total	46	263	3	30	70
Percent	1.7	10.0	0.1	1.1	2.7

The mean trajectories of participant 5 are shown in Figure 2.3. The trajectories are temporal averages of reaches in the forward position by the lateral position (the transverse plane). The starting positions and the two targets for each limb are shown for direct (Figure 2.3 top) and symbolic cues (Figure 2.3 bottom). For clarity, only three reach types are shown: control reaches to the middle targets in black (left limb solid, right limb dashed), on-line corrections with the left limb in green, and corrections with the right limb in magenta. The dashed green and magenta limbs made on-line corrections and are referred to as perturbed limbs, with the solid green and magenta limbs being the unperturbed limbs. Representative participant data is always from participant 5, and the same pattern and colour scheme will be used in all graphs.
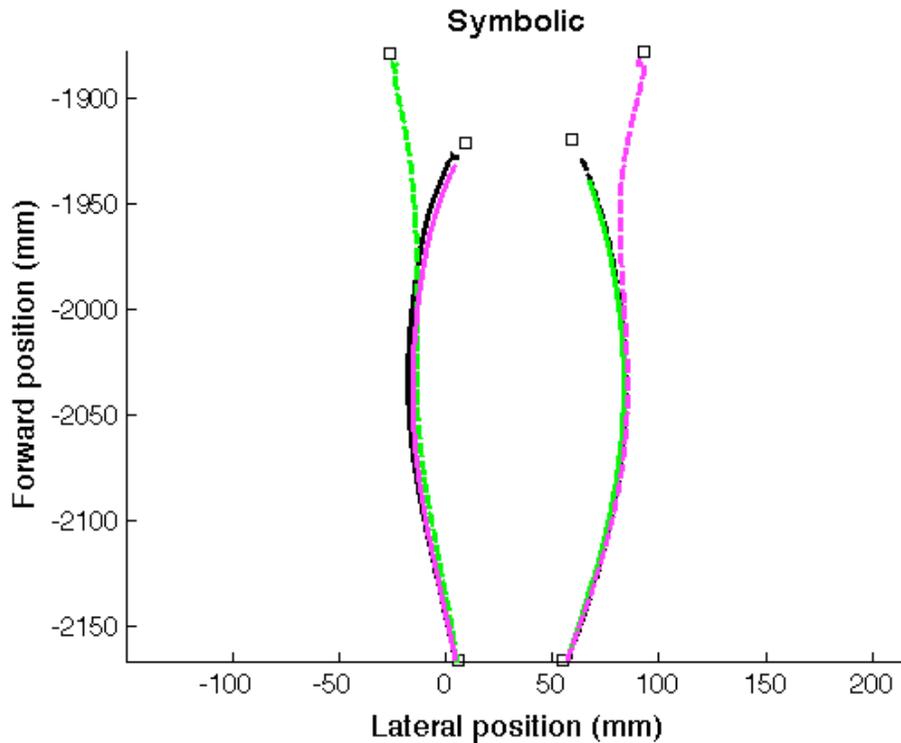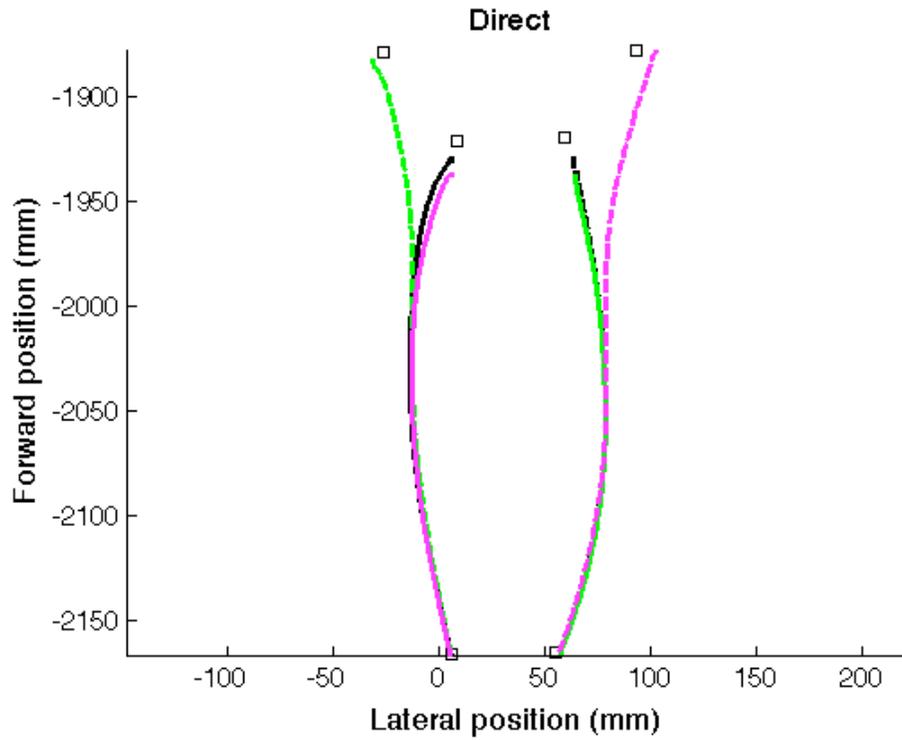
Figure 2.3. Bird's eye view of the mean reach trajectories in Direct (top) and Symbolic (bottom) conditions for participant 5. The perturbed left limb is dashed green, and the unperturbed right limb is solid green. The unperturbed left limb is solid magenta, and the perturbed right limb is dashed magenta. The left control is solid black, and the right control is dashed black. The centre of the targets and starting positions are represented by the black squares.

The same trajectories in Figure 2.3 are re-plotted as forward position by time in Figure 2.4, to emphasise the variables used in our analyses. Time zero is when the second pen was lifted from the starting position, which is also when target perturbations occurred. The last time point is the participant's mean movement time for each limb and reach type. As these are temporal averages, the variable endpoints and movement times of the perturbed limbs resulted in the end of perturbed trajectories being irregular. This occurred because shorter movements are not extended to the mean movement time and fluctuations can result as these trials no longer contribute to the average. It is important to note that the irregular portions of perturbed trajectories were not used in any analysis, and a temporal average is the best averaging technique to display two trajectories with disparate movement times.
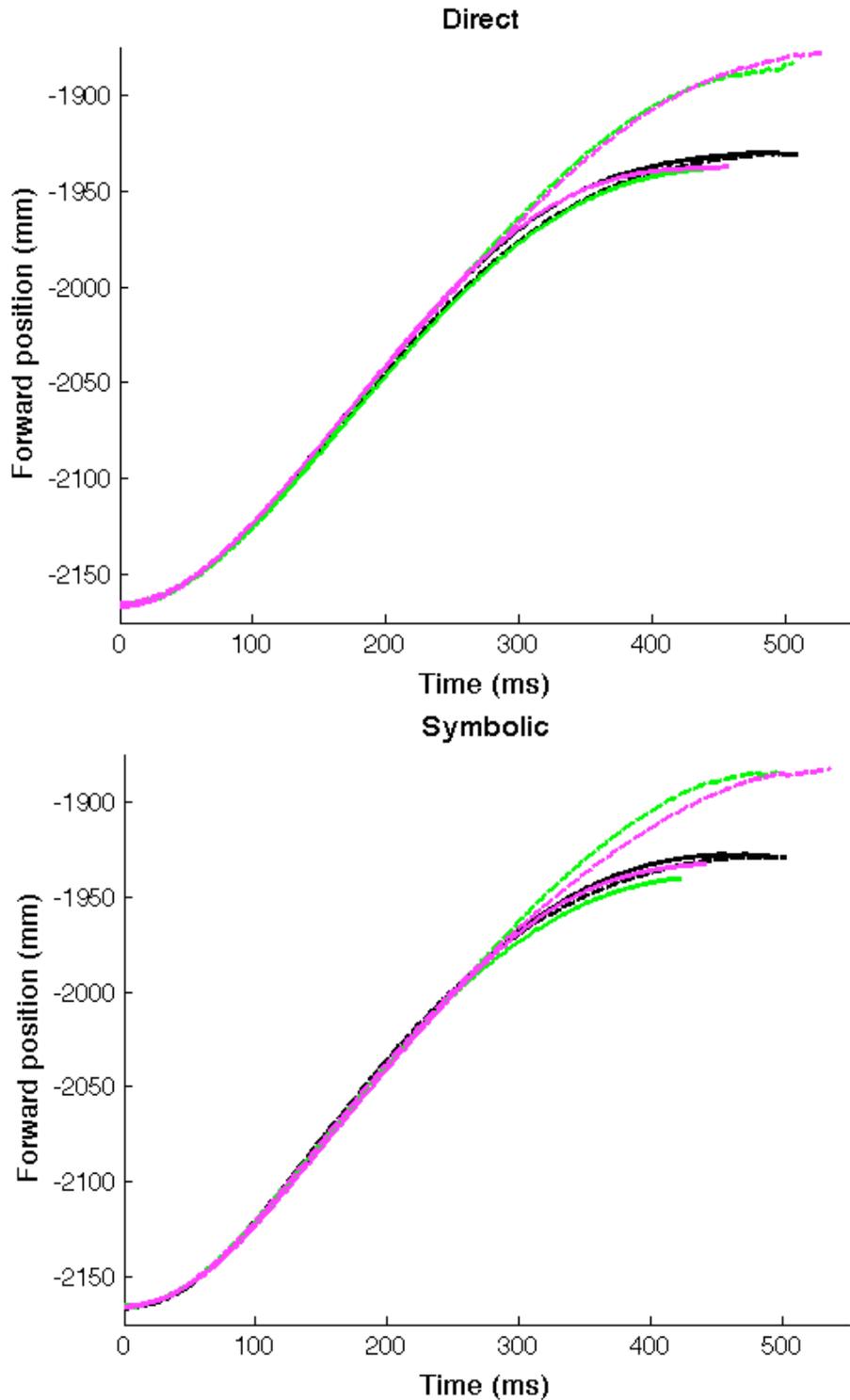
Figure 2.4. Mean forward position by time in Direct (top) and Symbolic (bottom) conditions for participant 5. The perturbed left limb is dashed green, and the unperturbed right limb is solid green. The unperturbed left limb is solid magenta, and the perturbed right limb is dashed magenta. The left control is solid black, and the right control is dashed black.

2.2.1 No difference in the onsets of adjustments with direct or symbolic cues

Onsets of adjustments were calculated by determining when the temporal average velocity of the perturbed limbs and controls diverged. Figure 2.5 shows the right perturbed limbs diverging from controls, with the onsets of adjustments displayed by the vertical lines. The onsets of adjustments were surprisingly similar with either direct or symbolic cues.
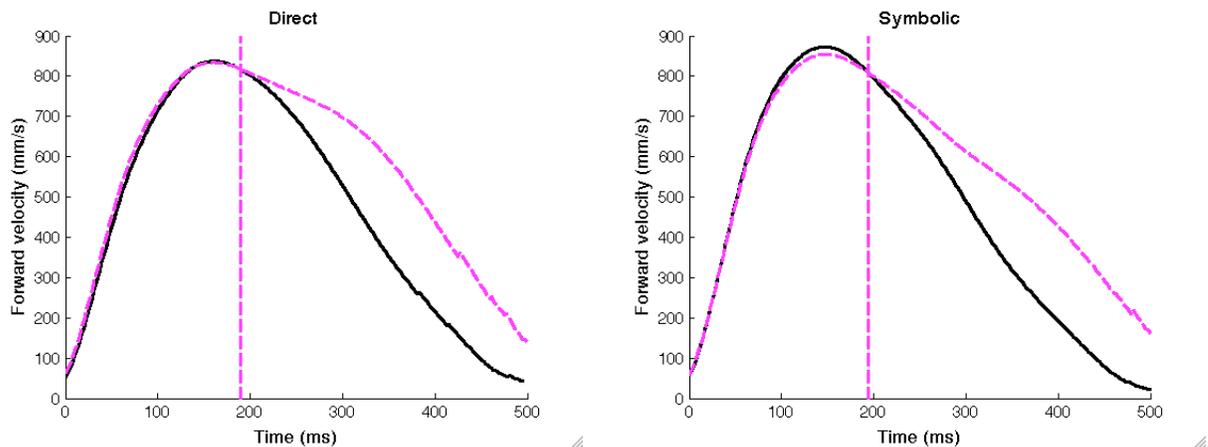
Figure 2.5. Forward velocity of the perturbed right limb (dashed magenta) in Direct (left) or Symbolic (right) conditions for participant 5. The onsets of adjustments (dashed vertical lines) shown above are when the forward velocity of the perturbed right limbs diverged from the velocity of the left controls (black).

