INFORMATION PROCESSING OF BIMANUAL REACHING MOVEMENTS

by

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Abstract

The information processing of bimanual reaching movements was investigated in this thesis. All of the studies tested symmetric and asymmetric bimanual reaching movements that were made to targets as quickly and accurately as possible. The duration of movement preparation was measured by reaction time (RT). Study one found that bimanual asymmetric movements had longer preparation than bimanual symmetric movements. Donders’ subtraction method was used to isolate this bimanual asymmetric cost to a stage, or stages, of movement preparation that are unique to choice RT tasks; these included target discrimination, response selection, and response programming. Many different movement parameters could cause bimanual asymmetric costs. The results from study two suggested that the relative contribution of three parameters to the asymmetric cost, from most to least important, was movement amplitudes, target locations, and then startling locations. The relationship between unimanual and bimanual movements was tested in the third study by precuing the target for the left arm of a bimanual movement. RT and the start-react effect were used to determine how movement preparation changed. These measures suggested: 1) that the precued movement was not fully programmed but partially programmed before the imperative stimulus, and 2) that the asymmetric cost was caused by increased processing demands on response programming. Overall, the results supported that bimanual movements are not the sum of two unimanual movements; instead; the two arms of a bimanual movement are unified into a functional unit. When one target is precued, this critical unification likely occurs during response programming. Study four used the additive factors method to determine which stages of movement preparation contributed to the asymmetric cost when both targets were cued by the imperative stimulus. The results supported that the asymmetric cost was caused by increased processing demands on response selection. Target discrimination and response programming – contrary to previous hypotheses – did not contribute to the asymmetric cost. The critical process of bimanual unification likely depends on how the task is presented and conceptualised. It occurs during response selection when both targets
are cued by the imperative stimulus, and it is deferred to response programming when one target is precued.
Preface

This thesis is the result of collaboration from many scientists. I was the principle investigator and led the experimental design, data collection and analysis, and manuscript preparation. My supervisor, Professor Romeo Chua, guided and supported me with all phases of the research. My thesis committee, Professor Ian M Franks and Associate Professor Mark G Carpenter, commented on all aspects of the research as proposed and completed studies. Dr. Brendan D Cameron has a similar role for the experiments presented in Chapters 2 and 3 and Associate Professor Erin K Cressman for the experiment in Chapter 2.

The UBC Research Ethics Board approved all of the studies. The experiments in Chapters 2, 3, and 5 were covered by ethics certificate H03-80057 (Sensory and perceptual contributions to the preparation and execution of goal-directed action), and Chapter 4 was covered by ethics certificate H10-01354 (Perceptual and motor contributions to the preparation and execution of goal-directed action: investigations using transcranial magnetic stimulation).


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A version of Chapter 5 is under review: Blinch J, Carpenter MG, Franks IM, Chua R (under review). Preparation cost for bimanual asymmetric movements is caused by response selection.
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<th>Description</th>
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<td>AFM</td>
<td>Additive factors method</td>
</tr>
<tr>
<td>ANOVA</td>
<td>Analysis of variance</td>
</tr>
<tr>
<td>CI</td>
<td>Confidence interval</td>
</tr>
<tr>
<td>RT</td>
<td>Reaction time</td>
</tr>
<tr>
<td>SE</td>
<td>Standard error</td>
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To Dara,
I may now be a decent scientist
but I am nothing without you

To the baby in Dara's belly,
Stay in school
but don't stay too long
1 Introduction

“The study of human movement coordination provides an ideal system to unravel multiple-task management and task integration by the central nervous system in general, and interactions between distributed neural assemblies in particular, because the consequences of these neural processes can be traced at the behavioural level with high kinematic resolution” Swinnen (2002, pp 359).

1.1 Concise literature review\(^1\)

One of the research problems in the field of motor control is determining how the nervous system accomplishes coordinated movements. Many studies have examined the coordination of bimanual reaching movements as an example of coordination in motor activities of daily life. Try keeping one arm behind your back at any point in your day and you will quickly realise how much we rely on bimanual movements. A foundational discovery about the nature of bimanual reaching movements is they are not the sum of two unimanual movements (Kelso et al. 1979a, b). If you perform two different unimanual movements at the same time with each arm, for example, a movement to an easy target with one arm and a movement to a hard target with the other arm, then temporal and spatial coupling occurs and alters the movement trajectories. More specifically, bimanual movements tend to have similar trajectories with similar timing. Examples of temporal coupling are that bimanual reaching movements begin, reach peak velocity, and end at around the same time (Kelso et al. 1979a, b). Spatial coupling is seen when one arm has to increase the height of its trajectory to go over an obstacle. The trajectory of the other arm often increases its trajectory, even though there is no obstacle in its path (Kelso et al. 1983). Temporal and spatial coupling are two examples of interference that can occur during bimanual reaches. Most forms of bimanual interference can be overcome with practice; athletes

\(^1\) The comprehensive literature review is in Appendix A.
and musicians learn to do complicated asynchronous and asymmetric bimanual movements. However, bimanual interference defines the default mode of coordination that typifies coordinated actions in daily life.

Bimanual interference has been hypothesised to occur in several neural pathways (reviewed by Carson 2005). The interference considered in this thesis likely occurs in the brain during the preparation of the motor command for a bimanual reaching movement. Bimanual interference could be the amount, or the complexity, of neural activity for one type of bimanual movement compared to another. A source of complexity is the communication between the hemispheres during movement preparation. One neural substrate for interhemispheric communication that causes bimanual interference is the corpus callosum (reviewed by Franz 2003; Gooijers and Swinnen 2014). In this thesis, I will not directly measure the amount of neural activity or the flow of information across the corpus callosum. However, the complexity of information processing during movement preparation can be indirectly measured by reaction time (RT). It has been shown in many different bimanual movements and studies that bimanual interference, or more complex movement preparation, causes longer RTs (reviewed by Wenderoth and Weigelt 2009).

In my thesis studies, I compared bimanual symmetric reaching movements to bimanual asymmetric reaching movements. Symmetric movements are ones that travel equal distances in the same direction, while movements that travel different distances or in different directions are examples of asymmetric movements. Symmetric and asymmetric movements were tested in simple and choice RT tasks. In choice RT tasks, the required response is unknown before the imperative stimulus. Therefore, the RT reflects the duration of all stages of movement preparation: imperative stimulus recognition, target discrimination, response selection, response programming, and response initiation (Figure 2.1).\(^2\) The required response is known before the imperative

\(^2\)To be precise, choice RT includes the stages of information processing, the transmission of the motor command from the brain to the muscles (transmission time), and the delay between the motor command arriving at the muscles and the initiation of the movement (motor RT). It is typically assumed that transmission time and motor RT are constant for similar movements, like symmetric and asymmetric reaching movements, and so these processes are often discounted from the notion of RT. Motor time can
stimulus in simple RT tasks, and so some movement preparation can occur in advance (Summers and Anson 2009). Target discrimination, response selection, and response programming can occur before the imperative stimulus. RT in simple RT tasks, therefore, reflects the duration of only imperative stimulus recognition and response initiation (Figure 2.1).

Illuminating a target for the left arm and a target for the right arm cued the bimanual reaching movements in this thesis; these are referred to as direct cues. Diedrichsen et al. (2001) compared the movement preparation of bimanual reaching movements with direct cues and symbolic cues in choice RT tasks. The symbolic cues were the letter “L”, to cue a long-distance movement, and the letter “S”, to cue a short-distance movement (Experiment 1). They found that with symbolic cues, bimanual asymmetric movements had longer movement preparation than bimanual symmetric movements. Subsequent studies have shown that this large RT cost (~100 ms) with symbolic cues is caused by increased processing demands on response selection (e.g. Albert et al. 2007; Diedrichsen et al. 2003; Hazeltine et al. 2003). The cost is caused by translating two different symbolic cues (for example, the letters L and S for a Long-Short movement) into target locations for asymmetric movements. Symmetric movements have shorter preparation than asymmetric movements because they involve translating the same symbolic cue twice (for example, the letters L and L for a Long-Long movement). Direct cues, in contrast, directly specify the target locations and decrease the processing demands on response selection. Diedrichsen et al. (2001) found the duration of movement preparation for symmetric and asymmetric movements with direct cues was comparable. However, later studies (even one by Diedrichsen) reported a small RT cost (~20 ms) for bimanual asymmetric movements compared to symmetric movements (e.g. Diedrichsen et al. 2006; Heuer and Klein 2006b; reviewed by Weigelt and Wenderoth 2009).

be excluded by measuring the time from the imperative stimulus to the onset of muscle activity (premotor RT). This was done in Chapter 3 and RT and premotor RT had the same pattern of results.

3 The target for the left arm is indicated before the hyphen and the right arm’s target is indicated after the hyphen. Short–Long, for example, cues a short-distance movement with the left arm and a long-distance movement with the right arm.
1.2 Overview of thesis studies

The discussion of potential movement preparation costs for bimanual reaching movement led us to the first thesis study (Chapter 2). I tested whether movement preparation was longer for bimanual symmetric movements compared to unimanual movements (a potential bimanual symmetric cost) and whether preparation was longer for bimanual asymmetric movements compared to bimanual symmetric movements (a potential bimanual asymmetric cost). RTs were measured in simple and choice RT tasks. Donders’ subtraction method (1969) was used to isolate any bimanual costs to stages of movement preparation that are unique to simple RT tasks (imperative stimulus recognition and response initiation) or choice RT tasks (target discrimination, response selection, and response programming). The results showed that RTs were comparable for all types of movements in simple RT; that is, there was neither a bimanual symmetric cost nor an asymmetric cost. Therefore, unimanual, bimanual symmetric, and bimanual asymmetric movements have comparable complexity during imperative stimulus recognition and response initiation. In choice conditions, there was no bimanual symmetric cost but there was a bimanual asymmetric cost, indicating the preparation of asymmetric movements is more complex than symmetric movements. This bimanual asymmetric cost could be caused by increased processing demands on target discrimination, response selection, or response programming.

The goals of the second study (Chapter 3) were to determine which symmetric movement parameters facilitate the preparation of bimanual movements and to compare the size of the facilitation for different parameters. Participants performed bimanual reaching movements that varied in terms of the symmetry/asymmetry of starting locations, movement amplitudes, and target locations. RT savings were examined by comparing movements that had one symmetric parameter (and two asymmetric parameters) to movements with all asymmetric parameters. I observed significant savings for movements with symmetric amplitudes and movements with symmetric target locations. RT costs were examined by comparing movements that had
two asymmetric parameters (and one symmetric parameter) to movements with all symmetric parameters. I observed significant RT costs for all movements with asymmetric amplitudes. These results suggest that movement preparation is facilitated when amplitudes or target locations are symmetric and that movement preparation suffers interference when amplitudes are asymmetric. The relative importance of the three parameters to movement preparation, from most to least important, is movement amplitudes, target locations, and then starting locations.