The onsets of adjustments were analysed with a 2 Cue (direct, symbolic) by 2 Limb (left, right) ANOVA. There were no significant main effects or interactions, $p > .05$. Most importantly, the onsets of adjustments with direct cues (260 ± 34.0 ms, mean $\pm$ standard deviation) were not significantly different from the onsets of adjustments with symbolic cues (277 ± 61.9 ms), $F_{1, 10} = 2.3$, $p = .158$, $\eta_p^2 = .19$.

A large and significant difference between the onsets of adjustments for direct and symbolic cues is fundamental to our experiment. Symbolic cues are expected to have increased processing demands for the cue-to-target translations compared to direct cues, which has been shown to significantly increase the onsets of adjustments (Diedrichsen et al., 2001, Blinch et al., 2008). One difference in this experiment compared to our pilot experiment (Appendx A) was that only one target perturbation could occur for either limb. When a target perturbation can occur in at least two directions, the perturbation is identified and then translated to determine the appropriate on-line correction. The difference in processing time for direct or symbolic cues results from the cue-to-target translation (Diedrichsen et al., 2003) and likely not the identification. When a

target perturbation can occur in only one direct, it is possible that participants only had to identify the perturbation and not translate it to determine the appropriate correction, as the correction was always the same. The lack of translation could have resulted in onsets of adjustments that were comparable with direct or symbolic cues. To establish a difference in the onsets of adjustments, Experiment 2 (presented later in this thesis) tested a new group of participants with target perturbations that required either longer or shorter movements than control.

2.2.2 Movement times of the perturbed limbs were longer than the unperturbed limbs

Movement time was calculated from the pen-up to the pen-down of each limb. A 2 Cue (direct, symbolic) by 2 Limb (left, right) by 3 Type (control, long perturbed, long unperturbed) ANOVA with repeated measures on all factors was used to analyse movement times. There was a main effect of type (Figure 2.6), $F_{1.5, 15.0} = 9.5$, $p < .01$, $\eta_p^2 = .49$, which was further analysed by pairwise comparisons using the Sidak adjustment for multiple comparisons. The long perturbed limb had a longer movement time than the unperturbed limb or control. The movement time of the perturbed limb was likely extended to allow for an on-line correction. It is interesting that the movement time of the unperturbed limb was not statistically different from control. Temporal interference in bimanual reaches can cause the two limbs to end at the same time (Kelso, Southard, & Goodman, 1979), but the perturbed limb did not result in a longer movement time for the unperturbed limb.

There was also a significant cue by type interaction (Figure 2.6), $F_{1.6, 15.8} = 7.9$, $p < .01$, $\eta_p^2 = .44$, that was further analysed using simple main effects on cue. The long unperturbed limb had a longer movement time with a symbolic cue than a direct cue, $F_{1, 10} = 7.1$, $p = .023$, $\eta_p^2 = .42$. Therefore, symbolically-cued on-line corrections resulted in longer movement times than directly-cued ones, despite the equivalent onsets of adjustments.
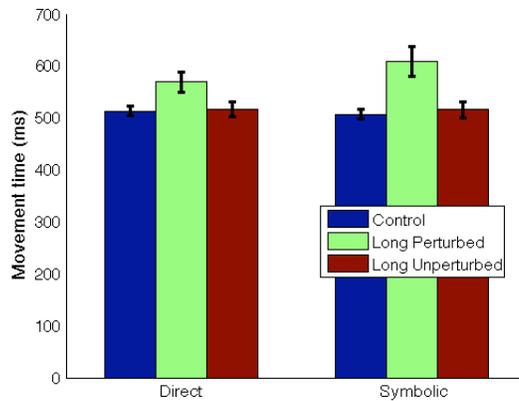
Figure 2.6. Mean movement times for the cue by type interaction. The error bars are plus or minus one standard error.

2.2.3 Constant and variable error were comparable with the unperturbed limbs and controls

Reach accuracy and consistency were measured by constant and variable error, which were calculated by the forward and lateral distances from the endpoint of each limb to the centre of the appropriate target. If there is spatial interference that lasts until the end of the movement, then the unperturbed limbs may be less accurate or less consistent than controls. In the forward direction, spatial interference should pull the unperturbed limb in the same direction as the perturbed limb, which is further than control. In the lateral direction, spatial interference may occur in an allocentric or egocentric reference frame. Allocentric interference will pull the unperturbed limb in the same lateral direction as the perturbed limb, so towards the midline. The unperturbed limb will move away from the midline, in the opposite lateral direction as the perturbed limb, if the interference occurs in egocentric coordinates.

Constant error and variable error in the forward direction were analysed separately with 2 Cue (direct, symbolic) by 2 Limb (left, right) by 3 Type (control, long perturbed, long unperturbed) ANOVAs. For constant error, there were significant main effects of limb and type, $F_{1, 10} = 12.8$, $p < .01$, $\eta_p^2 = .56$, $F_{1.3, 13.4} = 8.3$, $p < .01$, $\eta_p^2 = .46$. The right limb (-6.0 ± 7.4 mm) undershot the target more than the left limb (-3.9 ± 7.3 mm). The unperturbed limb (-8.2 ± 6.7 mm) undershot more than the perturbed limb (-0.7 ± 7.8 mm), but they were both comparable to control (-5.9 ± 5.5 mm).

For variable error, there were also significant main effects of limb and type, $F_{1, 10} = 15.5$, $p < .05$, $\eta_p^2 = .61$, $F_{2, 20} = 13.7$, $p < .01$, $\eta_p^2 = .58$. The left limb (7.4 ± 2.0 mm) was less consistent than the right limb (6.5 ± 1.3 mm), and the perturbed limb (8.1 ± 1.8 mm) was less consistent than the unperturbed limb or control (6.5 ± 1.7 mm, 6.2 ± 1.2 mm). The increased variability of the perturbed limb was likely the result of making on-line corrections to target locations that were never given endpoint feedback. Endpoint feedback was also withheld for the unperturbed limb, but its target did receive feedback in control trials.

The same ANOVAs were used to evaluate constant and variable error in the lateral direction. Constant error had a significant main effect of limb, $F_{1, 10} = 8.6$, $p = .015$, $\eta_p^2 = .46$, that showed the left limb was to the left of the targets (-3.9 ± 5.3 mm) and the right limb was to the right of the targets (1.8 ± 5.4 mm). For variable error, there were significant main effects of cue, limb, and type, $F_{1, 10} = 19.2$, $p < .01$, $\eta_p^2 = .66$, $F_{1, 10} = 7.1$, $p = .023$, $\eta_p^2 = .42$, $F_{1.5, 14.9} = 19.7$, $p < .01$, $\eta_p^2 = .66$. Movement endpoints in the Direct condition (5.4 ± 1.4 mm) were less variable than in the Symbolic condition (6.1 ± 1.9 mm), and the left limb (6.1 ± 1.8 mm) was more variable than the right limb (5.4 ± 1.5 mm). As with variability in the forward direction, the perturbed limb (7.1 ± 1.9 mm) was less consistent than the unperturbed limb and control (5.1 ± 1.2 mm, 5.1 ± 0.9 mm). The increased variability of the perturbed limb was likely the result of making on-line corrections to target locations that were never given endpoint feedback.

Constant and variable error did not reveal spatial interference from the perturbed limb that pulled the endpoint of the unperturbed limb in the forward or lateral directions; the accuracy and consistency of the unperturbed limbs were always comparable to controls. Spatial interference could have been transient, occurring sometime after the onset of adjustment and correcting itself before the movement endpoint. This possibility was investigated by comparing the forward positions of the unperturbed limbs to controls.

2.2.4 Forward and lateral positions did not reveal spatial interference

We were interested if on-line corrections of the perturbed limbs resulted in spatial interference that affected the position of the unperturbed limbs. As with reach accuracy, interference in the forward direction should pull the unperturbed limbs further than control, and lateral deviations

25

could be to either side of control depending on if the interference occurred in an egocentric or an allocentric reference frame.

Visual analysis of the forward or lateral positions did not support large spatial interference with direct or symbolic cues. As there was no obvious trend for spatial interference, a single point in time with the greatest spatial interference could not be identified and analysed. Instead, the positions of the unperturbed limbs were analysed in 20 ms intervals after movement onset (20, 40, etc.). For the Direct condition, the last complete data set was 460 ms after movement onset. The last complete data set in the Symbolic condition was 420 ms, so both conditions were analysed together from 20 to 420 ms to prevent losing data from any participant.

Forward and lateral positions were analysed separately with 2 Cue (direct, symbolic) by 21 Time (20, 40, 60…420 ms) by 2 Limb (left, right) by 2 Type (control, long unperturbed) ANOVAs. In the forward direction, there was a main effect of time, $F_{2.0, 20.4} = 2230$, $p < .01$, $\eta_p^2 = .99$. More interesting were the significant interactions of cue by time by type, cue by limb by type, and cue by time by limb by type, $F_{2.2, 22.4} = 3.6$, $p = .039$, $\eta_p^2 = .27$, $F_{1, 10} = 240$, $p = .049$, $\eta_p^2 = .33$, $F_{2.3, 23.1} = 3.9$, $p = .03$, $\eta_p^2 = .28$. Simple main effects on type were used to analyse the four-way interaction. This is similar to performing a one-way ANOVA on Type (control, long unperturbed) for each combination of cue, time, and limb.

In the Direct condition, the left unperturbed limb undershot the left control limb from 380 ms to the last time point of 420 ms, $p < .05$, with a peak difference of 3.0 ± 4.0 mm at 420 ms. This region is shown in Figure 2.7 top; the left unperturbed limb (solid magenta) undershoots the left control limb (solid black) from 380 to 420 ms. There are two reasons why this likely did not reflect transient spatial interference. First, it occurred in only the left limb. The counterargument is that interference is sometimes larger in the nondominant limb, and the interference in this movement is so small that it is only visible in the nondominant limb. Second, and more difficult to reconcile, spatial interference should occur in the opposite direction, resulting in the unperturbed limb overshooting control.
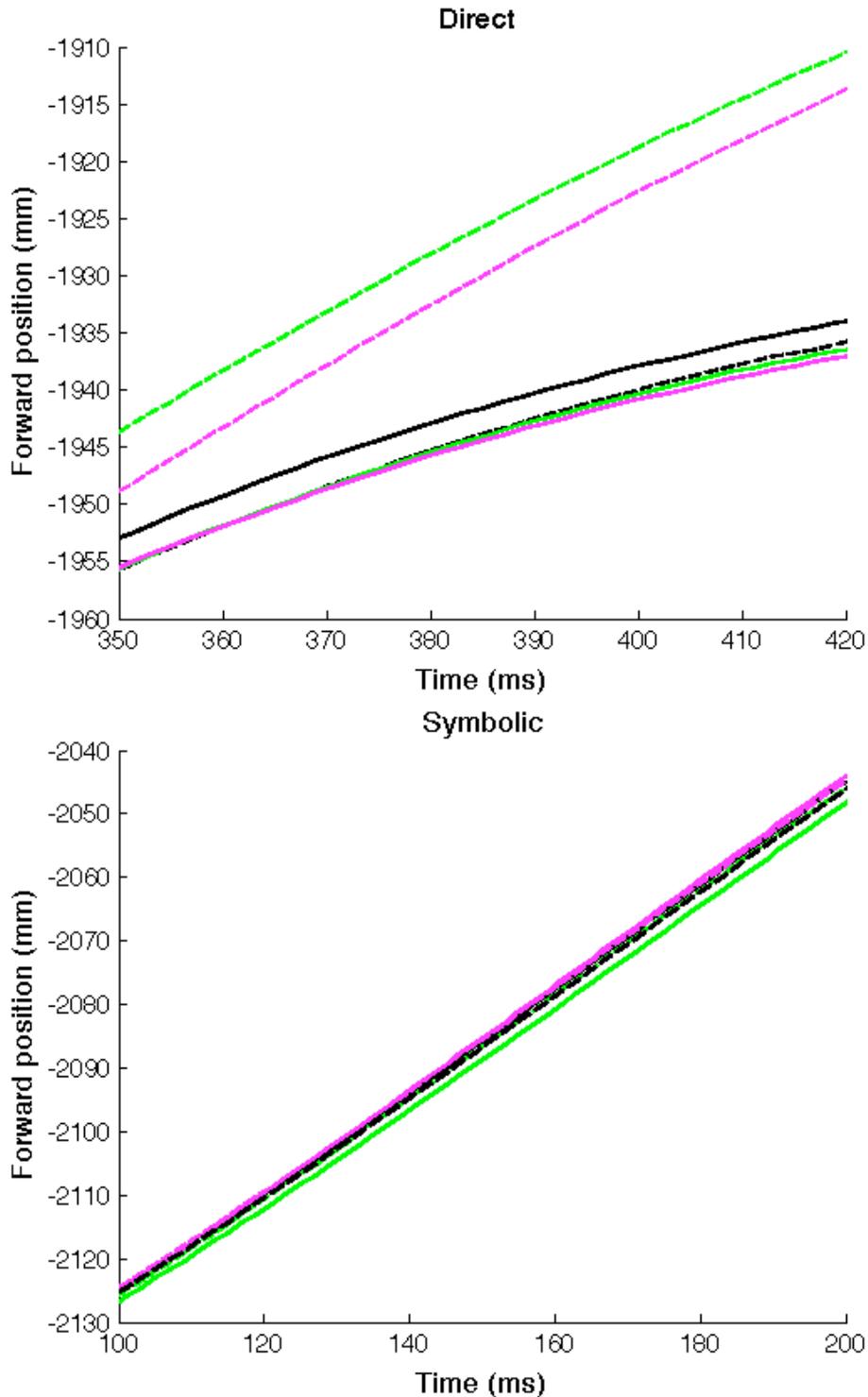
Figure 2.7. Magnified mean forward positions in the Direct (top) and Symbolic (bottom) conditions. The left perturbed limb is dashed green, and the right unperturbed limb is solid green. The left unperturbed limb is solid magenta, and the right perturbed limb is dashed magenta. The left control is solid black, and the right control is dashed black. Spatial interference is examined by comparing the control limbs to the unperturbed limbs: the left unperturbed limb (solid magenta) to the left control (solid black) or the right unperturbed limb (solid green) to the right control (dashed black).

In the Symbolic condition, the right unperturbed limb undershot the right control limb from 100 to 200 ms, p < .05, with a peak difference of 2.2 ± 2.8 mm at 180 ms. This region is shown in Figure 2.7 bottom; note how the right unperturbed limb (solid green) undershoots the right control limb (dashed black) from 100 to 200 ms. It is possible for spatial interference to occur early in the movement, possibly before the onset of adjustment. However, this undershoot may not be spatial interference as it occurred in only the right limb and was in the opposite direction as the predicted spatial interference.

As for the analyses on lateral position, there were significant main effects of time and limb, $F_{2.7, 27.1} = 3.6$, $p = .03$, $\eta_p^2 = .26$, $F_{1, 10} = 567$, $p < .01$, $\eta_p^2 = .98$, and a significant time by limb interaction, $F_{1.3, 13.4} = 42$, $p < .01$, $\eta_p^2 = .81$. These showed the typical lateral curvature away from each other as the limbs moved forward (Figure 2.3). There was also a significant cue by time by limb by type interaction, $F_{2.4, 23.9} = 3.4$, $p = .044$, $\eta_p^2 = .25$, that was further analysed with simple main effects on type. Control and the unperturbed left limb were significantly different in the Symbolic condition at 20 and 40 ms, p < .05. The unperturbed left limb was pulled to the left of control with a peak difference of 0.3 ± 0.4 mm at 40 ms; the direction of this pull was consistent with egocentric interference. However, this likely did not reflect transient spatial interference as it occurred too early in the movement.

To summarize, reach accuracy and consistency in the forward and lateral directions did not support spatial interference on the unperturbed limbs that lasted until the movement endpoint. We also did not find reliable evidence of transient interference in the forward or lateral directions of the unperturbed limbs. There were a few differences between control and one of the limbs, but in the forward direction it was always an undershoot compared to control, in the opposite direction than predicted by spatial interference. Instead of spatial interference, we found evidence to suggest primarily spatial independence between the perturbed and unperturbed limbs. We predicted larger spatial interference with symbolic cues than direct cues. However, having only one potential target perturbation instead of two decreased the uncertainty of the on-line corrections and resulted in comparable onsets of adjustments with direct or symbolic cues. In this case, we no longer expect different spatial interference, as the cues are too similar.

We anticipated small, transient spatial interference with direct cues, as was found by Diedrichsen and colleagues (2004) with lateral perturbations and Mason (2008) with anterior perturbations. It

is curious that we did not find consistent interference, but it is not a fundamental problem to our experiment as is the lack of difference in the onsets of adjustments with direct and symbolic cues. Perhaps the interference was attenuated or eliminated by one of the differences in our experiment. The important point is that we predict greater spatial interference with symbolic cues than with direct cues. This may be seen as no spatial interference with direct cues and some amount of interference with symbolic cues - be it small and transient or big and lasting - simply greater than with direct cues. Since a difference in the onsets of adjustments with direct and symbolic cues is required before we can compare the amount of spatial interference in each condition, we tested a new group of participants in Experiment 2 with target perturbations that required either longer or shorter movements than control to establish a difference in the onsets of adjustments.

3 EXPERIMENT TWO

3.1 Methods

The following changes were made to the methods from the first experiment.

3.1.1 Participants

The participants were 12 students from the University of British Columbia. The University of British Columbia Office of Research Services approved this study. All participants had normal or corrected-to-normal vision and were right handed based on self-report measures of the Edinburgh Handedness Inventory (Oldfield, 1971), with a laterality quotient greater than .60.

3.1.2 Task and apparatus

The dimensions of the stimulus display are shown in Figure 3.1. Unlike the first experiment, target perturbations required an on-line correction in only the forward direction, but it could be to either the anterior or the posterior target placeholders. This setup was used to create an on-line correction task that was similar to the preplanned task used by Diedrichsen and colleagues (2001) and Blinch and Chua (2009). Three target placeholder configurations were used (near, mid, far), and the distances from the starting locations to the middle target placeholders were 14.6, 19.8, and 25 cm; a difference of 5.2 cm between configurations, which was the same as the distances between the short and middle targets or the middle and long targets. These distances were selected so that, for example, the middle targets in the mid configuration were the long targets in the near configuration.

0.9

1.0

5.2

5.2

5.3

19.8
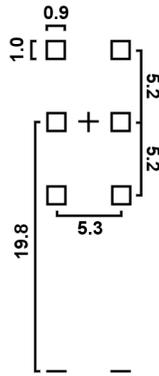
Figure 3.1. Dimensions of the stimulus display in the mid configuration. All dimensions are in centimeters.

The target perturbations in Symbolic conditions were no longer changes in the colour of the middle targets. Instead, the middle targets could change at movement onset to the letter L or S. The participant was instructed that if the right target changed to the letter L than they should perform an on-line correction with the right limb to the long target placeholder. The letter S required a correction to the short target placeholder. The type of symbolic target perturbation was changed to replicate the type of symbolic cue used by Diedrichsen and colleagues (2001) and Blinch and Chua (2009). However, both colour change and identity change symbolic perturbations increase the processing demands for cue-to-target translation and are an appropriate contrast to direct cues (Cressman, Franks, Enns, & Chua, 2006; Diedrichsen et al., 2001; Diedrichsen et al., 2003).

3.1.3 Design

The experiment was divided into four sections: practice, direct, practice, and symbolic (Table 3.1). The experiment began with 31 practice trials to familiarize the participant with control and perturbation trials and to achieve a movement time of 500 ms ± 50 ms. The perturbation trials were the same as the type used in the following direct or symbolic section. These trials were added to practice as we found that in the first experiment, most participants were unable to make on-line corrections in the first two perturbation trials and this reduced the number trials that contributed to the mean. The number of trials in the second practice section was reduced to 16, as the participant only needed familiarization with the new type of target perturbation. The order of the direct and symbolic sections was counterbalance. These sections consisted of 160 trials, with a randomization of 60% control trials and 40% target perturbations, with an equal number

of the four types of perturbations (left limb long, left limb short, right limb long, right limb short). Target perturbations occurred in all the target placeholder configurations (near, mid, far).

Table 3.1. The experimental design.

Practice	Direct		Practice	Symbolic	
23 control	*Mid*	*Near or Far*	8 control	*Mid*	*Near or Far*
8 perturbation	72 control	12 control	8 perturbation	72 control	12 control
	12 x 4 perturbation	2 x 4 perturbation		12 x 4 perturbation	2 x 4 perturbation
	Symbolic			**Direct**	
	Mid	*Near or Far*		*Mid*	*Near or Far*
	72 control	12 control		72 control	12 control
	12 x 4 perturbation	2 x 4 perturbation		12 x 4 perturbation	2 x 4 perturbation

3.1.4 Data analysis

The control trajectories and the trajectories of the on-line corrections were primarily in the forward direction, so the analyses were in the forward direction. The endpoint accuracy exclusion criterion (the absolute forward distance from the movement endpoint to the centre of the target placeholder) was increased from 25 mm in the first experiment to 30 mm, as the target placeholders were further apart. The reaction time asynchrony criterion was also increased from 25 ms to 30 ms to decrease the number of trials recycled to the end of the section. Target perturbations in the near or far configurations were excluded from the analyses.

As there were on-line corrections in opposite directions, the onsets of adjustments were calculated with the same method used by Diedrichsen and colleagues (2004). The onset of adjustment was measured by comparing the mean velocity of the perturbed limb to the long target to the mean velocity of the perturbed limb to the short target, and this was done separately for each limb. The onset of adjustment was the time from movement onset to when these trajectories diverged.

3.2 Results

The number of trials excluded for each participant is shown in Table 3.2. We successfully decreased the occurrence of asynchronous trials from 10.0% in the first experiment to 4.1% in the second experiment by increasing the asynchronous reaction time criterion from 25 to 30 ms.

Table 3.2. The number of excluded trials for each participant and for each exclusion criterion.