The third study (Chapter 4) tested the demands on the movement preparation of bimanual movements by temporally separating the preparation of each arm. This was achieved by precuing the target of one arm before the imperative stimulus. We asked: What was prepared in advance when one arm was precued? The answer to this question suggested which process caused the bimanual asymmetric cost. Movement preparation before the imperative stimulus was examined by comparing RTs with and without a precue for the left target and by using the start-react effect. Participants made bimanual symmetric and asymmetric reaching movements in simple and 2-choice RT conditions and a condition with a precue for the left target. I found a bimanual asymmetric cost in 2-choice conditions, and the asymmetric cost was significantly smaller when the left target was precued. These results suggested: 1) that the precued movement was not fully programmed but partially programmed before the imperative stimulus, and 2) that the asymmetric cost was caused by increased processing demands on response programming. The results of the startle trials also supported these two conclusions. Overall, the results support the notion that bimanual movements are not the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit. When one target is precued, this critical unification likely occurs during response programming.

In the final study (Chapter 5), I asked: Which stages of movement preparation contribute to the bimanual asymmetric cost with direct cues? The bimanual asymmetric cost may be caused by increased processing demands on any stage (or stages) of movement preparation that are unique to choice RT: specifically, target discrimination, response selection, or response programming. The additive factors method (Sternberg
was used to test the contributions of each stage. This involved: altering the stimulus contrast (bright or dim), the response compatibility (compatible or incompatible), and the response complexity (reaches or reversals). These manipulations changed the processing demands on target discrimination, response selection, and response programming, respectively. Incompatible bimanual asymmetric movements were the only movements that had an over-additive RT interaction. This suggested that the bimanual asymmetric cost was caused by increased processing demands on response selection and that target discrimination and response programming did not contribute to the cost. The asymmetric cost was caused by response selection despite the use of direct cues that place fewer processing demands on translation processes compared to symbolic cues. Selecting or integrating two different, asymmetric responses could have increased the processing demands on response selection. Although response selection contributed to the asymmetric cost in this task, altering movement preparation may change when the bimanual asymmetric cost occurs or the magnitude of the cost.
2 Comparing movement preparation of unimanual, bimanual symmetric, and bimanual asymmetric movements

2.1 Introduction

Bimanual movements are typically thought to require more complex movement preparation than their unimanual counterparts (Swinnen and Wenderoth 2004). This complexity may stem from concurrent selection of more than one response (Diedrichsen et al. 2001), from concurrent assembly of multiple motor commands (Heuer and Klein 2006b; Spijkers et al. 1997; Spijkers and Heuer 1995; Stelmach et al. 1988), or from some combination of these. Whatever the source of the complexity, a reasonable assumption is that more complex movement preparation requires more processing time; therefore, increased reaction time (RT) in a reach task can be used as an indicator of increased complexity.

The majority of studies that have investigated the preparation of bimanual movements have compared bimanual symmetric movements (i.e. the arms travel equivalent distances in the same directions) to unimanual movements in simple reaction-time tasks with direct cues (Anson and Bird 1993; Di Stefano et al. 1980; Hughes and Franz 2007; Nagelkerke 2002; Ohtsuki 1981; Shen and Franz 2005; Taniguchi 1999a, b). The results from these studies have been inconsistent; some have shown simple reaction-time costs for bimanual symmetric movements (Anson and Bird 1993, finger extension; Di Stefano et al. 1980; Hughes and Franz 2007; Ohtsuki 1981; Shen and Franz 2005; Taniguchi 1999b) while others have not (Anson and Bird 1993, elbow flexion; Nagelkerke 2002; Taniguchi 1999a). Furthermore, other studies did not statistically compare RTs of bimanual symmetric movements to unimanual movements.

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Studies that have measured choice RTs with direct cues (Blinch et al. 2011; Diedrichsen et al. 2001, 2006; Heuer and Klein 2006b; Stelmach et al. 1988; Weigelt and Cardoso de Oliveira 2003) have focused on the movement preparation of bimanual asymmetric movements (i.e. the arms travel different distances or directions) compared to symmetric movements. Diedrichsen et al. (2001) compared symmetric and asymmetric movements that were cued by direct and symbolic cues. They found large bimanual asymmetric costs with symbolic cues (55 ms in Experiment 1 and 94 ms in Experiment 2) and no costs with direct cues. They argued that the asymmetric costs were the result of increased processing demands on response selection when two different symbolic cues required translation, which has been supported by other studies (reviewed by Wenderoth and Weigelt 2009).

Recent research has questioned whether there might be small asymmetric costs with direct cues. Heuer and Klein (2006b) and Diedrichsen et al. (2006) found small asymmetric costs (15–55 ms) and suggested the asymmetric costs are attenuated, but not eliminated, with direct cues. They argued that the large and small asymmetric costs with symbolic and direct cues revealed two forms of interference. The small costs with direct cues might be the result of increased processing demands on response programming for asymmetric movements. The large costs with symbolic cues include the small costs and the larger interference from the translation of two different symbolic cues. We focused on bimanual costs with direct cues in this study. In regard to direct cues, the results from previous studies on the asymmetric costs have been inconsistent. Some have shown choice reaction-time costs for bimanual asymmetric movements (Diedrichsen et al. 2006; Heuer and Klein 2006b; Stelmach et al. 1988, young participants; Weigelt and Cardoso de Oliveira. 2003, non-transformed conditions) while others have not (Blinch et al. 2011; Diedrichsen et al. 2001). The current study also examined potential bimanual symmetric costs in choice reaction-time conditions, which have not been looked at in great detail (Diedrichsen et al. 2001, 2006; Stelmach et al. 1988).
The bimanual symmetric and asymmetric reaction-time costs deserve further investigation, as these effects have been inconsistent and difficult to detect due to the small sample sizes used in the majority of previous studies on bimanual costs (Maxwell 2004). An examination of bimanual symmetric and bimanual asymmetric costs across simple and choice reaction-time tasks *within a single study* and with sufficient power is needed if we want to isolate the processes of movement preparation where bimanual reaches produce interference.

Our logic for isolating these processes in the current study was the following. Simple RT reflects the time required to recognise the imperative stimulus and initiate a response, assuming that participants fully program their movements prior to the imperative stimulus (Figure 2.1). Furthermore, stimulus recognition is unlikely to be longer for bimanual tasks (which involve two visual onsets and therefore, more stimulus energy) than for unimanual ones. Therefore, if we find bimanual costs in simple reaction-time tasks, then it is probably the result of increased processing during response initiation. Choice RT, on the other hand, reflects the time required to recognise the imperative stimulus, discriminate the targets, select an appropriate response, program that response, and initiate the response (Figure 2.1). With direct targets, we eliminate or attenuate the effects of response selection (Diedrichsen et al. 2001; Goodman and Kelso 1980). Furthermore, we can reasonably assume that imperative stimulus recognition and response initiation demands are equivalent between simple and choice reaction-time tasks. Therefore, if there is a bimanual cost in choice RT, but not in simple reaction-time tasks, then it is probably the result of target discrimination, response programming, or both processes.
2.2 Method

2.2.1 Participants

Twenty participants were tested from the university community (mean age of 25.1 years, 8 females). All participants reported being right-handed and had normal or corrected-to-normal vision. The research ethics board at the University of British Columbia approved the study, and participants gave written informed consent before participation.

2.2.2 Apparatus

Participants were seated at a table in a dimly lit room (Figure 2.2), and each participant rested their head in a chin rest. Virtual stimuli were projected on the surface of the table by an LCD monitor positioned over the table. Midway between the table and the monitor was a half-silvered mirror; it created the illusion that the stimuli appeared on the table. Participants were seated so that their mid-sagittal plane was in the middle of a three-row by two-column array of circle outlines displayed on the table. The circles
in the closest row were the two home positions, and they had a radius of 3.4 mm. The remaining four circles were the short- and long-distance targets for the left and right arms. Each target had a radius of 15.3 mm, and the short and long targets were 100 and 200 mm from the home positions. The distance between the two columns of targets was 150 mm. A fixation cross was displayed in the middle of the four targets. Filling any of the circle outlines cued that target; this is subsequently referred to as illuminating a target (Figure 2.2a). A light was always on under the mirror so that the participants could see their arms and the hand-held styli that they moved to the targets without obstructing the stimuli.

Figure 2.2 Apparatus and display. Participants reached to target positions on the table surface beneath the mirror. The mirror set-up allowed for the unobstructed presentation of visual stimuli. A light was always on under the mirror so that the participants’ arms and the hand-held styli were visible during the entire experiment. a The stimuli and the imperative stimuli seen by the participants on bimanual asymmetric Long–Short trials. Reprinted with permission from Springer Science+Business Media

2.2.3 Procedure

Bimanual trials began with the outlines of the four potential targets and the two home positions appearing on the surface of the table. The home positions were illuminated as a cue for the participants to press the tips of the hand-held styli in them. Participants could see their arms, the styli, and two small circles that were displayed on the table surface to represent the locations of tips of the styli in real time. Once the styli were in the home positions, the real-time feedback disappeared and the 1–2 s variable foreperiod began. A fixation cross appeared between the four targets, and participants
were instructed to fixate on it until after they reached for the targets. In simple reaction-time blocks, the outlines of the correct targets would change colour (from blue to yellow) during the foreperiod to encourage movement preparation before the imperative stimulus. The eight different types of unimanual and bimanual movements were tested in eight, separate simple reaction-time blocks.

Two targets, one for each arm, were illuminated (by filling the circle in with blue) as the imperative stimuli. Participants were instructed to “hit the targets as fast as possible”. At the end of the bimanual movement (the tips of the styli were pressed down on the surface), the fixation disappeared and the endpoint of each movement was displayed. Each endpoint and the correct target were displayed in green for a target hit and red for a target miss. Participants were encouraged to use this feedback to help them with subsequent trials. The trial was then labelled as “good” or “bad”. Bad trials were recycled to the end of the block. Examples of bad trials were target misses, anticipation (RT <100 ms), distraction (RT or movement time >1,000 ms), and asynchronous movement initiation (>60 ms RT difference between the pens). If it was a bad trial, then a message explained the problem, but the participants were not told that these trials were recycled. In total, 4.5% of all the trials were recycled. Every trial ended with a blank screen, and then the next trial would begin when the participants lifted the styli.

Unimanual blocks were similar except that only one home position was illuminated and the imperative stimulus consisted of illuminating one target. The participants held only the required stylus for each unimanual block.

2.2.4 Design

The experiment consisted of testing unimanual, bimanual symmetric, and bimanual asymmetric movements in simple and 2-choice reaction-time conditions. Each combination of these conditions was tested in a separate block, which resulted in 12 blocks (Table 2.1). The order of these blocks was counterbalanced first by the type of RT (simple or 2-choice) and then by the type of movement (unimanual or bimanual).
The order of the blocks that fell within this counterbalance was randomised; for example, the order of the four unimanual simple blocks (left long, right long, right short, right long) was randomised.

A block consisted of a practice phase and a test phase. In simple RT, there were 9 practice trials (1 was a catch trial with no imperative stimulus) and 36 test trials (4 were catch trials). The number of trials was doubled in 2-choice RT (18 practice, 72 test trials). There were two potential movements in 2-choice blocks, so half of the trials were one type of movement. The order of these movements was randomised in each block, and the same randomisation was used for each participant.