Participant	Missing Markers	Asynchronous Reaction Time	Slow Movement Initiation	Slow Movement Termination	Poor Accuracy
1	10	12	0	0	2
2	1	24	2	9	1
3	0	26	0	0	2
4	2	11	0	1	5
5	0	5	0	0	2
6	26	18	0	1	3
7	0	3	0	0	5
8	9	9	1	3	1
9	0	8	1	0	4
10	0	6	0	0	4
11	0	15	2	2	6
12	3	10	0	0	3
Total	51	147	6	16	38
Percent	1.4	4.1	0.2	0.4	1.1

The mean trajectories of participant 8 are shown in Figure 3.2. The trajectories are temporal averages of reaches in the forward position by the lateral position (the transverse plane). The starting positions and the three targets for each limb are shown for direct (Figure 3.2 top) and symbolic cues (Figure 3.2 bottom). For clarity, only three reach types are shown: control reaches to the middle targets in black (left solid, right dashed), on-line corrections with the right limb to the long target in magenta, and corrections with the right limb to the short target in cyan. The dashed magenta and cyan right limbs made on-line corrections and are referred to as perturbed limbs, with the solid magenta and cyan left limbs being the unperturbed limbs. Representative participant data are always from participant 8, and the same pattern and colour scheme will be used in all graphs.
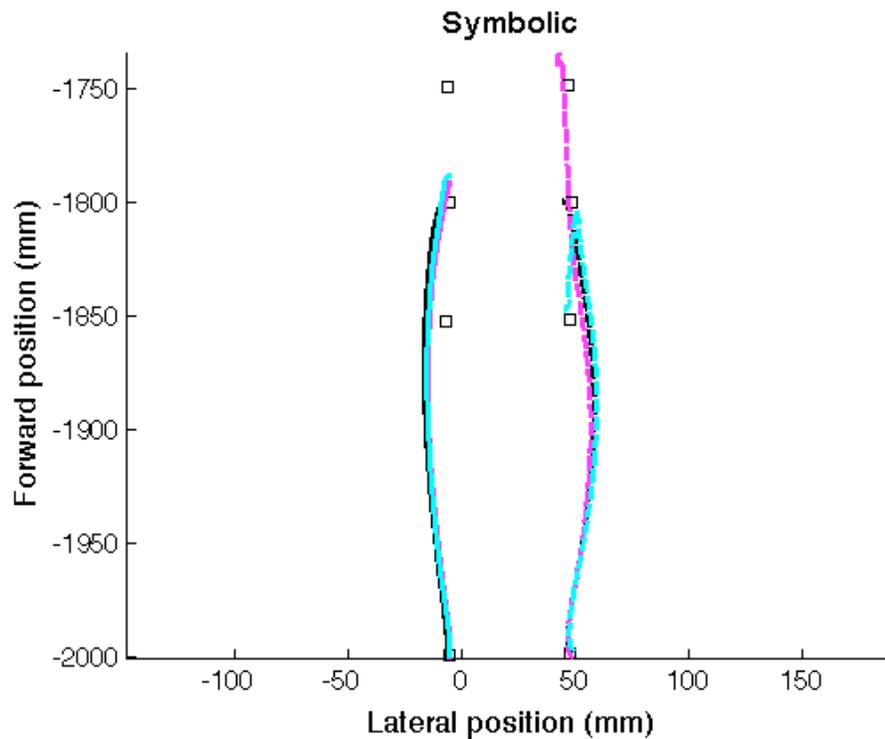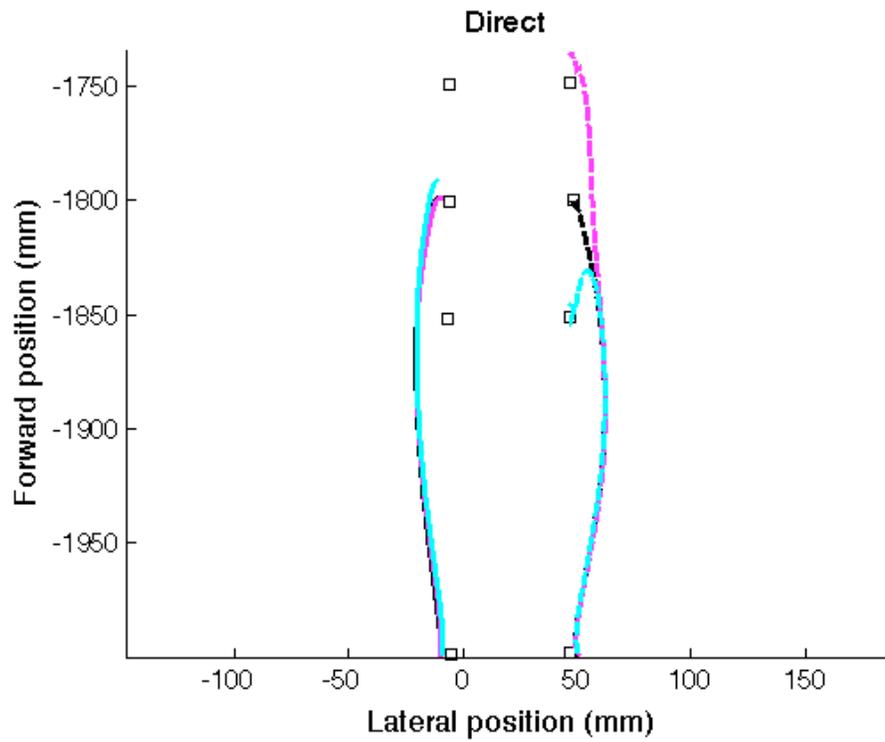
Figure 3.2. Bird's eye view of the mean reach trajectories in Direct (top) and Symbolic (bottom) conditions for participant 8. The short unperturbed left limb is solid cyan, and the short perturbed right limb is dashed cyan. The long unperturbed left limb is solid magenta, and the long perturbed right limb is dashed magenta. The left control is solid black, and the right control is dashed black. The centre of the targets and starting positions are represented by the black squares.

The same trajectories in Figure 3.2 are re-plotted as forward position by time in Figure 3.3, to emphasise the variables used in our analyses. Time zero is when the second pen was lifted from the starting position, which is also when target perturbations occurred. The last time point is the participant's mean movement time for each limb and reach type. As these are temporal averages, the variable endpoints and movement times of the perturbed limbs resulted in the end of perturbed trajectories being irregular. As with the first experiment, irregular portions of perturbed trajectories were not used in any analysis.
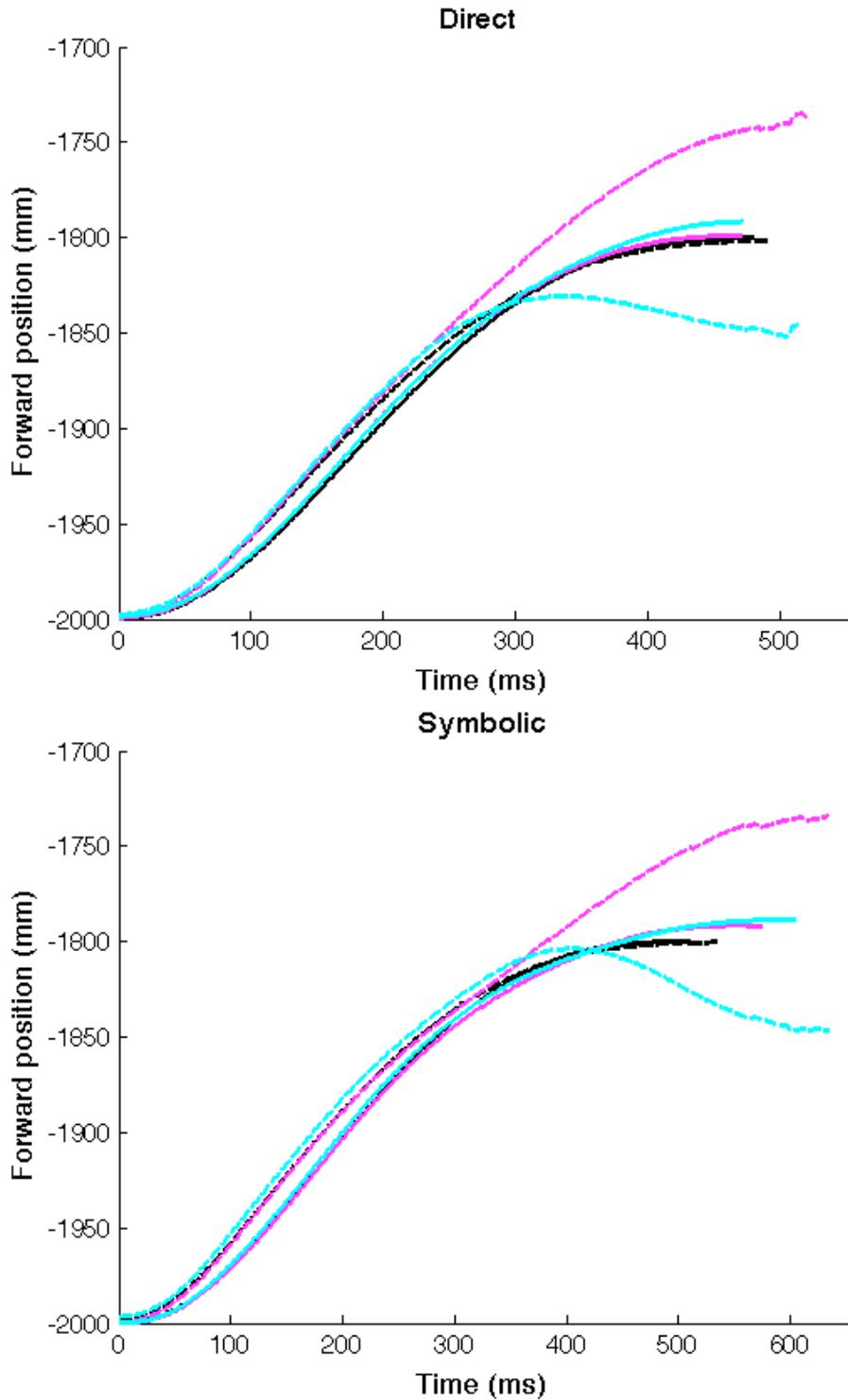
Figure 3.3. Mean forward position by time in Direct (top) and Symbolic (bottom) conditions for participant 8. The short unperturbed left limb is solid cyan, and the short perturbed right limb is dashed cyan. The long unperturbed left limb is solid magenta, and the long perturbed right limb is dashed magenta. The left control is solid black, and the right control is dashed black.

3.2.1 Movement times of the perturbed limbs were longer than the unperturbed limbs

Movement time was calculated from the pen-up to the pen-down of each limb. A 2 Cue (direct, symbolic) by 2 Limb (left, right) by 5 Type (control, long perturbed, long unperturbed, short perturbed, short unperturbed) ANOVA with repeated measures on all factors was performed on the movement time data. There was a significant main effects of cue, $F_{1, 11} = 38$, $p < .01$, $\eta_p^2 = .78$, that showed movement times were slower in symbolic than direct conditions (Figure 3.4). The significant main effect of type, $F_{1.6, 17.1} = 27$, $p < .01$, $\eta_p^2 = .71$, was further analysed by pairwise comparisons using the Sidak adjustment for multiple comparisons. Movement times of the perturbed limbs (long or short) were slower than the unperturbed limbs or control. The short unperturbed limb was slower than control, but the long unperturbed limb was not statistically different from control. Thus, a target perturbation resulted in temporal interference that slowed the unperturbed limb, but not to the same extent as the perturbed limb. There was also a significant cue by type interaction, $F_{2.6, 28.1} = 15.9$, $p < .01$, $\eta_p^2 = .59$. The cue by type interaction was further analysed using simple main effects on cue. Movement times were significantly longer for all types with symbolic cues compared to direct cues, $F_{1, 11} > 1$, $p < .05$. The interaction was likely the result of larger increases in movement time for the perturbed limbs.
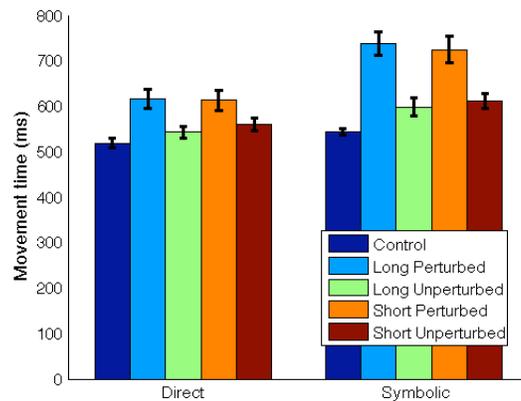

Figure 3.4. Mean movement times for the cue by type interaction. The error bars are plus or minus one standard error.