Two important considerations for choice conditions are the number and kind of movement choices. It is important to have the same number of choices in unimanual and bimanual conditions as the number of choices can influence RT (Hick 1952; Hyman 1953; cf. Favilla 1996; Wright et al. 2007). However, there may be an unequal number of choices when comparing unimanual movements in 4-choice to bimanual symmetric and asymmetric movements in 4-choice. Unimanual 4-choice requires the participant to select the arm that will move (left or right) as well as the distance of the movement (long or short). The arms do not need to be selected in bimanual 4-choice because both arms are required on all trials. In other words, unimanual 4-choice requires one arm to be selected after the imperative stimulus, whereas both arms can be selected before the imperative stimulus in bimanual 4-choice. This difference could lengthen RTs in unimanual 4-choice and eliminate a potential bimanual symmetric cost. Our solution was to test unimanual and bimanual movements in 2-choice blocks (unimanual left, unimanual right, bimanual symmetric, bimanual asymmetric). This ensured that the arm (unimanual blocks) or arms (bimanual blocks) could be selected before the imperative stimulus in all blocks.

As for the kind of movement choice, if both symmetric and asymmetric bimanual movements are tested in one 4-choice block, then participants may strategically prepare for the harder, asymmetric movements. That is, participants might always prepare asymmetric movements in order to decrease the potential RT difference between movement types. Strategically preparing for the worst-case scenario has been shown
when movements are made with or without visual feedback (cf. Elliott and Allard 1985; Zelaznik et al. 1983). We did not alter visual feedback in the current study, but the principle of preparing for the worst-case scenario may still apply. Therefore, we tested symmetric and asymmetric movements in separate 2-choice blocks.

**Table 2.1** Movements performed in each of the 12 blocks in the experiment. Reprinted with permission from Springer Science+Business Media

<table>
<thead>
<tr>
<th>Unimanual</th>
<th>Bimanual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simple</td>
<td>2-Choice</td>
</tr>
<tr>
<td>Long–</td>
<td>Long–</td>
</tr>
<tr>
<td>Short–</td>
<td>Short–</td>
</tr>
<tr>
<td>–Long</td>
<td>–Long</td>
</tr>
<tr>
<td>–Long</td>
<td>–Short</td>
</tr>
</tbody>
</table>

The target for the left arm is indicated before the hyphen and the right arm’s target is indicated after the hyphen. Short–Long, for example, cues a short-distance movement with the left arm and a long-distance movement with the right arm.

### 2.2.5 Data acquisition and analysis

A microswitch in each stylus was sampled at 250 Hz to determine when the stylus tip was pressed against the table and when it was lifted. The signal from the microswitch was used to calculate RT (time from the imperative stimulus to stylus lift).

Mean RTs for each participant were calculated for each arm, distance, and movement type in the twelve blocks. These were then collapsed into three movement types (unimanual, bimanual symmetric, bimanual asymmetric) for the two reaction-time conditions (simple, choice). The bimanual symmetric and asymmetric costs were investigated by statistical analysis on RTs in simple and choice conditions with a 3 movement type (unimanual, bimanual symmetric, and bimanual asymmetric) repeated-measures ANOVA. When local sphericity was violated (as indicated by Mauchly’s test, \( p < .10 \)), the Huynh–Feldt correction was used when the \( \epsilon \) was greater than or equal to .75 and the Greenhouse–Geisser correction was used otherwise. The uncorrected degrees
of freedom and the $\varepsilon$ values were reported (Huynh–Feldt $\varepsilon_{HF}$, Greenhouse–Geisser $\varepsilon_{GG}$). When the effect of movement type was significant, two a priori comparisons were performed: unimanual movements were compared to bimanual symmetric movements and symmetric movements were compared to asymmetric movements. The Sidak correction was used to control the familywise error rate.

The analyses on RTs were also performed on the probabilities of target misses. Probabilities were normalised with the arcsine square-root transformation before statistical analysis; the data reported are percentages. Between-arm movement time and amplitude correlations were calculated for the four types of bimanual movements (Long–Long, Short–Short, Long–Short, and Short–Long). These correlations were transformed with Fisher’s $r$ to $z$ transformation before analysis with movement type (Long–Long, Short–Short, Long–Short, and Short–Long) repeated-measures ANOVAs. Simple and choice conditions were analysed with separate ANOVAs. The data reported are $r$ values.

There may be a bias when comparing the mean choice RT of bimanual asymmetric movements to symmetric movements. Choice RTs are influenced by the duration of the movement, with long duration movements resulting in longer RTs than short duration movements (Klapp 1995, 2003). As Long–Long movements have longer movement times than Short–Short movements, we predicted that Long–Long movements would also have longer RTs. For asymmetric movements, temporal assimilation occurs that results in movement times for the long- and short-distance movements that are similar to Long–Long movements (Kelso et al. 1979b). If we consider only the influence of movement times on RTs, then Long–Long, Long–Short, and Short–Long movements should have comparable RTs that are longer than Short–Short movements. These differences could result in a bimanual asymmetric cost, as Short–Short movements have shorter RTs than the other movements. We, therefore, compared the RTs of only Long–Long movements to asymmetric movements with a repeated measures $t$ test. This isolated the asymmetric costs that are the result of greater processing demands for asymmetric movements compared to symmetric
movements (and not the result of the influence of movement duration on RTs). Values are reported as the mean ± standard error.

2.3 Results

RTs in simple and choice conditions for unimanual, bimanual symmetric, and asymmetric movements are shown in Figure 2.3. One obvious difference is that RTs were visually longer in 2-choice (287 ± 7.0 ms) than simple conditions (258 ± 6.1 ms). Movement times are shown in Figure 2.4; these data were collapsed across choice (simple, 2-choice) and the unimanual data were also collapsed across arm (left, right). The movement times of unimanual long (311 ± 11.4 ms) and bimanual Long–Long movements (334 ± 12.9, 328 ± 12.3 ms) were visually longer than unimanual short (234 ± 9.0) and bimanual Short–Short movements (260 ± 10.7, 252 ± 10.2 ms). Asymmetric Long–Short (331 ± 12.8, 306 ± 12.1 ms) and Short-Long movements (309 ± 12.4, 319 ± 11.7 ms) had movement times that were more like bimanual Long–Long movements than Short–Short movements. This last result was indicative of temporal assimilation for asymmetric movements.

Figure 2.3 Mean RTs (±SE) for unimanual, bimanual symmetric, and bimanual asymmetric movements in simple and 2-choice conditions. *p < .01. Reprinted with permission from Springer Science+Business Media
2.3.1 No costs in simple RT

In simple RT, the effect of movement type was not significant, $F(2, 38) = 2.4, p = .11$. Thus, RTs were not significantly different between unimanual (261 ± 6.0 ms), bimanual symmetric (254 ± 6.7 ms), and asymmetric movements (259 ± 6.3 ms; Figure 2.3). These results suggested that there was neither bimanual symmetric costs nor bimanual asymmetric costs in simple reaction-time tasks.

2.3.2 Bimanual asymmetric costs in choice RT

In 2-choice RT, there was a tendency for RTs to increase from unimanual (276 ± 8.1 ms), to bimanual symmetric (284 ± 6.5 ms), to asymmetric movements (300 ± 8.1 ms; Figure 2.3). Statistical analysis showed that the effect of movement type was significant, $F(2, 38) = 11.0, p < .001$. The a priori comparisons showed that RTs were not significantly different between unimanual and bimanual symmetric movements ($p = .21$), which suggest that there were no bimanual symmetric costs. There was support for asymmetric costs, as asymmetric movements had significantly longer RTs compared to symmetric movements ($p < .01$). We controlled for the influence of movement duration on the asymmetric cost in choice conditions by comparing only Long–Long
movements to asymmetric movements and found that asymmetric movements (300 ± 8.1 ms) had longer RTs than Long–Long movements (289 ± 6.6 ms), $t(19) = 2.4$, $p = .03$.

### 2.3.3 Target misses, movement amplitudes, and between-arm correlations

Statistical analysis on target misses revealed that they were not significantly different for unimanual, symmetric, and asymmetric movements in simple and choice conditions ($ps > .23$; Table 2.2). This supported that the RTs were not influenced by a speed-accuracy trade-off.

Movement amplitudes were relatively consistent in all conditions; long amplitudes ranged from 200.2 ± 0.40 to 202.0 ± 0.43 mm and short amplitudes ranged from 97.1 ± 0.38 to 99.8 ± 0.41 mm. The amplitudes showed no trend towards amplitude assimilation, which is more often seen when fast reversal movements are made without emphasis on accuracy.

Between-arm movement time and amplitude correlations were also examined (Table 2.3). These correlations were larger for movement times compared to amplitudes. The movement time correlations were not significantly different for any of the bimanual movements in simple or choice conditions ($ps > .26$). Amplitude correlations in simple and choice conditions showed the typical result that symmetric movements (Long–Long, Short–Short) had larger correlations than asymmetric movements (Long–Short, Short–Long).

<table>
<thead>
<tr>
<th>Table 2.2</th>
<th>Mean target misses ± SE (%)</th>
<th>Simple</th>
<th>2-Choice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unimanual</td>
<td>2.6 ± 1.1</td>
<td>2.6 ± 0.7</td>
<td></td>
</tr>
<tr>
<td>Bimanual symmetric</td>
<td>1.8 ± 0.6</td>
<td>2.0 ± 0.4</td>
<td></td>
</tr>
<tr>
<td>Bimanual asymmetric</td>
<td>2.1 ± 0.6</td>
<td>1.9 ± 0.3</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.3 Mean between-arm movement time and amplitude correlations ± SE (r). Reprinted with permission from Springer Science+Business Media

<table>
<thead>
<tr>
<th>Symmetric</th>
<th>Movement time</th>
<th>Amplitude</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Simple</td>
<td>2-Choice</td>
<td>Simple</td>
<td>2-Choice</td>
</tr>
<tr>
<td>Long–Long</td>
<td>.67 ± .05</td>
<td>.76 ± .04</td>
<td>.47 ± .03</td>
<td>.43 ± .04</td>
</tr>
<tr>
<td>Short–Short</td>
<td>.70 ± .03</td>
<td>.73 ± .03</td>
<td>.37 ± .04</td>
<td>.49 ± .03</td>
</tr>
<tr>
<td>Asymmetric</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Long–Short</td>
<td>.72 ± .04</td>
<td>.70 ± .04</td>
<td>.20 ± .04</td>
<td>.15 ± .05</td>
</tr>
<tr>
<td>Short–Long</td>
<td>.70 ± .03</td>
<td>.70 ± .03</td>
<td>.20 ± .04</td>
<td>.20 ± .04</td>
</tr>
</tbody>
</table>

2.4 Discussion

The goal of this study was to determine the process or processes most likely to be involved in reaction-time costs for directly cued bimanual reaching. The advantage of this experiment, compared to previous experiments, was that bimanual symmetric costs and bimanual asymmetric costs were examined in simple and choice reaction-time tasks within a single study. The simple reaction-time task allowed us to isolate bimanual symmetric and asymmetric costs related to response initiation, and the choice reaction-time task allowed us to isolate bimanual costs related to target discrimination, response selection, and response programming.

In simple RT, there was neither a bimanual symmetric cost nor a bimanual asymmetric cost. This suggests that the total duration of imperative stimulus recognition and response initiation was comparable for unimanual, symmetric, and asymmetric movements. The first novel finding of this experiment is, therefore, that the duration of response initiation is comparable for unimanual, bimanual symmetric, and asymmetric movements. In this regard, unimanual movements are as complex as bimanual movements.

In choice RT, there were no bimanual symmetric costs but there were bimanual asymmetric costs. Importantly, there were still bimanual asymmetric costs when we
controlled for the influence of movement duration on RTs. Thus, the asymmetric costs are likely the result of greater processing demands for asymmetric movements compared to symmetric movements. These asymmetric costs suggest a form of bimanual interference. We should, more accurately, refer to this interference as bimanual asymmetric interference, as there were no bimanual symmetric costs.

Why did we find small but significant bimanual asymmetric costs when previous studies (e.g. Diedrichsen et al. 2001; Hazeltine et al. 2003) have suggested that there are no asymmetric costs with direct cues? Diedrichsen et al. (2001) found large bimanual asymmetric costs (~100 ms) with symbolic cues and they did not find asymmetric costs with direct cues. The costs with symbolic cues have been attributed to increased processing demands on response selection in several studies (e.g. Albert et al. 2007; Diedrichsen et al. 2003; Weigelt et al. 2007). Two recent studies found small but significant asymmetric costs with direct cues (Diedrichsen et al. 2006; Heuer and Klein 2006b). They showed that asymmetric costs are attenuated, but not eliminated, with direct cues. Both studies argued that the large and small asymmetric costs reveal two components of interference. The large costs with symbolic cues are mostly caused by increased processing demands on response selection, and the small costs with direct cues are caused by increased processing demands on response programming. Heuer and Klein suggested that the small costs with direct cues escaped discovery in previous studies because of their small effect size. This present study confirms that there are small but significant asymmetric costs with direct cues.

Diedrichsen et al. (2006) and Heuer and Klein (2006b) reasoned that the asymmetric costs with direct cues were caused by increased processing demands on response programming, but this has not been tested. The asymmetric costs could be the result of increased processing demands on any process or processes of movement preparation (imperative stimulus recognition, target discrimination, response selection, response programming, and response initiation). From the present results, we now have evidence that it is unlikely that imperative stimulus recognition and response initiation contributed to the bimanual asymmetric costs. This is supported by a comparable total duration of imperative stimulus recognition and response initiation.
for unimanual, symmetric, and asymmetric movements in simple RT. Therefore, the bimanual asymmetric costs are most likely the result of one or more preparation processes that are unique to choice conditions. These processes are target discrimination, response selection, and response programming.

Discrimination of symmetric targets may take less time than asymmetric targets as symmetric targets can become grouped as a gestalt because of their horizontal alignment and closer proximity than asymmetric targets (Han et al. 1999). However, it has been shown that the perceptual similarity or dissimilarity of the bimanual targets does not affect RT (Albert et al. 2007). Given that perceptually dissimilar targets are unlikely to be grouped as a gestalt, this argues against a role for target discrimination in the bimanual asymmetric cost.

For response selection, symmetric movements involve the selection of the same response for both arms. This is either a long-distance movement (Long–Long) or a short movement (Short–Short). Asymmetric movements involve the selection of a different response for each arm (Long–Short or Short–Long). It has been argued that there is a savings to response selection when selecting identical responses for both arms (Albert et al. 2007; Diedrichsen et al. 2003; Hazeltine et al. 2003). This, however, has been shown when the targets are cued symbolically. An example of a symbolic cue is presenting the word “Long” or “Short” to indicate a long- or short-distance target. Symbolic cues result in greater processing demands on response selection compared to the direct, direct cues used in this experiment (Diedrichsen et al. 2001). It has been shown that preparation costs with symbolically cued movements are either eliminated or attenuated with direct cues (Diedrichsen et al. 2001; Goodman and Kelso 1980). As we used direct cues that place minimal demands on response selection, it is unlikely that response selection results in the bimanual asymmetric cost observed in this experiment.

It has been suggested that there is a savings to response programming when programming identical responses for both arms (Spijkers et al. 1997), so response programming of two movements with identical distances (symmetric) may be shorter than two movements with different distances (asymmetric). Stelmach et al. (1988) and
Heuer and Klein (2006b) also argued that the asymmetric cost was the result of interference during response programming. Stelmach et al. (1988) reasoned that the programming of asymmetric movements are more complex than symmetric movements, as asymmetric movements require the programming of two different amplitudes and symmetric movements require the programming of the same amplitude twice. Heuer and Klein (2006b) argued that concurrently programming two different amplitudes resulted in the asymmetric cost, a process they referred to as “transient parametric coupling during amplitude specification” (pp. 238; cf. Heuer 1986). Therefore, the bimanual asymmetric cost that we observed is most likely the result of increased processing demands on response programming.

The increased processing demands on response programming are related to the movement parameters for asymmetric movements compared to symmetric movements. Compared to symmetric movements, the asymmetric movements used in this study had asymmetric movement amplitudes and asymmetric target locations. Thus, asymmetric amplitudes, asymmetric targets, or both could have caused the asymmetric cost. Two studies have attempted to determine the contributions of various asymmetric movement parameters to the bimanual asymmetric cost (Heuer and Klein 2006a; Weigelt 2007). The issue with these studies is that the changes in RTs with symmetric and asymmetric parameters were confounded by other changes that influenced RTs. In the study by Heuer and Klein, the number of movement choices depended on the starting locations of the movements. This is a problem because RTs can increase with the number of movement choices (Hick 1952; Hyman 1953; cf. Favilla 1996; Wright et al. 2007). In the study by Weigelt, the movements were cued symbolically, so movements with two different symbolic cues had longer RTs than movement with two identical cues. Further studies are required to determine the contribution of various asymmetric movement parameters to the asymmetric cost.

In summary, we observed neither bimanual symmetric costs nor asymmetric costs in simple RTs. We can conclude that unimanual, bimanual symmetric, and bimanual asymmetric movements have comparable complexity for response initiation. There was also no bimanual symmetric costs for choice reaction-time tasks, so
unimanual and bimanual symmetric movements have comparable preparation complexity. We did observe bimanual asymmetric costs in choice RTs, so the preparation of asymmetric movements is more complex than symmetric movements. The bimanual asymmetric costs in the choice task could be the result of increased processing demands on target discrimination, response selection, or response programming. Our results support that the most likely source of the asymmetric costs is response programming. The strength of our study was its use of direct targets and a simple reaction-time task control condition, for they allowed us to examine bimanual reach costs that were independent of response selection and response initiation costs. However, further experiments are needed to confirm that response programming is the source of the asymmetric costs.

2.5 Bridging summary

The remainder of this thesis investigated the bimanual asymmetric costs in choice RT tasks. Studies 3 and 4 (Chapters 4 and 5) investigated which stages of movement preparation (target discrimination, response selection, response programming) contribute to the bimanual asymmetric costs. These results were used to hypothesise which processes cause the bimanual asymmetric costs. But first, study 2 (Chapter 3) investigated how various movement parameters differentiate bimanual movements as either symmetric or asymmetric. Bimanual symmetric movements in study 1 (Chapter 2) had symmetric movement amplitudes and target locations, whereas bimanual asymmetric movements had asymmetric movement amplitudes and target locations. Therefore, asymmetric amplitudes, asymmetric targets, or both could have caused the bimanual asymmetric costs. The contributions to bimanual asymmetric costs from various movement parameters are investigated in the next study.
3 Facilitation and interference during the preparation of bimanual movements: contributions from starting locations, movement amplitudes, and target locations

3.1 Introduction

Coordinated movements with the two arms are important for a plethora of activities of daily living. As common as these movements are, it is difficult to move each arm with different spatio-temporal features; for example, think of how much practice is needed to coordinate your arms while cascade juggling. One approach to studying bimanual coordination has been to test bimanual reaching movements where the arms have the same (symmetric) or different (asymmetric) movement amplitudes [reviewed by Wenderoth and Weigelt (2009)]. Kelso et al. (1979b) compared the movement times of bimanual symmetric movements with short or long movement amplitudes to bimanual asymmetric movements where one arm had a short movement amplitude and the other had a long amplitude. The finding of interest was that during bimanual asymmetric movements the movement time of a short amplitude movement was lengthened to be comparable to the movement time of a long movement. Kelso et al. argued that this temporal assimilation of movement times suggested that bimanual movements are not simply the sum of two unimanual movements; instead, the two arms of a bimanual movement are prepared as a functional unit.

Subsequent studies probed the complexity of movement preparation for bimanual symmetric and asymmetric reaching movements. It was reasonably assumed that more complex movement preparation requires more processing time. Therefore, increased reaction time (RT) was used as an indicator of increased complexity. Spijkers et al. (1997) compared the RTs of bimanual symmetric and asymmetric reversal

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5 A version of Chapter 3 is in press: Blinch J, Cameron BD, Franks IM, Carpenter MG, Chua R (in press) Facilitation and interference during the preparation of bimanual movements: contributions from starting locations, movement amplitudes, and target locations. Psychol Res
movements. The movements were cued symbolically; for example, in the first experiment, the German words for short and long were used to indicate the target movement amplitudes for the left and right arms. They found longer RTs for bimanual asymmetric movements compared to symmetric movements. Spijkers et al. argued that intermanual cross-talk during the response programming of asymmetric amplitudes caused more complex movement preparation for bimanual asymmetric movements.

A potential confound was investigated by Diedrichsen et al. (2001). They reasoned that the bimanual asymmetric costs could be caused by symbolic cues and not bimanual interference during response programming. Asymmetric movements were cued with two different symbolic cues and this may place greater processing demands on response selection compared to two identical cues for symmetric movements. Diedrichsen et al. compared the bimanual asymmetric costs for symbolically and directly cued movements, with the assumption that direct cues place minimal processing demands on response selection. They found large bimanual asymmetric costs with symbolic cues (55 ms, Experiment 1) and non-significant asymmetric costs with direct cues (6 ms, Experiment 1). These results were used to argue that there are large costs to translate two different symbolic cues and that there are no costs to prepare bimanual asymmetric movements.

More recently, several studies have shown that there are small processing costs (typically 10–20 ms) to prepare bimanual asymmetric movement, even when movements are directly cued (Blinch et al. 2014; Diedrichsen et al. 2006; Franz and McCormick 2010; Heuer and Klein 2006b; Stelmach et al. 1988; Weigelt and Cardoso de Oliveira 2003). Collectively, the findings support the position that movement preparation is more complex for bimanual asymmetric movements than symmetric movements. A common feature of these previous studies is that the bimanual symmetric movements had symmetric starting locations, movement amplitudes, and target locations. The bimanual asymmetric movements had the hands starting at symmetric locations but travelling asymmetric amplitudes to asymmetric target locations. This difference in parameters between symmetric and asymmetric movements raises the following question: Do asymmetric movement amplitudes,
asymmetric target locations, or both cause the bimanual asymmetric costs? In this study, we examined three kinds of spatial symmetry in bimanual reaching: starting location symmetry, movement amplitude symmetry, and target location symmetry to assess whether these parameters influence movement preparation. Two studies (Heuer and Klein 2006a; Weigelt 2007) have tried to isolate the independent effects of these parameters.