3.2.2 Onsets of adjustments were longer with symbolic cues than direct cues

The dashed vertical lines in Figure 3.5 are the onsets of adjustments for the perturbed right limbs. These were calculated by determining when the temporal averages of the velocity for long and short perturbed limbs diverged (Diedrichsen et al., 2004). The onsets of adjustments are visible as the divergence of the long (magenta) and short (cyan) perturbed right limbs.
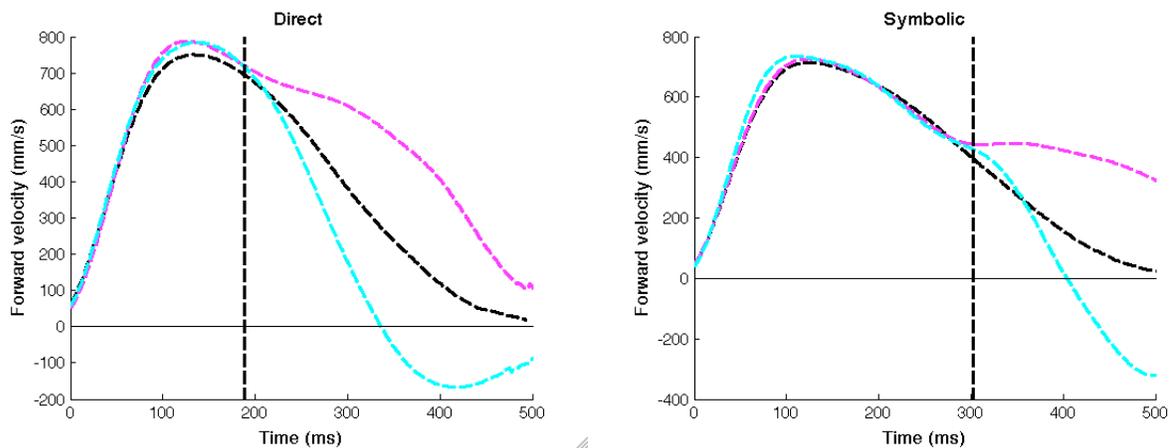
Figure 3.5. Forward velocity of the short perturbed right limb (dashed cyan), the long perturbed right limb (dashed magenta), and right control (dashed black) in Direct (left) and Symbolic (right) conditions for participant 8. The onsets of adjustments (dashed vertical lines) shown above are when the forward velocity of the short perturbed right limb diverged from the velocity of the long perturbed right limb.

Onsets of adjustments were analysed with a 2 Cue (direct, symbolic) by 2 Limb (left, right) ANOVA. A significant main effect of cue, $F_{1, 11} = 152$, $p < .01$, $\eta_p^2 = .93$, revealed that adjustments began earlier for directly-cued perturbations (236 ± 34.7 ms, mean $\pm$ standard deviation) compared to symbolically-cued perturbations (370 ± 46.5 ms).

The onsets of adjustments can be related to the movement times of the perturbed limbs. As the onsets of adjustments occurred later in Symbolic than Direct conditions, the movement times of the perturbed limbs in Symbolic conditions will also be slower than direct conditions to allow enough time for the on-line corrections. When subtracting Direct from Symbolic conditions, the onsets of adjustments differed by 134 ms and the movement times had a similar difference of 117 ms.

3.2.3 Constant and variable error were comparable with the unperturbed limbs and controls

Reach accuracy and consistency were measured by constant and variable error, which were calculated by the distance in the forward position from the endpoint of each limb to the centre of the appropriate target. If spatial interference occurred and it resulted in a lasting effect on the unperturbed limbs, then the unperturbed limbs should be less accurate or less consistent than controls.

Constant error was analysed with a 2 Cue (direct, symbolic) by 2 Limb (left, right) by 5 Type (control, long perturbed, long unperturbed, short perturbed, short unperturbed) ANOVA. The main effect of limb, $F_{1, 11} = 5.4$, $p = .04$, $\eta_p^2 = .33$, showed that the left limb (2.4 ± 7.6 mm) slightly overshot the target and the right limb (-0.7 ± 6.6 mm) was more distributed around the target. Simple main effects on cue were used to analyse the significant cue by type interaction, $F_{2.1, 22.6} = 4.6$, $p = .02$, $\eta_p^2 = .30$. Cue only had an impact on the long unperturbed limb, $F_{1, 11} = 11.4$, $p < .01$, $\eta_p^2 = .51$, which undershot with a direct cue and was more distributed around the target with a symbolic cue (Figure 3.6).
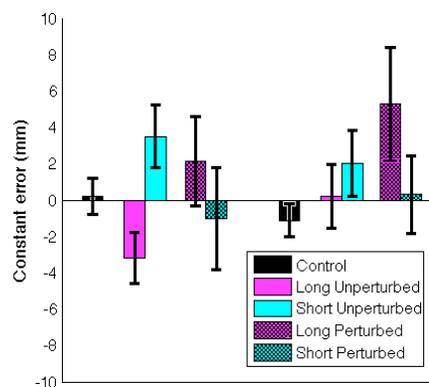
Figure 3.6. Mean constant error for the cue by type interaction. The error bars are plus or minus one standard error.

Variable error was analysed with the same ANOVA as constant error. There was a significant main effect of type, $F_{4, 44} = 7.4$, $p < .01$, $\eta_p^2 = .40$, which was the result of greater variable error for the long perturbed limb (8.1 ± 2.5 mm) than control (6.5 ± 1.2 mm). The lack of endpoint feedback in perturbed trials likely resulted in the increased variability.

Constant and variable error did not reveal consistent spatial interference from the perturbed limb that pulled the endpoint of the unperturbed limb in the same direction. The long unperturbed limb did undershoot with a direct cue compared to a symbolic cue, but spatial interference from the long perturbed limb should result in an overshoot. Spatial interference could have been transient, occurring after the onset of adjustment and correcting itself before the movement endpoint. This possibility was investigated by comparing the forward positions of the unperturbed limbs to controls.

3.2.4 Forward positions revealed small, transient spatial interference that was larger with symbolic cues than direct cues

The on-line corrections of the perturbed limbs resulted in large differences from control by the end of the movement. We were interested if these corrections resulted in spatial interference that affected the position of the unperturbed limbs. It was hypothesized that if spatial interference occurred, it would pull the unperturbed limb in the same direction as the perturbed limb: the position of the long unperturbed limb would be greater than control, and the short unperturbed limb would be less than control.

Visual analysis of the forward positions did not support large spatial interference with direct or symbolic cues. As there was no obvious trend for spatial interference, a single point in time with the greatest spatial interference could not be identified and analysed. Instead, the positions of the unperturbed limbs were analysed in 20 ms intervals after movement onset (20, 40, etc.). For the Direct condition, the last complete data set was 460 ms after movement onset. The last complete data set in the Symbolic condition was 440 ms. This was extended to 460 ms to match the Direct condition by excluding the one participant (participant 10) that began to lose data at 440 ms.

A 2 Cue (direct, symbolic) by 23 Time (20, 40, 60…460 ms) by 2 Limb (left, right) by 3 Type (control, long unperturbed, short unperturbed) ANOVA was used to analyse forward positions. There were significant main effects of cue and time, $F_{1, 10} = 21$, $p < .01$, $\eta_p^2 = .68$, $F_{2.0, 20.1} = 4023$, $p < .01$, $\eta_p^2 = .99$. The significant two-way interactions were cue by time, time by limb, cue by type, and time by type, $F_{2.0, 19.9} = 11.6$, $p < .01$, $\eta_p^2 = .54$, $F_{2.0, 19.7} = 4.2$, $p = .03$, $\eta_p^2 = .30$,

$F_{2, 20} = 3.7$, $p = .044$, $\eta_p^2 = .27$, $F_{4.2, 42.5} = 3.9$, $p < .01$, $\eta_p^2 = .28$. Most of these main effects and interactions were captured by the significant three-way cue by time by type interaction, $F_{4.2, 41.8} = 3.6$, $p = .013$, $\eta_p^2 = .26$. This interaction was further analysed with simple main effects on type. This is similar to performing a one-way ANOVA on Type (control, long unperturbed, short unperturbed) for each combination of cue and time, so 23 levels of time for each cue.

With direct cues, the three reach types were significantly different at 340 and 360 ms, $p < .05$. At these two times, the short unperturbed limbs undershot control (2.3 ± 3.5 mm at 340 ms, 2.3 ± 3.5 mm at 360 ms). This small undershoot was in the same direction as the perturbed limb and is therefore consistent with transient spatial interference. Notice in Figure 3.7 top how the short unperturbed limb (solid cyan) is close to control (solid black) at 260 ms, undershoots control by 2.3 mm at 340 and 360 ms, and then overlaps control at 440 ms. It was interesting that the long unperturbed limb was not pulled longer than control.
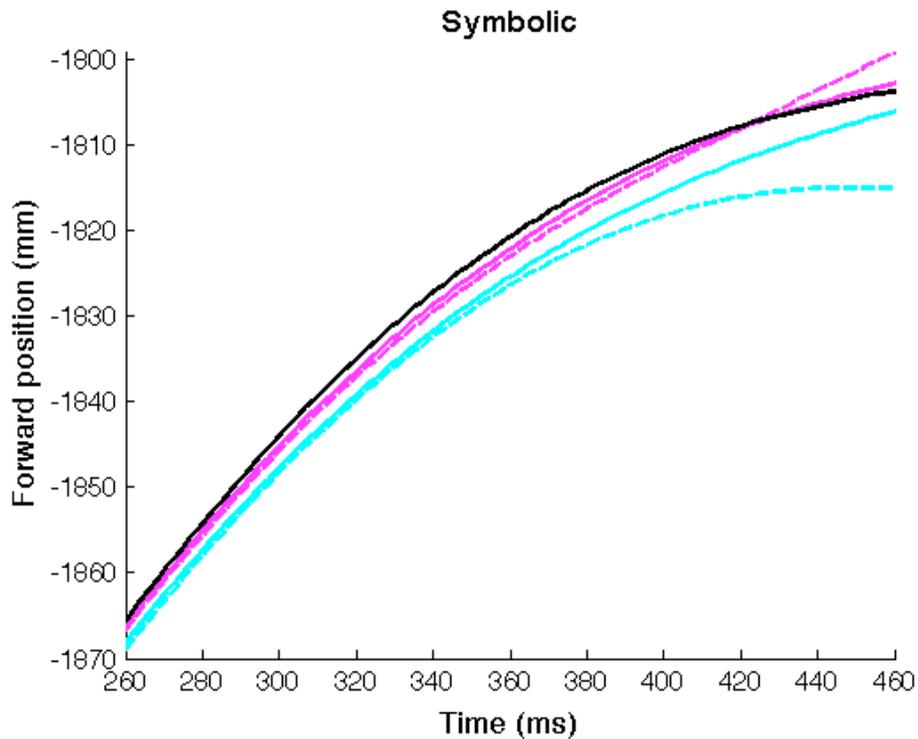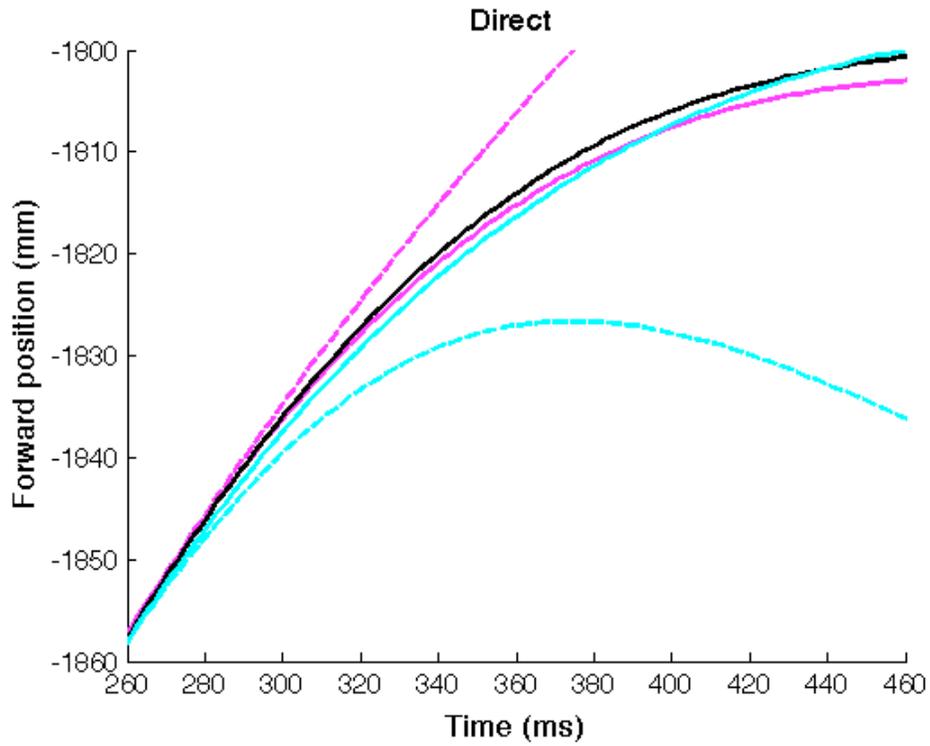
Figure 3.7. Magnified mean forward positions in the Direct (top) and Symbolic (bottom) conditions. The trajectories have been collapsed across limb to match the significant cue by time by type interaction. The long perturbed limbs are dashed magenta, and the short perturbed limbs are dashed cyan. The long unperturbed limbs are solid magenta, and the short unperturbed limbs are solid cyan. The controls are solid black. Spatial interference is examined by comparing the control limbs to the unperturbed limbs: the long unperturbed limb (solid magenta) to the control (solid black) or the short unperturbed limb (solid cyan) to the control (solid black).

42

A similar trend emerged in the Symbolic condition, but the spatial interference of the short unperturbed limb lasted longer and was slightly larger in magnitude. The three reaches types were significantly different from 300 ms to the last time point (460 ms), p < .05. It was the short unperturbed limb that undershot control at these time points, reaching a maximum undershoot of 4.9 ± 4.6 mm at 380 ms. In Figure 3.7 bottom, the short unperturbed limb (solid cyan) is below control (solid black) from 300 to 460 ms. As in the Direct condition, the long unperturbed limb was not pulled further than control. Therefore, spatial interference appeared to occur for the short unperturbed limb but not the long unperturbed limb.

We compared the peak undershoot of the short unperturbed limbs compared to controls in the Direct condition (at 340 and 360 ms) to the Symbolic condition (380 ms) to determine if the Symbolic condition had a larger undershoot. The symbolic undershoot was not significantly different from the direct undershoot at 340 or 360 ms, $t(11) = 1.98$, $p = .073$, $d = 0.81$, $t(11) = 1.86$, $p = .090$, $d = 0.80$. Although the magnitudes of the peak undershoot were not significantly different, the duration of the undershoot was at least 160 ms in the Symbolic condition and only 20 to 40 ms in the Direct condition.

In summary, the onsets of adjustments with symbolic cues were later than with direct cues. In contrast to the first experiment, this allowed us to compare temporal and spatial interference in Direct and Symbolic conditions. In both conditions, the movement times of the perturbed limbs increased compared to control to allow for the on-line corrections. This resulted in longer movement times for the unperturbed limbs, but the movement times did not increase to the same extent as the perturbed limbs. Pointing accuracy and consistency of the unperturbed limbs were comparable to controls, so if there was spatial interference in either condition, then it was corrected before the end of the movement. Small, transient spatial interference was seen when the unperturbed limbs were compared to controls. The interference had comparable magnitudes in both conditions but lasted longer with symbolic cues than with direct cues. In both conditions, interference was found for the short unperturbed limb but not the long unperturbed limb.

4 GENERAL DISCUSSION

In Experiments 1 and 2, we sought to determine if there was larger spatial interference in the unperturbed limb when the perturbed limb responded to a symbolically-cued on-line correction compared to a directly-cued correction. Participants made bimanual reaches to targets that were occasionally perturbed at movement onset. These perturbations required on-line corrections with the perturbed limb to the new target location. The new target location was indicated by illuminating the new target as a direct cue (Experiments 1 and 2) or symbolically cueing the target with a colour change (Experiment 1) or displaying the letter L or S (Experiment 2). Symbolically-cued on-line corrections should have longer onsets of adjustments than directly-cued corrections due to the increased processing demands on response selection for the cue-to-target translations (Diedrichsen et al., 2001; Diedrichsen et al., 2003).

Surprisingly, there was no difference in the onsets of adjustments with direct or symbolic cues in the first experiment. We suggested this occurred because the correction was always made to the same target. Uncertainty of the correction may be required for the target perturbation to be translated and a difference to exist between direct and symbolic cues. Two potential targets for the on-line correction were included in the second experiment to ensure that onsets of adjustments with symbolic cues occurred later than direct cues. The onsets of adjustments were longer with symbolic cues (370 ± 46.5 ms) than direct cues (236 ± 34.7 ms) in the second experiment, so the second experiment can be used to compare spatial interference with direct and symbolic cues.

4.1 Spatial interference

The accuracy and consistency of pointing with the unperturbed limbs and controls were comparable in both experiments, so if there was spatial interference then it would have to be transient, correcting itself before the end of the movement. In the first experiment, comparison of the forward positions of the unperturbed limbs and controls revealed some differences. We do not believe that these were reliable evidence for transient spatial interference as they were in the

opposite direction as the predicted interference; the unperturbed limbs were pulled in the opposite direction as the perturbed limbs.

In contrast, there were indications of small, transient spatial interference in the second experiment. When the short perturbed limb made an anterior on-line correction, the short unperturbed limb was pulled towards the correction. With direct cues, the transient interference lasted between 20 and 40 ms and pulled the unperturbed limb 2.3 ± 3.5 mm anterior. This is similar to the 2.1 ± 1.4 mm of lateral deviation in the experiment by Diedrichsen and colleagues (2001), but their transient spatial interference lasted around 100 ms. It is interesting that transient spatial interference occurred for the short unperturbed limbs but not the long unperturbed limbs. One explanation is that reversing directions with an on-line correction to the short target requires a greater change in the preplanned movement than extending the movement to the long target. It is the larger change in the preplanned movement for the short perturbed limbs compared to the long perturbed limbs that may result in interference. Mason (2008) made the same suggestion when comparing the longer duration of transient spatial interference in her experiment to Diedrichsen and colleagues' (2001). Mason's on-line corrections required a reversal in direction compared to Diedrichsen's lateral corrections.

Notably, the transient spatial interference with symbolic cues had a similar magnitude but a longer duration than with direct cues. The interference lasted at least 160 ms, pulling the short unperturbed limb anterior by 4.9 ± 4.6 mm. This greater interference is likely the result of the increased processing demands for the cue-to-target translations of symbolic cues. This processing begins after movement onset when the target is perturbed, so interference could occur anytime after movement onset. Symbolic interference began 300 ms after movement onset, which was 70 ms before the mean onset of adjustment. It is the difference in the cue-to-target translation for symbolic cues that likely increased the transient spatial interference compared to direct cues. If interference was the result of response programming or movement execution, then it should be similar with direct or symbolic cues.

Our asymmetric movements did have larger spatial interference with symbolic cues than direct cues, but the interference was much smaller than in asymmetric movements that are planned in advance of movement execution (Kelso, Putnam, & Goodman, 1983; Marteniuk & MacKenzie, 1980, Marteniuk, MacKenzie, & Baba 1984). For example, Blinch and Chua (2009) tested

symmetric and asymmetric bimanual reaches that were directly- or symbolically-cued in a reaction time task. This is similar to the second experiment except the target perturbation became the imperative stimulus and the short and long targets were 7 and 14 cm from the starting positions (Figure 4.1).
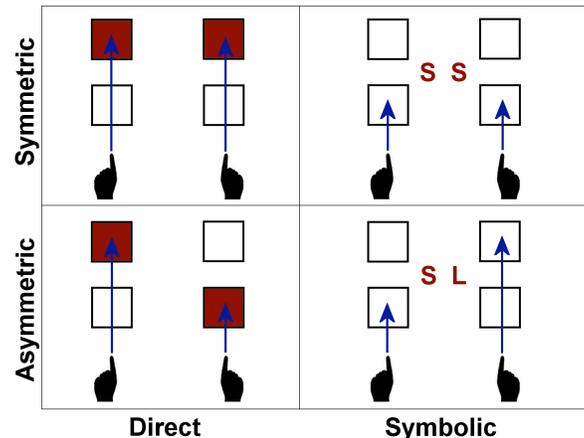

Figure 4.1. In Blinch and Chua (2009), participants made bimanual reaching movements that were cued directly (left) or symbolically (right) in a reaction time paradigm. The movements were either symmetric with both targets at equal distances (top) or asymmetric with targets at different distances (bottom). From Blinch and Chua (2009).

Blinch and Chua (2009) replicated Diedrichsen and colleagues (2001) and found longer reaction times with direct cues than symbolic cues, as well as longer reaction times for asymmetric movements than symmetric movements with symbolic cues. More importantly, transient spatial interference was evident in the trajectories of the asymmetric movements with symbolic cues (Figure 4.2). When the short asymmetric movements (red) were compared to short symmetric movements (cyan), the short asymmetric movement overshot by 13.5 ± 8.3 mm. This is larger than the 4.9 ± 4.6 mm of spatial interference that we found for symbolically-cued on-line corrections that resulted in asymmetric movements. Our interference was found when comparing the participants' means but the same trend was difficult to identify in mean trajectories of individual participants. Subsequent statistical analysis on the trials of each participant did not find any participant with greater interference (magnitude or duration) in Symbolic compared to Direct conditions. In contrast, the interference in preplanned movements found by Blinch and Chua was seen in mean participant trajectories as well as individual trials. Since we found spatial interference that was quite small and subtle, we are more inclined to conclude at this point that on-line control of the limbs during bimanual reaching is mostly independent. This was found even with increased processing demands on response selection to

translate symbolic cues. It remains to be seen whether on-line control of the limbs is truly independent, or what conditions are necessary and sufficient to induce spatial interference during on-line control of bimanual reaching.
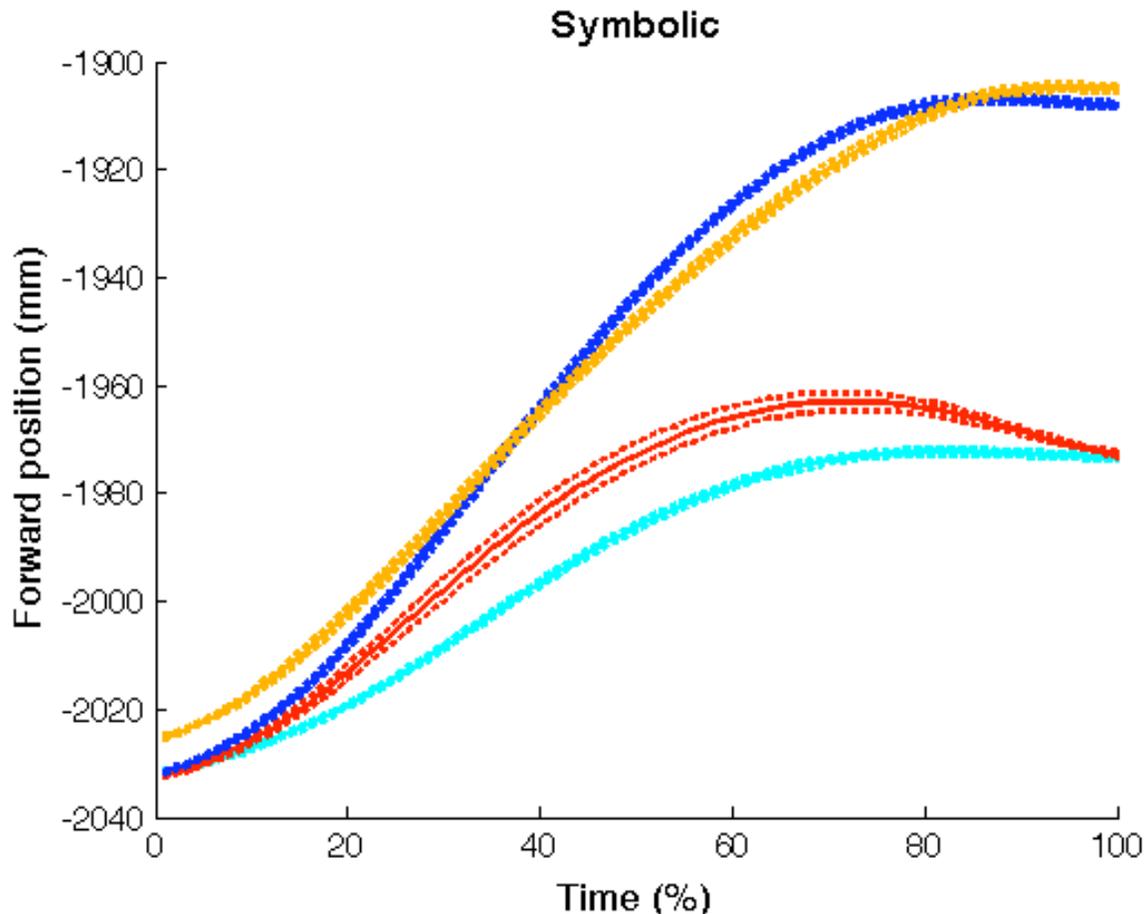