Heuer and Klein (2006a) investigated the contribution of asymmetric movement amplitudes and target locations to the bimanual asymmetric costs. They tested all possible combinations of bimanual reversal movements with symmetric or asymmetric starting locations, amplitudes, and target locations (Figure 3.1). The order of the various movement combinations was randomized for each block of trials. Although starting locations were manipulated, their contribution to the bimanual asymmetric costs was not analysed. Heuer and Klein concluded that asymmetric amplitudes and asymmetric target locations contributed additively to the asymmetric costs.
The 16 movements tested by Heuer and Klein (2006a). Symmetric and asymmetric starting locations, movement amplitudes, and target locations were tested, but only the effects of amplitudes and target locations on RTs were evaluated. The label above each column indicates the symmetric parameters (lowercase letters) and the asymmetric parameters (uppercase letters). The number at the bottom of each cell indicates the number of movement choices for those starting locations. Adapted from Heuer and Klein (2006a). Reprinted with permission from Springer Science+Business Media

The interaction between amplitudes and target locations could not be fully dissociated because of a confound in the study: the number of movement choices depended on the starting locations. This ranged from 4-choice RT to simple RT. (The number at the bottom of each cell in Figure 3.1 indicates the number of movement choices for those starting locations.) This is a problem because RTs can increase with the number of movement choices (Hick 1952; Hyman 1953; Favilla 1996; Wright et al. 2007).

Weigelt (2007) re-examined the contributions from movement amplitudes and target locations in bimanual reaches, and he also considered the contribution from starting locations. Another advantage to Weigelt’s design was that it included four movement choices in all of the starting locations. As with the previous study, the order of the various movement combinations was randomized for each block of trials. A symbolic cue (the letter A or B) indicated the movement for each arm. The letter A cued the short distance target and B cued the long target. The sixteen bimanual movements were divided into five types of movements based on the symmetry/asymmetry of the movement parameters. The five movement types were:

1. All parameters symmetric (sat)
2. Symmetric movement amplitudes (asymmetric starting and target locations; SaT)
3. Symmetric starting locations (asymmetric amplitudes and target locations; sAT)
4. Symmetric target locations (asymmetric starting locations and amplitudes; SAt)
5. All parameters asymmetric (SAT)

The bimanual asymmetric costs can also be thought of as RT savings for symmetric movements. Potential RT savings were investigated by comparing the RTs of movements with one symmetric parameter (and two asymmetric parameters; SaT, sAT, SAt) to movements with all asymmetric parameters (SAT). These comparisons yielded
three results: (1) RT savings for movements with symmetric target locations [SAt vs. SAT], (2) no RT savings for movements with symmetric amplitudes [SaT vs. SAT], and (3) RT costs for movements with symmetric starting locations [sAT vs. SAT].

The limitation with Weigelt’s, (2007) use of symbolic cues is that RTs are longer when the cues are different for each arm (AB or BA) compared to when they are the same (AA or BB; see Diedrichsen et al. 2001). The types of movements in Weigelt’s, (2007) experiment that had different symbolic cues (SAT, 579 ms; sAT, 600 ms; SaT, 583 ms) had substantially longer RTs than movements with the same cues (SAt, 554 ms; sat, 551 ms). The first comparison was confounded by comparing movements with different symbolic cues to movements with the same cues (SAt vs. SAT). Therefore, it was not surprising that there were RT savings for movements with symmetric target locations (identical symbolic cues) compared to movements with all asymmetric parameters (different symbolic cues). The same symbolic cues, symmetric target locations, or both could have caused these savings.

The goals of this study were to determine which symmetric movement parameters facilitate the preparation of bimanual movements and to compare the size of the facilitation for different parameters. The contributions from starting locations, movement amplitudes, and target locations were considered. We eliminated confounds from previous experiments by equating the number of movement choices in each starting location and by directly illuminating the targets. Movements with one symmetric parameter and two asymmetric parameters were compared to movements with all asymmetric parameters for potential RT savings and to movements with all symmetric parameters for potential RT costs. The effects of the three symmetric and asymmetric parameters on the movement times of bimanual movements were also investigated.
3.2 Method

3.2.1 Participants

Thirty volunteer participants were tested from the university community (mean age of 23.6 years, 13 female). All participants reported being right-handed and had normal or corrected-to-normal vision. The research ethics board at the University of British Columbia approved the study, and participants gave informed written consent before participation.

3.2.2 Apparatus

Participants were seated at a table and their midsagittal plane was aligned with the middle of a button box placed on the table. On the surface of the button box was a four-row by two-column array of square pushbuttons (1.4 by 1.4 cm). The distance from the middle of one row of buttons to the next row was 10 cm and the distance between the two columns was 15 cm. The buttons could be either starting locations or target locations of bimanual reaches. Illuminating an LED inside the button served as a direct cue for the starting and target locations.

3.3.3 Design

The experiment consisted of testing six blocks of bimanual reaches in 2-choice RT conditions (Figure 3.2). The starting locations in each block were held constant, and the left and right arms could be cued to reach for either a short distance (10 cm) or a long distance (20 cm) target. The blocks were also designed to isolate the various parameters of bimanual reaches (starting locations, movement amplitudes, and target locations). There was one block where all parameters of the movements were symmetric (symmetric starting locations, amplitudes, and target locations; Figure 3.2, sat). By symmetric starting and target locations, we are referring to buttons in the same row; symmetric amplitudes imply that both arms reached similar distances (either 10
cm or 20 cm). There were two blocks with symmetric amplitudes and asymmetric starting and target locations (Figure 3.2, SaT), and one block with symmetric starting locations and asymmetric amplitudes and targets (Figure 3.2, sAT). The last two blocks included one movement with symmetric targets and asymmetric starting locations and amplitudes and one movement with all asymmetric parameters (Figure 3.2, SAt and SAT). The order of these blocks was counterbalanced with a balanced Latin square design.

A block consisted of practice trials followed by test trials. The first block had 32 practice trials (16 of each movement choice) and the remaining blocks had 16 practice trials (8 of each movement choice); there were 40 test trials in every block (20 of each movement choice). The order of the movement choices was randomized in each block, and the same randomisation was used for each participant.

### 3.3.4 Procedure

At the start of each block the experimenter covered the unused buttons with black construction paper that matched the surface of the button box. Participants were then shown (with gestures) the starting locations and the target locations for the two

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**Figure 3.2** The twelve movements tested in this study and their symmetric and asymmetric parameters. The six columns represent the six blocks with two movement choices. The label above each movement indicates the symmetric parameters (*lowercase letters*) and the asymmetric parameters (*uppercase letters*). Reprinted with permission from Springer Science+Business Media
potential movement choices in that block. Using gestures instead of words prevented the potential bias of using conceptually unified or separate language to describe the bimanual movements (Franz and McCormick 2010). Trials began with the illumination of the starting locations for the left and right arms. This was the cue for the participants to press and hold these buttons down. Each participant decided at the beginning of the experiment whether they would press the buttons with either their index fingers or their index and middle fingers, based on whichever was more comfortable. This decision was enforced for the entire experiment. When the buttons were depressed, the lights inside the starting locations were turned off and a 1–2 s variable foreperiod began. The imperative stimuli consisted of illuminating the target locations, and participants were instructed to “react and hit the targets as fast as possible.” The target lights were turned off when the target buttons were depressed, and the participants were told to keep the buttons depressed. The starting locations for the next trial were illuminated 2 s after the targets were pressed, at which point the participants could release the target buttons and begin the next trial when ready.

Each trial was labelled as “good” or “bad,” with bad trials being recycled to the end of the block and excluded from subsequent analyses. Types of bad trials were target errors (missing the target button or hitting an incorrect button), anticipation (RT < 100 ms), inattention (RT > 750 or movement time > 500 ms) and asynchronous movement initiation (>60 ms RT difference between the arms). If it was a bad trial, then the experimenter explained the reason to the participants, but participants were not told that these trials were recycled. In total, 0.6 % of all the trials were recycled.

A “speed score” was given to participants after every six good trials. This score gave participants feedback on their total response time (RT + movement time) and was intended to motivate them to react and hit the targets as fast as possible. It was calculated by comparing the mean total response time of the last six good trials to the previous six good trials. The percent change was calculated and multiplied by ten; for example, if the total response time decreased from 300 to 270 ms (a 10 % change), then the speed score would be -100 [-100 = 1,000 * (270/ 300 - 1)]. A multiple of ten was
used to make the small changes in total response time (typically less than 5%) more salient to the participants.

3.3.5 Data acquisition and analysis

The state of each button (open or closed) was sampled with a 12-bit digital input–output card. These states were used to calculate the RT (from imperative stimulus to release of the starting button) and movement time (from release of the starting button to depression of the target button) of the left and right arms. Mean RTs for each participant were calculated for each arm and movement choice in the six blocks. Means were then calculated for the five movement types (sat, SaT, sAT, SAT, SAT), collapsing across hand and movement choice, to isolate the parameters of bimanual reaches. These RTs were analysed with a one-way repeated-measures ANOVA with five levels. If there was a significant difference in RTs for the five movement types, then three sets of post hoc comparisons were performed.

First, potential RT savings were examined by comparing the RTs of movements with one symmetric parameter (SaT, sAT, SAT) to movements with all asymmetric parameters (SAT). Second, the RTs of the movements with one symmetric parameter (SaT, sAT, SAT) were contrasted with three comparisons. This allowed us to make inferences about the size of the relative savings for each symmetric parameter. Third, potential RT costs were examined by comparing the RTs of movements with two asymmetric parameters (SaT, sAT, SAT) to movements with all symmetric parameters (sat). An advantage for evaluating RT savings compared to costs is that a savings can be isolated to the change in one movement parameter; for example, the only difference between the SaT and the SAT movement types is that amplitudes are either asymmetric

6 Statistically, it does not make a difference whether we analyse the RT savings [(SaT, sAT, SAT) - SAT] or the RTs (SaT, sAT, SAT). Subtracting SAT from the RTs to calculate the RT savings affects the participant variance but neither the treatment variance nor the error variance. The results of these analyses are identical because repeated-measures ANOVAs disregard the participant variance. The variances that are used are the treatment and error variances and these are identical in both calculations. Therefore, analysis of the RTs allowed us to make inferences about the relative RT savings.
or symmetric. RT costs are somewhat more complicated because they involve a change in two movement parameters. These three sets of post hoc tests each involved three comparisons, for a total of nine, two-tailed comparisons. The familywise error rate was controlled with the Šidák correction based on nine comparisons.

Mean movement times for each participant were calculated for each arm and movement choice in the six blocks. Means were then calculated for the five movement types (sat, SaT, sAT, SAT) and the two movement amplitudes (long, short), collapsing across hand and movement choice. These movement times were analysed with a five Movement Type (sat, SaT, sAT, SAT) by two Movement Amplitude (long, short) repeated-measures ANOVA. The significant interaction was examined with simple main effects on Movement Type. The familywise error rate was controlled with the Šidák correction.

When local sphericity was violated (as indicated by Mauchly's test, \( p < 0.10 \)), the Huynh–Feldt correction was used when \( \varepsilon \) was greater than or equal to 0.75 and the Greenhouse-Geisser correction was used otherwise (Huynh and Feldt 1976). The uncorrected degrees of freedom and the \( \varepsilon \) values were reported (Huynh–Feldt \( \varepsilon_{HF} \), Greenhouse-Geisser \( \varepsilon_{GG} \)). Reported values are means ± the standard errors.

### 3.3 Results

Mean RTs for the five movement types are shown in ascending order in Figure 3.3. Movements with all symmetric parameters had the shortest mean RTs (sat, 256 ± 3.9 ms) and movements with all asymmetric parameters had the longest RTs (SAT, 275 ± 4.0 ms). The three movement types with one symmetric parameter (and two asymmetric parameters) fell in between these conditions; in ascending order of mean RTs, they were symmetric movement amplitude (SaT, 262 ± 4.1 ms), symmetric starting locations (sAT, 268 ± 3.9 ms), and symmetric target locations (SAt, 269 ± 4.0 ms). Statistical analysis of the RTs for the five types of movements revealed a significant main effect, \( F(4, 116) = 14, p < 0.001, \varepsilon_{HF} = 0.86 \).


3.3.1 Facilitation for symmetric amplitudes or symmetric target locations

Post hoc comparisons were used to analyse the potential RT savings for movements with one symmetric parameter (and two asymmetric parameters) compared to movements with all asymmetric parameters. There were significant RT savings for movements with symmetric amplitudes (SaT, -13.0 ± 2.8 ms, p < 0.001) and for movements with symmetric target locations (SAt, -5.9 ± 1.8 ms, p = 0.021). There were no significant RT savings for movements with symmetric starting locations (sAT, -7.5 ± 2.9 ms, p = 0.143). These results suggested that movement preparation was facilitated when movement amplitudes or target locations were symmetric.
3.3.2 Relative savings for symmetric starting locations, amplitudes, and target locations

RTs of the three movements with one symmetric parameter were not significantly different from each other. RTs for movements with symmetric amplitudes were comparable to RTs for movements with symmetric starting locations, \( p = 0.364 \). RTs for movements with symmetric starting locations were comparable to RTs for symmetric target locations, \( p = 1.000 \), and RTs for symmetric amplitudes were comparable to RTs for symmetric target locations, \( p = 0.106 \). These results, in isolation, suggested that the relative size of facilitation during movement preparation did not differ for symmetric starting locations, amplitudes, or target locations. However, this must be integrated with the results of the RT savings and costs to appreciate the contributions from each parameter.

3.3.3 Interference for movements with asymmetric amplitudes

There were significant costs for movements with asymmetric amplitudes and target locations (sAT, 11.8 ± 3.5 ms; \( p = 0.019 \)) and for movements with asymmetric starting locations and amplitudes (SA, 13.3 ± 2.5 ms; \( p < 0.001 \)). The one common parameter for these two types of movements was asymmetric amplitudes, so movement amplitude may be the most important parameter for RT costs. In fact, there were no significant RT costs for movements with symmetric amplitudes even when the starting and target locations were asymmetric (SaT, 6.3 ± 2.5 ms, \( p = 0.176 \)). These results suggested that movement preparation suffers interference when movement amplitudes are asymmetric.

3.3.4 Movement amplitudes determined movement times

Mean movement times for all movements are shown in Figure 3.4. One visible difference was that movements with long amplitudes had longer movement times than movements with short amplitudes. This occurred for movements with symmetric...
amplitudes (Long–Long vs. Short–Short) and to a lesser degree for movements with asymmetric amplitudes (Long movements in Long-Short and Short-Long vs. Short movements in Long-Short and Short-Long). These differences were statistically confirmed with a significant main effect of Movement Amplitude, $F(1,29) = 386, p < 0.001$, that showed that long amplitude movements had longer movement times ($155 \pm 6.5$ ms) than short amplitude movements ($120 \pm 5.9$ ms).

![Figure 3.4 Mean movement times (± the standard errors) for each movement type and amplitude. Reprinted with permission from Springer Science+Business Media](image)

There was also a significant main effect of Movement Type, $F(4,116) = 16, p < 0.001, \varepsilon_{HF} = 0.81$, and a significant Movement Type by Movement Amplitude interaction, $F(4,116) = 22, p < 0.001, \varepsilon_{GG} = 0.56$. The interaction was analysed with simple main effects on Movement Type (Figure 3.5). Long ($149 \pm 6.3$ ms) and short ($106 \pm 5.0$ ms) amplitude movements with all symmetric parameters were the baseline movement times for comparisons to the four conditions with asymmetric parameters (SaT, sAT, SaT, SAT).
First, we compared the movement times of long amplitude movements. Movements with symmetric amplitudes and movements with symmetric starting locations had long amplitude movement times (156 ± 7.3, 155 ± 6.4 ms) that were comparable to movements with all symmetric parameters, $p = 0.306$, $p = 0.341$. Long amplitude movement times of movements with symmetric target locations (157 ± 6.4 ms) and movements with all asymmetric parameters (160 ± 7.3 ms) were significantly longer than movements with all symmetric parameters, $p = 0.030$, $p = 0.028$, but they were comparable to movements with symmetric amplitudes and movements with symmetric starting locations, $ps > 0.617$.

Next, we compared the movement times of short amplitude movements. Movements with symmetric amplitudes had short amplitude movement times (109 ± 5.3 ms) that were comparable to movements with all symmetric parameters, $p = 0.620$. Short amplitude movement times of movements with symmetric starting locations (126 ± 6.7 ms), symmetric target locations (125 ± 6.4 ms), and all parameters asymmetric (133 ± 7.6 ms) were significantly longer than movements with all parameters symmetric and movements with symmetric amplitudes, $ps < 0.001$. In other words, when paired with long amplitude movements, short amplitude movements showed the typical pattern of partial temporal assimilation to the long amplitude movement times.
Overall, these results suggested that the movement times were determined by the movement amplitudes and not by the symmetry/asymmetry of the starting or target locations.

3.4 Discussion

The goals of this study were to determine which symmetric movement parameters facilitate the preparation of bimanual movements and to compare the size of the facilitation for different parameters. There were significant RT savings for movements with symmetric amplitudes and movements with symmetric target locations compared to movements with all asymmetric parameters. This pattern of savings suggests that movement preparation is facilitated when movement amplitudes or target locations are symmetric. The analyses of RT costs showed significant costs for all movements with asymmetric amplitudes compared to movements with all symmetric parameters. These costs suggest that movement preparation suffers interference when movement amplitudes are asymmetric.

How do these results compare to those from previous studies? Heuer and Klein (2006a) could not fully analyse the interaction between movement amplitudes and target locations due to a confound in the number of movement choices. However, they did compare conditions with a balanced number of movement choices in an attempt to partially separate the effects of amplitudes and target locations. In one of these comparisons, they found significantly longer RTs for a group of movements that included movements with all asymmetric parameters (SAT) and movements with asymmetric amplitudes and target locations (sAT) compared to movements with all symmetric parameters (sat). Movements with all asymmetric parameters were tested in simple reaction conditions, movements with asymmetric amplitudes and target locations were tested in 4-choice RT conditions, and movements with all symmetric parameters were tested in either simple or 4-choice conditions. We have previously shown comparable RTs for all bimanual movements in simple RT conditions, regardless of the symmetry or asymmetry of the movement parameters (Blinch et al. 2014).
Therefore, the significant difference found by Heuer and Klein (2006a) was likely caused by RT differences in the 4-choice conditions. If we omit movements in simple RT conditions from the comparison by Heuer and Klein, then their result becomes longer RTs for movements with asymmetric amplitudes and target locations than movements with all symmetric parameters. In other words, our interpretation of Heuer and Klein’s result is RT costs for movements with asymmetric amplitudes and target locations. The present study also found RT costs for the same movements. Therefore, both studies suggest that movement preparation suffers interference when movement amplitudes and target locations are asymmetric.

The results by Weigelt (2007) can also be compared to our results, as both studies compared movements with one symmetric parameter to movements with all asymmetric parameters (RT savings). A common finding was RT savings for movements with symmetric target locations (SAT). This comparison in Weigelt’s study was confounded by the use of same or different symbolic cues, as RTs are shorter when two of the same symbolic cues are used compared to two different cues (Diedrichsen et al. 2001). Movements with symmetric targets had two of the same symbolic cues and movements with all asymmetric parameters had two different cues. Thus, it is not surprising that movements with symmetric targets (two identical symbolic cues) had RTs that were 25 ms shorter than movements with all asymmetric parameters (two different symbolic cues). This confound was eliminated in our study using direct cues. The RT savings for symmetric targets were much smaller in this study (-5.9 ± 1.8 ms) than in Weigelt’s study, suggesting that the cost to translate two different symbolic cues produced most of the difference between movement with symmetric targets and movements with all asymmetric parameters. However, the small but significant RT savings for symmetric targets that we found in the present study suggest that the spatial alignment of the targets does matter. A small savings for symmetric targets and a large savings for two identical symbolic cues likely caused the larger savings in Weigelt’s study.

Weigelt (2007) also compared movements with symmetric amplitudes (SaT) and movements with symmetric starting locations (sAT) to movements with all asymmetric
parameters (SAT). These comparisons were not confounded by the use of identical or different symbolic cues because all these movements had two different symbolic cues. For movements with symmetric amplitudes, Weigelt found a non-significant difference in RTs, while we found significant savings. The presence of this significant effect in our study, but not in Weigelt’s study, may be due to increased statistical power afforded by our study’s larger sample size (30 participants vs. 10). Another explanation is that symbolic cues cause longer RTs than direct cues (Diedrichsen et al. 2001), and small differences in RTs between conditions could be masked by longer RTs.

In contrast to our present results, Weigelt, (2007) found unexpected RT costs for movements with symmetric starting locations. He argued that the same starting locations might facilitate assimilation between the arms and increase interference during preparation. The present study found non-significant RT savings, and not costs, for movements with symmetric starting locations.

In a recent study (Blinch et al. 2014), we used the subtraction method (Donders 1969) to isolate the costs for movements with symmetric starting locations and asymmetric amplitudes and target locations (sAT) to processes that are unique to choice RT. These processes include target discrimination, response selection, and response programming, and evidence from that study favoured response programming as the source of the interference during movement preparation. If we assume that bimanual interference occurs primarily during response programming, then the interference may be caused by concurrently programming two unimanual movements with asymmetric parameters (a bimanual asymmetric movement). In support of this hypothesis for interference during concurrent programming, we found that RT costs were eliminated when programming of the two arms was temporally separated (Blinch et al. under review).

Our previous studies (Blinch et al. 2014, under review) suggest that RT costs for directly cued asymmetric bimanual movements are caused by interference during response programming. So what do the current results suggest about the response programming of bimanual movements? The RT savings suggest that response programming considers the movement amplitudes and target locations. Movement
preparation was facilitated when either amplitudes or target locations were symmetric. Starting locations, in contrast, did not consistently facilitate movement preparation. Starting locations may have had minimal impact on movement preparation because they were always known in advance of the imperative stimulus and could potentially be accounted for ahead of the upcoming movement. We have previously shown that the RT savings for bimanual movements with symmetric amplitudes and target locations are eliminated when those movement parameters are known in advance (i.e. in simple RT conditions; Blinch et al. 2014). In the present study, knowing the starting locations before the imperative stimuli may have reduced or eliminated any RT savings for symmetric starting locations.