Figure 4.2. Grand mean trajectories of the left limb for reaches with symbolic cues graphed in forward position by percent time. Long and short symmetric movements are shown in blue and cyan. Short asymmetric movements are red, and long asymmetric movements are orange. Notice how the short asymmetric movement (red) overshoots the short symmetric movement (cyan). The dotted lines are plus or minus one standard error. Adapted from Blinch and Chua (2009).

Directly- and symbolically cued movements place different processing demands on the cue-to-target translations during response selection (Diedrichsen et al., 2003). When these cues are part of premovement planning symbolically-cued asymmetric movements result in bimanual interference during movement initiation (Diedrichsen et al, 2001; Spijkers et al., 1997). The interference is not the result of motor programming or execution, as the required movements are very similar with direct or symbolic cues. Rather, symbolic cues change how the action goals are represented and this result in bimanual interference (Franz, 2003; Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004; Serrien, Ivry, & Swinnen, 2006; Serrien, Ivry, & Swinnen, 2007).

Blinch and Chua (2009) showed that a symbolic representation had a downstream influence on movement execution. However, we found only minimal interference when the symbolically-cued movement is a modification to a currently executing movement. Why does the action representation result in bimanual interference for a preplanned movement and not on-line control? It is possible that there are two different types of movement selection: one for preplanned movements and one for online control, with the latter being more immune to cortical crosstalk. Perhaps both types of movements share the same selection process and then some other process differs before movement execution. For example, specifying the initial movement parameters during planning may differ from adding an on-line correction to a currently executing movement. This is an interesting area for future research.

4.2 Challenges to independent on-line control

There are two extensions to these experiments that could yield results that challenge the notion of independent on-line control during bimanual reaching. First, if on-line control is independent, then both limbs should be able to make on-line corrections at the same time without the corrections interfering with each other. In our pilot experiment (Appendix A), we included trials where both limbs were required to make on-line corrections. The onsets of adjustments and other performance measures were comparable to bimanual reaches when only one limb made an on-line correction. Therefore, independent on-line control was still supported.

Second, it is possible the amount of on-line control for the unperturbed limbs decreased compared to controls, relying on a more open-loop or ballistic mode of control, which could result in spatial interference. In different terms, there may have been a tradeoff between on-line control for each limb, and as the perturbed limbs required on-line control, the unperturbed limbs relied on open-loop control and the reach trajectories differed compared to controls. This tradeoff was likely temporary, as the spatial interference was transient and the unperturbed limbs were no different from control by the end of the movement. The tradeoff may even be larger with symbolic cues than direct cues, which could explain the different amounts of spatial interference. The possibility of a tradeoff between the limbs could be investigated with variability analysis or endpoint correlation analysis (Khan, Franks, Elliott, Lawrence, Chua, Bernier, Hansen, & Week, 2006).

4.3 Cue-to-target translation

The onsets of adjustments were longer with symbolic cues (370 ± 46.5 ms) than direct cues (236 ± 34.7 ms) in the second experiment. Symbolic cues have longer onsets of adjustments because of the increased processing demands on response selection for the cue-to-target translations (Diedrichsen et al., 2003). When there is no uncertainty to the location of the on-line adjustment for each limb (as in the first experiment), the target perturbation need only be detected and not translated to perform the on-line correction. Without translation, it follows that the onsets of adjustments with direct or symbolic cues will be the same. In the second experiment, two potential targets for the on-line correction ensured the cues were translated and the difference between direct and symbolic cues emerged.

The onsets of adjustments in the second experiment with direct cues (236 ± 34.7 ms) were slower than the direct onsets of adjustments (173 ± 11 ms) reported by Diedrichsen and colleagues (2004). One difference was our on-line corrections were in the forward direction and Diedrichsen's were in the lateral direction. It has been shown that corrections in the forward direction occur later than lateral corrections (Sarlegna & Sainburg, 2008), which supports our slower onsets of adjustments.

The delayed onsets of adjustments with symbolic cues compared to direct cues reflects increased processing during the initiation of an on-line correction (Diedrichsen et al., 2003). This is similar to the increased reaction time for symbolically-cued movements compared to directly-cued movements, except that processing occurs during premovement planning. Diedrichsen and colleagues (2004) have shown that the onsets of adjustments with direct cues are comparable for unimanual or bimanual reaches with a correction in one limb or both limbs. In other words, there is no bimanual cost for on-line corrections compared to unimanual conditions. Blinch and colleagues (2008) found comparable onsets of adjustments with symbolic cues for bimanual reaches with a correction in one limb or both limbs, but baseline performance in unimanual conditions was untested. It is possible that there is a bimanual cost for symbolically-cued on-line corrections. This would be a form of bimanual interference and would argue against

independent on-line bimanual control when processing demands are increased with symbolic cues.

4.4 Temporal interference

When a short duration unimanual movement with one limb is combined with a long duration unimanual movement with the other limb, temporal interference typically occurs that results in the disparate timing of the movements becoming comparable under bimanual performance. This has been shown for preplanned bimanual reaches (Kelso, Putnam, & Goodman, 1983; Kelso, Southard, & Goodman, 1979; Marteniuk & MacKenzie, 1980, Marteniuk, MacKenzie, & Baba 1984; Swinnen, Walter, & Shapiro, 1988), as both limbs beginning their movements and ending their movements at approximately the same time. In contrast, the movement times of the perturbed and unperturbed limbs were different with direct or symbolic cues. The perturbed limbs had longer movement times than controls to allow for the on-line corrections. Temporal interference should extend the movement times of the unperturbed limbs. The movement times of the short unperturbed limbs were longer than controls, but still not as long as the short perturbed limbs, and the long unperturbed limbs were comparable to controls. There was some temporal interference, but the movement times of the two limbs were mostly independent. It seems that on-line control escapes much of the temporal interference experienced by preplanned movements in the same way that on-line control appears relatively immune to spatial interference.

4.5 Conclusion

We found larger spatial interference for symbolically-cued on-line corrections compared to directly-cued corrections. Symbolic cues place greater demands on response selection for the cue-to-target translations than direct cues (Diedrichsen et al., 2003). This increases cortical crosstalk and results in spatial interference. Although there was greater interference with symbolic cues, the interference was small and transient with direct or symbolic cues, and it occurred in only the short unperturbed limb and not the long unperturbed limb. It was also subtle in comparison to spatial interference during preplanned bimanual reaches. Since a correction in one limb can be accomplished without a large or lasting effect on the other limb, we therefore

conclude that on-line control of the limbs during bimanual reaching is mostly independent. The independence of on-line control fits with our expectations in daily life; we do not miss either target when making asymmetric reaching movements. Perhaps we use on-line control to correct the spatial interference that is sometimes introduced by premovement planning.

REFERENCES

Bernstein, N (1967). *The coordination and regulation of movements*. Oxford, England: Pergamon Press.

Blinch, JPG, Cameron, B, Lam, MY, Hua, S, Cory, M, & Chua, R (2008, November). Bimanual interference during on-line control to symbolically- vs. directly-cued target locations. Poster session presented at the annual meeting of the Canadian Society for Psychomotor Learning and Sport Psychology, Canmore, Alberta.

Blinch, JPG, & Chua, R (2009, November). Symbolically-cued asymmetric reaches result in spatial interference during initiation and execution. Poster session presented at the annual meeting of the Canadian Society for Psychomotor Learning and Sport Psychology, Toronto, Ontario.

Cressman, EK, Frank, IM, Enns, JT, & Chua, R (2006). No automatic pilot for visually guided aiming based on colour. *Experimental Brain Research, 171(2)*, 174-183.

Diedrichsen, J, Grafton, S, Albert, N, Hazeltine, E, & Ivry, RB (2006). Goal-selection and movement-related conflict during bimanual reaching movements. *Cerebral Cortex, 16(12)*, 1729-1738.

Diedrichsen, J, Hazeltine, E, Kennerley, S, & Ivry, RB (2001). Moving to directly cued locations abolishes spatial interference during bimanual actions. *Psychological Science, 12(6)*, 493-498.

Diedrichsen, J, Ivry, RB, Hazeltine, E, Kennerley, S, & Cohen, A (2003). Bimanual interference associated with the selection of target locations. *Journal of Experimental Psychology: Human Perception and Performance, 29(1)*, 64-77.

Diedrichsen, J, Nambisan, R, Kennerley, SW, & Ivry, RB (2004). Independent on-line control of the two hands during bimanual reaching. The European Journal of Neuroscience, 19(6), 1643-1652.

Fitts, PM (1954). The information complexity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology, 47*, 381-391.

Franz, EA (1997). Spatial coupling in the coordination of complex actions. Quarterly Journal of Experimental Psychology, 50A, 684-704.

Franz, EA (2003). Bimanual action representation: A window on human evolution. In SH Johnson-Frey (Ed.), *Taking action: Cognitive neuroscience perspectives on intentional acts* (pp. 259-288). Cambridge: The MIT Press.

Franz, EA, Eliassen, JC, Ivry, RB, & Gazzaniga, MS (1996). Dissociations of spatial and temporal coupling in the bimanual movements of callosotomy patients. *Psychological Science, 7(5)*, 306-310.

Glover, S (2004). Separate visual representations in the planning and control of action. *The Behavioral and Brain Sciences, 27(1)*, 3-24.

Goodale, MA, Pelisson, D, & Prablanc, C (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature, 320,* 748-750.

Goodman, D, & Kelso, JAS (1980). Are movements prepared in parts? Not under compatible (naturalized) conditions. *Journal of Experimental Psychology: General, 109(4)*, 475-495.

Hazeltine, E, Diedrichsen, J, Kennerley, SW, & Ivry, RB (2003). Bimanual cross-talk during reaching movements is primarily related to response selection, not the specification of motor parameters. *Psychological Research, 67(1)*, 56-70.

Ivry, RB, Diedrichsen, J, Spencer, R, Hazeltine, E, & Semjen, A (2004?). A cognitive neuroscience perspective on bimanual coordination and interference. In SP Swinnen & J Duysens (Eds.), *Neural behavioral determinants of interlimb coordination: A multidisciplinary approach* (pp. 259-295). Massachusetts: Kluwer Academic Publishers.

Khan, MA, Franks, IM, Elliott, D, Lawrence, GP, Chua, R, Bernier, P-M, Hansen, S, & Weeks, DJ (2006). Inferring online and offline processing of visual feedback in target-directed movements form kinematic data. *Neuroscience and Biobehavioral Reviews, 30*, 1106-1121.