From our results, we can also examine whether the RT savings for movement amplitudes, starting locations, and target locations are additive. Recall that the RT savings were -13.0 ± 2.8 ms for symmetric amplitudes, -7.5 ± 2.9 for symmetric starting locations, and -5.9 ± 1.8 ms for symmetric target locations. Adding these savings together gives a summed RT savings of -26.4 ± 6.0 ms. In comparison, the RT savings for movements with all symmetric parameters compared to movements with all asymmetric parameters (sat–SAT) were -19.2 ± 2.8 ms, which was not significantly different from the summed savings, t(29) = 1.4, p = 0.164, Cohen’s d = 0.28 (calculated with the pooled standard deviation). As the individual savings for amplitudes and targets summed to be similar to the savings for all symmetric parameters, the individual savings may be additive. The additivity of these savings suggests that the savings for symmetric movement amplitudes and target locations occur during separate preparation processes (Sternberg 1969).

The RT costs suggest that response programming considers the movement amplitudes, as movement preparation suffered interference with asymmetric amplitudes. This occurred for movements with asymmetric amplitudes and either asymmetric target locations or asymmetric starting locations (sAT or SAt). When the amplitudes were symmetric, the RT costs were not significant even when starting and target locations were asymmetric (SaT). Movement amplitude is also the primary determinant of the duration of movement execution; specifically, movement times were
determined by the movement amplitudes and not by the symmetry/asymmetry of the starting or target locations.

Taken together, the RT costs and RT savings analyses suggest that movement amplitudes and target locations appear to be more important parameters for movement preparation than starting locations. It is interesting that many of the studies that have shown facilitation for bimanual symmetric movements (sat) compared to bimanual asymmetric movements (sAT) had symmetric starting locations for both types of movements (Blinch et al. 2014; Diedrichsen et al. 2006; Heuer and Klein 2006b; Stelmach et al. 1988; Weigelt and Cardoso de Oliveira 2003). These studies manipulated what we now believe are the more important parameters: movement amplitudes and target locations.

Previous research has argued that response programming of bimanual movements is facilitated when movement amplitudes are symmetric (Heuer 1986; Stelmach et al. 1988). When movement amplitudes are asymmetric there may be cross-talk between concurrent processes of amplitude specification that causes transient interference (Heuer et al. 1998). This cross-talk is overcome and asymmetric amplitudes are specified at the cost of increased processing demands on response programming. It is possible that the contribution of target locations to response programming is similar to the contribution from movement amplitudes. When the target locations are symmetric, the same location can be coded for both arms and response programming is facilitated. When the target locations are asymmetric, there may be cross-talk between concurrent processes of target location specification (Heuer 1993).

A fascinating aspect of the costs for bimanual asymmetric movements is that they can be affected by how the task is conceptualised by the participants [reviewed by Swinnen and Wenderoth (2004)]. Various forms of bimanual interference have been reduced, or even eliminated, when a difficult bimanual movement is conceptualised as a single unified movement. Examples of unified bimanual movements that decrease interference are when a single goal is shared by the two arms (Franz et al. 2001), when
a single stimulus represents that position of both arms (Kovacs et al. 2009; Swinnen et al. 1997), or both (White and Diedrichsen 2010).

It was recently shown that the costs for bimanual reaching movements with asymmetric movement amplitudes and target locations, movements that were similar to the present experiment, were eliminated by two manipulations that encourage bimanual unification (Franz and McCormick 2010). The first manipulation was a change to the target stimuli; connecting the two, circular targets with a line (resembling a dumbbell) virtually abolished the RT costs for bimanual asymmetric movements. RT costs were also abolished when the instructions before each trial were changed from encouraging separate representations of each arm (move one hand and move the other hand to their respective targets) to a unified representation (move both hands to their respective targets). In the present experiment, the bimanual movements were likely conceptualised as two separate unimanual movements as the targets were visually disconnected and the instructions did not use unified language (the targets were illustrated during the instructions by gesturing). Our results of bimanual interference for asymmetric movement amplitude or target locations remain valid, but it is important to appreciate that the magnitude of any form of bimanual interference will likely depend on how the task is conceptualised.

In summary, we investigated the influence of movement amplitudes, target locations, and starting locations on the preparation of bimanual reaching movements. Our findings suggest that movement preparation, or more specifically, response programming, is facilitated when movement amplitudes or target locations are symmetric. Conversely, response programming suffers interference when the movement amplitudes are asymmetric. The relative importance of these parameters to response programming, from most to least important, is movement amplitudes, target locations, and then starting locations. Interference with asymmetric amplitudes or target locations may be caused by cross-talk between concurrent processes of parameter specification. There are, of course, other parameters we did not investigate that may also have an impact on movement preparation, such as movement direction (Heuer 2006; Heuer and Klein 2006c). Future experiment could investigate these
parameters and determine where they fit in the apparent hierarchy of parameters that influence the programming of bimanual movements.

3.5 Bridging summary

An extension to this study would be to compare the relative contributions of movement directions and movement amplitudes to bimanual asymmetric costs. These studies are ongoing and they are described in section 6.6, Future directions. Studies 3 and 4 (Chapters 4 and 5) investigated the stages of movement preparation – and the processes within these stages – that cause bimanual asymmetric costs. The next study tested the demands on the movement preparation of bimanual movements by temporally separating the preparation of each arm. This was achieved by precuing the target of one arm before the imperative stimulus. RTs and the start-react effect were used to determine what was prepared in advance when one target was precued. This offered insight into the stages and processes that cause bimanual asymmetric costs.
4 Unified nature of bimanual movements revealed by separating the preparation of each arm

4.1 Introduction

It can be challenging to coordinate our two arms, especially when each arm requires different timing or spatial paths. Swinnen and Wenderoth (2004) aptly summarised this challenge as “two hands, one brain,” in their review on bimanual coordination research. We recently compared the movement preparation of asymmetric bimanual reaching movements with different target amplitudes to symmetric bimanual reaching movements with the same amplitudes (Blinch et al. 2014). An important distinction was that illuminating the targets cued these movements. These types of cues are referred to as direct or spatial cues and they decrease processing demands on movement preparation compared to symbolic cues (reviewed by Wenderoth and Weigelt 2009). Movement preparation occurs after the imperative stimulus in choice reaction-time (RT) conditions and its duration is reflected in the RT (Donders 1969; Klapp and Jagacinski 2011; Sternberg 1969). The movement preparation processes include imperative stimulus recognition, target discrimination, response selection, response programming, and response initiation. Substantial movement preparation can occur before the imperative stimulus in simple RT conditions. This advanced preparation occurs before the imperative stimulus and causes a reduction in RT. The preparation after the imperative stimulus, which is measured by RT, includes imperative stimulus recognition and response initiation. The duration of movement preparation was comparable for symmetric and asymmetric movements in simple RT conditions. The lack of cost in simple RT suggested that the duration of imperative stimulus recognition and response initiation is comparable for symmetric and asymmetric movements. In choice RT conditions, the time for movement preparation

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7 A version of Chapter 4 is under review: Blinch J, Franks IM, Carpenter MG, Chua R (under review) Unified nature of bimanual movements revealed by separating the preparation of each arm
preparation of bimanual asymmetric movements was longer than bimanual symmetric movements (Blinch et al. 2014). The asymmetric cost in choice RT is likely caused by increased processing demands on one or more preparation processes unique to choice conditions (Donders 1969). These are target discrimination, response selection, and response programming. We argued that response programming was the most likely source of interference (Blinch et al. 2014), but this requires further investigation.

Preparing two different unimanual movements (i.e. a bimanual asymmetric movement) at the same time, likely causes the bimanual asymmetric cost. Is it possible to prepare each arm of a bimanual movement at different times? This was tested in the present experiment by temporally separating the preparation of each arm by precuing the target of one arm before the imperative stimulus. We asked the following question: what was prepared in advance when one arm was precued? The answer to this question would suggest which process is associated with the bimanual asymmetric cost and offer insight into the preparation of bimanual movements.

Our experimental predictions were related to how movement preparation may change when one target is precued (Figure 4.1). We began with two predictions. The first prediction is that the precued arm is prepared before the imperative stimulus, and the other arm is prepared after the imperative stimulus (Figure 4.1, left). This should eliminate the asymmetric cost, as the two unimanual movements are prepared at different times. As all preparation processes are temporally separated, an elimination is predicted regardless of which process causes the asymmetric cost. It may not, however, be possible to fully separate the preparation of each arm, and this leads to the second prediction (Figure 4.1, right). This may be the case as bimanual movements are not simply the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit (Kelso et al. 1979b; Swinnen and Wenderoth 2004). This could prevent the precued arm from being prepared before the other arm. Both targets must be discriminated and the movements selected before they

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8 As imperative stimulus recognition and response initiation are unlikely to contribute to asymmetric costs in choice RT (Blinch et al. 2014), they have been excluded from subsequent discussion of the processes during movement preparation in choice RT.
can be programmed as a single, bimanual movement. Movement preparation in this prediction is the same as in choice RT conditions. Therefore, the size of the asymmetric cost in choice RT and with one precue should be comparable.

![Figure 4.1](image)

**Figure 4.1** Two possibilities for movement preparation when the left target is precued. The stages of information processing are target discrimination (TD), response selection (RS), and response programming (RP). In the first prediction (left), the precued arm and the other arm are fully prepared at different times as two unimanual movements. In the second (right), a single, bimanual movements is prepared after the imperative stimulus when the targets for both arms have been cued

We also used a unique technique as a second measure of the relative amount of movement preparation that occurred in advance. The “go” tone was occasionally and unpredictably replaced with a loud, startling tone (120 dB). A startle tone can elicit two effects: the startle reflex and the start-react effect. The startle reflex consists of a stereotyped set of bilateral muscle contractions that is described as a generalised flexion response. A reliable indicator of the startle reflex is activation of the sternocleidomastoid (SCM) muscles (Carlsen et al. 2011). The start-react effect consists of the release of a prepared movement with an RT much shorter than control trials (Carlsen et al. 2012; Valls-Solé et al. 1999).

The start-react effect has been explained by the hypothesis that a startling acoustic stimulus increases neural activation of a prepared response, raising it to the threshold to be released (reviewed by Carlsen et al. 2012). The increase in neural activation has distinct effects in simple and choice RT conditions, which allows the start-react effect to probe the relative level of movement preparation. In simple conditions, the required movement is fully prepared before the imperative stimulus. This advance preparation causes a high level of neural activation that is close to the threshold required to release the movement. A startle tone quickly increases this neural
activation the small amount required to reach threshold, thus releasing the prepared movement with a much-reduced RT. It has also been shown that there is a high probability of a startle reflex (as indicated by activation of the SCM) in simple conditions (Maslovat et al. 2012). In choice RT conditions, the exact movement is unknown before the imperative stimulus and it cannot be fully prepared in advance. The result is a low level of neural activation that is far from threshold. A startle tone quickly increases the neural activation, but it takes longer to reach threshold. This delay affords an opportunity to finish movement preparation after the imperative stimulus, which can have two possible outcomes. For the majority of trials, the required response is prepared and initiated. For a minority of trials, movement preparation is disrupted by the loud, startling tone and a movement error is made (Carlsen et al. 2004, 2009; Forgaard et al. 2011; Maslovat et al. 2011). There is also a lower probability of a startle reflex in choice compared to simple conditions (Maslovat et al. 2012).