Kelso, JA, Putnam, CA, & Goodman, D (1983). On the space-time structure of human interlimb co-ordination. Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology, 35(2), 347-375.

Kelso, JA, Southard, DL, & Goodman, D (1979). On the coordination of two-handed movements. *Journal of Experimental Psychology: Human Perception and Performance, 5(2)*, 229-238.

Marteniuk, RG, & MacKenzie, CL (1980). A preliminary theory of two-hand coordination control. In GE Stelmach & J Requin (Eds.), *Tutorials in motor behavior* (pp. 185-197). Amsterdam: North-Holland.

Marteniuk, RG, MacKenzie, CL, & Baba, DM (1984). Bimanual movement control: Information processing and interaction effects. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 36A(2)*, 335-365.

Mason, AH (2008). Coordination and control of bimanual prehension: Effects of perturbing object location. *Experimental Brain Research, 188(1)*, 125-139.

Milner, AD, & Goodale, MA (2008). Two visual systems re-viewed. *Neuropsychologia, 46(3)*, 774-785.

Oldfield, R.C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97-113.

Pisella, L, Gréa, H, Tilikete, C, Vighetto, A, Desmurget, M, Rode, G, Boisson, D, & Rossetti, Y (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: Toward reinterpreting optic ataxia. Nature, 3(7), 729-736.

Rosenbaum, DA, Dawson, AM, & Challis, JH (2006). Haptic tracking permits bimanual independence. *Journal of Experimental Psychology: Human Perception and Performance, 32(5)*, 1266-1275.

Sarlegna, FR, & Sainburg, RL (2008). The roles of vision and proprioception in the planning of reaching movements. In D Sternad (Ed.), *Progress in motor control: A multidisciplinary approach* (pp. 317-335). New York, NY: Springer.

Serrien, DJ, Ivry, RB, & Swinnen, SP (2006). Dynamics of hemispheric specialization and integration in the context of motor control. *Nature Reviews: Neuroscience, 7(2)*, 160-167.

Serrien, DJ, Ivry, RB, & Swinnen, SP (2007). The missing link between action and cognition. *Progress in Neurobiology, 82(2)*, 95-107.

Spijkers, W, Heuer, H, Kleinsorge, T, & van der Loo, H (1997). Preparation of bimanual movements with same and different amplitudes: Specification interference as revealed by reaction times. *Acta Psychologica, 96(3)*, 207-227.

Sherwood, DE (1994**)**. Hand preference, practice order, and spatial assimilations in rapid bimanual movement. *Journal of Motor Behavior, 26(2),* 123-143.

Swinnen, SP (1992). Coordination of upper-limb movement: A neuro-dynamics account. In GE Stelmach & J Requin (Eds.), *Tutorials in motor behavior II* (pp. 695-711). Amsterdam: North-Holland.

Swinnen, SP, Verschueren, SMP, Bogaerts, H, Dounskaia, N, Lee, TD, Stelmach, GE, & Serrien, DJ (1998). Age-related deficits in motor learning and differences in feedback processing during the production of a bimanual coordination pattern. *Cognitive Neuropsychology, 15(5)*, 439-466.

Swinnen, SP, Walter, CB, Shapiro, DC (1988). The coordination of limb movements with different kinematic patterns. *Brain and Cognition, 8(3)*, 326-347.

Swinnen, SP, & Wenderoth, N (2004). Two hands, one brain: Cognitive neuroscience of bimanual skill. *Trends in Cognitive Sciences, 8(1)*, 18-25.

Turvey, MT (1977). Preliminaries to a theory of action with reference to vision. In R Shaw & J Bransford (Eds.), *Perceiving, acting, and knowing (pp. 211-265)*. Hillsdale, NJ: Erlbaum.

APPENDICIES

Appendix A: Pilot experiment

Blinch, Cameron, Lam, Hua, Cory, and Chua (2008) tested ten participants on bimanual reaching movements with a movement time goal of 500 ms. The imperative stimulus was the appearance of a number 8 inside the middle target placeholder for the left and right limbs. At movement onset for 50% of the trials, an on-line correction was directly or symbolically cued by a target jump (Figure A.1d) or a target identity change (Figure A.1e). For directly-cued on-line corrections, the target 8 would jump to the left or right target placeholder and the participant would reach to the new target location. If the right target box changed to a rightward facing "E", then the right limb (the perturbed limb) would make an on-line correction to the right target placeholder. A leftward facing "E" was used for corrections to the left target placeholder. Comparing the lateral deviation to control trials tested the effect of the target perturbation on the unperturbed limb when only one limb was required to change direction.
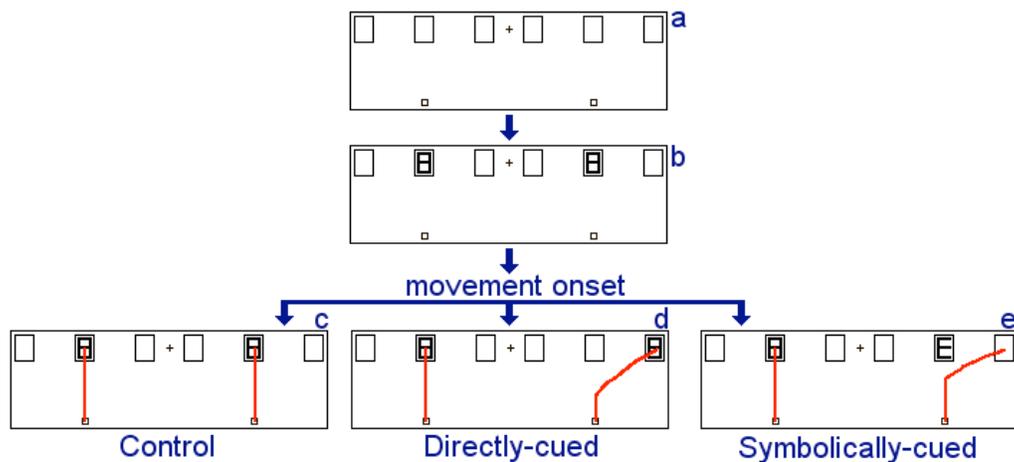

Figure A.1. Stimulus progression for each type of trial. The fixation point appeared in the middle of the target boxes (a). A target number "8" appeared in the middle target box for each limb as the movement cue (b). In control trials, the participant reached to the original targets (c). Both the direct (d) and symbolic (e) cues shown above required an on-line correction of the right limb to the right target box. The red lines represent the trajectories of the limbs. Adapted from Blinch and colleagues (2008).

All participants successfully made on-line corrections to symbolically- or directly-cued target locations. The mean onset of adjustment was earlier in direct (303 ms) than symbolic (412 ms)

conditions. A small, transient perturbation of 2.9 mm was seen in one of the direct conditions (Figure A.2 left). A larger perturbation of 4.8 mm that remained uncorrected was seen in one of the symbolic conditions (Figure A.2 right), but the magnitude of the spatial interference was smaller than expected when compared to spatial interference in preplanned bimanual movements (Kelso, Putnam, & Goodman, 1983; Kelso, Southard, & Goodman, 1979; Marteniuk & MacKenzie, 1980, Marteniuk, MacKenzie, & Baba 1984; Swinnen, Walter, & Shapiro, 1988). When spatial interference occurred, it always resulted in allocentric symmetry. The significant difference in the magnitude of spatial interference supported the conclusion that high processing demands on response selection for symbolically-cued on-line corrections results in more spatial interference than directly-cued corrections.
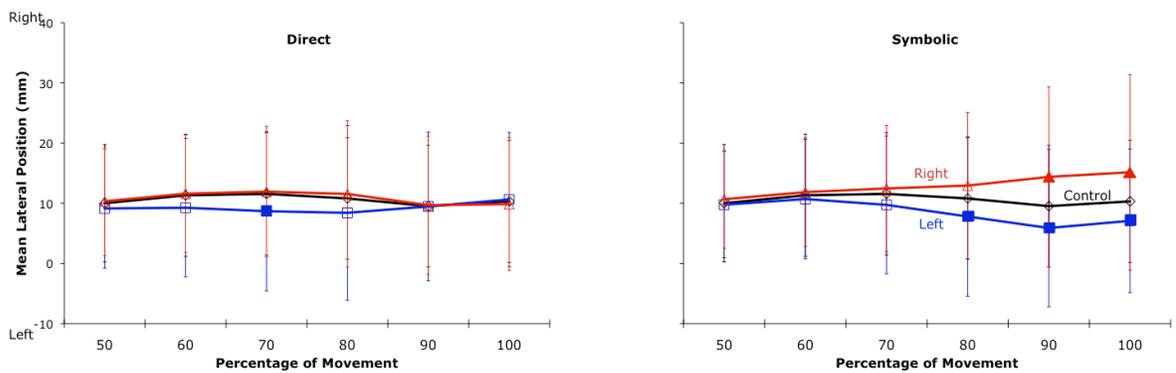

Figure A.2. Mean lateral position of the right, unperturbed limb by the percentage of movement. Directly-cued on-line corrections are on the left graph and symbolically-cued corrections are on the right. The position of the unperturbed limb is shown when the correction of the left, perturbed limb is to the right (red), left (blue), or control (black). Filled points are significantly different from control; vertical lines are standard deviations of the means. From Blinch and colleagues (2008).

It is possible the true magnitude of spatial interference (in both conditions) may have been suppressed by the experimental methods. Therefore, we proposed the following refinements to the methods used in this thesis. First, we tested larger target perturbations to smaller targets. Both of these changes have increased interference in bimanual reaching movements (Marteniuk & MacKenzie, 1980; Marteniuk, MacKenzie, & Baba, 1984; Sherwood, 1994). Second, we tested lateral perturbations that were also posterior to the initial target. More cortical crosstalk may occur when a correction is made in the same direction as the original movement (Mason, 2008) and may increase the spatial interference. Third, we created a larger difference between direct and symbolic conditions by using a colour change of the initial target as a symbolic cue instead of a target identity change. The leftward and rightward facing "E" may have been coded as arrows, with the prongs of the letter pointing towards the target change. In comparison, a

colour change will require more translation during response selection and potentially result in larger spatial interference. Fourth, to prevent highly practiced, automatic movements in the unperturbed limb that may avoid spatial interference, the target placeholders appeared in a randomized order between three slightly different configurations.

Appendix B: Ethics certificate

The University of British Columbia
Office of Research Services
Behavioural Research Ethics Board
Suite 102, 6190 Agronomy Road, Vancouver, B.C. V6T 1Z3

CERTIFICATE OF APPROVAL- MINIMAL RISK RENEWAL

PRINCIPAL INVESTIGATOR: Romeo Chua	DEPARTMENT: UBC/Education/Human Kinetics	UBC BREB NUMBER: H03-80057

INSTITUTION(S) WHERE RESEARCH WILL BE CARRIED OUT:

Institution	Site
UBC	Vancouver (excludes UBC Hospital)

Other locations where the research will be conducted:
N/A

CO-INVESTIGATOR(S):

Melanie L Lam
Brendan Cameron
Ian M. Franks
James T. Enns
Jarrod P.G. Blinch

SPONSORING AGENCIES:

Natural Sciences and Engineering Research Council of Canada (NSERC) - "Sensory and perceptual contributions to the preparation and execution of goal-directed action"

PROJECT TITLE:
Sensory and Perceptual Contributions to the Preparation and Execution of Goal-Directed Action

EXPIRY DATE OF THIS APPROVAL: February 27, 2010

APPROVAL DATE: February 27, 2009

The Annual Renewal for Study have been reviewed and the procedures were found to be acceptable on ethical grounds for research involving human subjects.

Approval is issued on behalf of the Behavioural Research Ethics Board

Dr. M. Judith Lynam, Chair
Dr. Ken Craig, Chair
Dr. Jim Rupert, Associate Chair
Dr. Laurie Ford, Associate Chair
Dr. Anita Ho, Associate Chair

Figure B.1. Ethics certificate.