The predictions for startle trials depend on the possible effects of the precue on movement preparation. If the precued arm is fully prepared before the imperative stimulus and the other arm is prepared after the imperative stimulus (Figure 4.1, left), the effects of the startle tone on the precued movement should be comparable to bimanual movements in simple RT conditions, with shorter RTs and a lower probability of a movement error. At the same time, the movements for the arm without the precue should be comparable to movements in choice conditions with longer RTs and a higher probability of a movement error compared to simple conditions. In other words, we predicted that the bimanual movement would be decomposed into two unimanual movements. Alternatively, if the bimanual movement is prepared after the imperative stimulus, the effects of the startle on the precued movement should be comparable to choice RT conditions, with shorter RTs than control trials but longer RTs than startle trials in simple RT conditions. The two arms are prepared as a single, bimanual movement, and so the arms should be initiated as synchronously on startle trials as control trials. The probability of a startle reflex should be lower than simple and comparable to choice conditions. Finally, the number of movement errors should be higher than in simple and comparable to choice conditions.
4.2 Method

4.2.1 Participants

Twenty-three volunteer participants were tested from the university community. All participants reported being right-handed and had normal or corrected-to-normal vision. Data from only 18 participants (mean age of 24.7 ± 5.1 years, 6 female) were analysed [5 participants lacked the startle reflex in simple RT conditions; see Carlsen et al. (2011) for detection and classification guidelines]. The research ethics board at the University of British Columbia approved the study, and participants gave informed written consent before participation.

4.2.2 Apparatus

Participants were seated at a table in a dark room, and each participant rested their head in a chin rest. On the surface of the table were two linear slides (Low Profile Redi-Rail, PBC Linear) that were perpendicular to the front edge of the table. The linear slides were 150 mm apart, and participants were seated so that their midsagittal plane was in the middle of the slides. Participants held the handles of the left and right slides with their left and right hands. The slides allowed forward and backward movements of the arms with minimal friction and prevented movements in other directions. There was an Optotrak marker at the top of each handle, and these were sampled at 750 Hz by an Optotrak system (3020; Northern Digital).

Virtual stimuli were projected on the surface of the table by an LCD monitor positioned over the table. Midway between the table and the monitor was a half-silvered mirror; it created the illusion that the stimuli appeared on the table. The stimuli created a three-row by two-column array of circle outlines (Figure 4.2), and the two columns were aligned with the linear slides. The circles in the closest row to the participants were the two backward targets, and the two forward targets were the circles in the farthest row; the targets had a radius of 15.3 mm. The circles in the middle
row were the home positions, and they had a radius of 3.4 mm. The distance from the center of the home positions to the center of the forward or backward targets was 100 mm. Filling any of the circle outlines directly cued that target; this is subsequently referred to as illuminating a target.

**Figure 4.2** Visual stimuli at the time of the imperative stimuli in the unilateral 2-choice condition. The left forward target was precued by changing the colour of the outer circle from cyan to yellow. In this example, the left forward target and the right backward target are illuminated as the imperative stimuli.

Testing occurred in a dark room that prevented visual feedback of the participants’ arms and the linear slides. The position of the handle for each slide was displayed on the surface of the table in real-time as a magenta circle with a 1.7 mm radius. There was a 16.7 ms time lag between receiving the current positions of the Optotrak markers and displaying the feedback on the monitor that was determined by the 60 Hz refresh rate of the LCD monitor. To compensate for this lag, the positions of the markers in the next frame were predicted based on the current and previous positions.

Surface electrodes were used to collect electromyography (EMG) data bilaterally from the following three muscles: SCM (startle indicator), anterior deltoid (agonist for forward movements), and posterior deltoid (agonist for backward movements). The muscles on the left and right sides of the body were grounded to the left and right clavicles, respectively. The recording sites were scrubbed and cleansed to reduce
electrical impedance. The EMG data were band-pass filtered between 30 and 1000 Hz, amplified (P511 AC Amplifier, Grass Technologies), sampled at 3000 Hz by an Optotrak Data Acquisition Unit (3020; Northern Digital), and then rectified.

### 4.2.3 Procedure

Trials began with the outlines of the four potential targets and the two home positions appearing on the surface of the table. The home positions were illuminated as a cue for the participants to move the handles into the home positions. Participants could not see their arms or the handles for the entire trial. They could always see two small circles that were displayed on the table surface to represent the positions of the handles in real-time. A 1-2 s variable foreperiod began when the handles were in the home positions. During the foreperiod, a fixation cross appeared between the home positions, and participants were instructed to fixate on it while they awaited the imperative stimuli. In simple RT blocks, the outlines of the correct targets would change colour (from cyan to yellow) during the foreperiod to encourage movement preparation before the imperative stimulus. Preprogramming was also encouraged in the block where only one target was precued. We will refer to this block as the unilateral 2-choice block, and the left, forward target was always precued during the foreperiod. Importantly, the right target was not precued, so participants did not know whether the target for the right arm would be the forward or backward target until the imperative stimuli.

The imperative stimuli consisted of illuminating the targets (by filling the circles in with blue) and sounding a 1000 Hz tone for 40 ms. The tone was 85.7 ± 1.29 dB on practice and control trials and startle trials were 120.2 ± 0.44 dB. Participants were instructed to “react and hit the targets as quickly as possible.” The positions of the handles at the end of the bimanual movement were displayed after the 2.0 s recording interval of the Optotrak. These endpoints and the correct targets were displayed in green for a target hit and red for a target miss. Participants were encouraged to use this feedback to help them with subsequent trials.
Each trial was labeled as “good” or “bad,” with bad trials being excluded from subsequent analyses. The types of bad trials were different for control and startle trials. For control trials, types of bad trials were anticipation (RT < 100 ms), inattention (RT or movement time > 500 ms) and asynchronous movement initiation (> 60 ms RT difference between the arms). For startle trials, the only type of bad trials was anticipation (RT < 50 ms). Movements with asynchronous initiation were included as the precued movement may be released by the startle tone and the other arm initiated later. In total, 1.51% of all control trials and 0.52% of all startle trials were excluded. If it was a bad trial, then a message explained the reason to the participant. Every trial ended with a blank screen for 1 s.

A “speed score” was given to participants after every six good trials. This score gave participants feedback on their total response time (RT + movement time) and was intended to motivate them to react and hit the targets as quickly as possible. It was calculated by comparing the mean total response time of the last six good trials to the previous six good trials. The percent change was calculated and multiplied by ten; for example, if the total response time decreased from 300 ms to 270 ms (a 10% change), then the speed score would be -100 \[-100 = 1000 \times (270/300 - 1)\]. A multiple of ten was used to make the small changes in total response time (typically less than 5%) more salient to the participants.

4.2.4 Design

The experiment consisted of testing bimanual symmetric and asymmetric movements in simple, 2-choice, and unilateral 2-choice RT conditions. There were two simple blocks (Forward-Forward, Forward-Backward), two 2-choice blocks (symmetric, asymmetric), and one unilateral 2-choice block (unilateral 2-choice), for a total of five blocks (Table 4.1). Note that symmetric and asymmetric movements were tested in different blocks in simple and 2-choice conditions, whereas they were tested in the same block in the unilateral 2-choice condition. The order of these blocks was counterbalanced by the type of RT (simple, 2-choice, unilateral 2-choice). The blocks
that fell within this counterbalance were randomised; for example, the order of the two 2-choice blocks (symmetric, asymmetric) was randomised.

<table>
<thead>
<tr>
<th>Simple</th>
<th>2-Choice</th>
<th>Unilateral 2-choice</th>
</tr>
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<tbody>
<tr>
<td>Symmetric</td>
<td>Forward-Forward</td>
<td>Forward-Forward</td>
</tr>
<tr>
<td></td>
<td>Backward-Backward</td>
<td></td>
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<tr>
<td>Asymmetric</td>
<td>Forward-Backward</td>
<td>Forward-Backward</td>
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<tr>
<td></td>
<td>Backward-Forward</td>
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Symmetric and asymmetric movements were tested in separate blocks in the simple and 2-choice conditions. Both of these types of movements were combined in one block in the unilateral 2-choice condition. The target for the left arm is indicated before the hyphen and the right arm’s target is indicated after the hyphen. Forward-Backward, for example, means a forward movement with the left arm and a backward movement with the right arm.

Each block consisted of practice trials followed by test trials. In simple RT, there were 16 practice trials and 32 test trials. Four of the test trials were randomly selected as startle trials with the stipulation that two startle trials never occurred in a row. The same randomisation of startle trials was used for each participant. The number of test trials was doubled in 2-choice and unilateral 2-choice RT (16 practice, 64 test trials). There were two potential movements in these blocks, so each type of movement was used on half the trials. The order of these movements was randomised in each block. Eight of the test trials were randomly selected as startle trials, with four startle trials for each movement. The number of practice trials on the participant’s first block was doubled to 32.

There were two important aspects of the experimental design. First, movements were either forwards or backwards. We have previously tested bimanual movements that were in the same direction to either short- or long-amplitude targets (Blinch et al. 2014). The problem with those movements is that default forward movements could be preprogrammed even in choice conditions, as all movements begin in the same direction (Forgaard et al. 2011). Forward and backward movements were used in this experiment to prevent preprogramming in 2-choice conditions and for the arm without
a precue in unilateral 2-choice. Second, the requirement of ensuring safe noise exposure from startle trials prevented us from testing all possible precues in unilateral 2-choice. Any of the four targets could have been precued: left-forward, left-backward, right-forward, or right-backward. Deciding to precue only the left, forward target reduced the number of startle trials in the entire experiment from 64 to 32 trials.

4.2.5 Analysis

The position data from the Optotrak were filtered with a dual-pass, second-order, low-pass Butterworth filter with a cut-off frequency of 10 Hz. When an Optotrak marker was missing for four frames or fewer, the position was linearly interpolated. Velocity and acceleration in the forward-backward direction were calculated with a three-point central difference method. A trajectory analysis of control and startle trials was performed with emphasis on detecting movement errors, and this is described in the Results.

RT for each arm was calculated as the time from the imperative stimuli until movement onset. The difference between left and right arm RTs was the delta RT, and a negative delta RT indicated that the left arm was initiated before the right arm. Movement onset was determined by finding the first time after the imperative stimuli that forward or backward displacement exceeded 5 mm from the starting location. This is a relatively late criterion for movement initiation; for example, displacement exceeded 5 mm about 30 ms after the velocity exceeded 50 mm/s. This conservative measure was used to prevent small movements related to the startle reflex as opposed to the true movement onset from exceeding the criteria. Movement offset was determined by finding the first time after peak velocity that the absolute value of velocity was less than 50 mm/s. The difference between movement offset of the left and right arms was the delta total response time, and a negative value indicated that the left arm was terminated before the right arm.

Significant SCM EMG was determined by calculating a 99.999% confidence interval (4.4172 standard deviations) from the SCM activity for 100 ms before the
startle tone. This confidence interval was then compared to the SCM activity from 30 ms after the imperative stimuli to either 120 ms or movement onset, whichever was first. If SCM activity was outside the confidence interval, then the startle reflex was deemed to be present. This algorithm was also checked by visual inspection of all startle trials.

Mean RTs were calculated for each arm and then they were collapsed across arm. All dependent variables in 2-choice conditions were collapsed across the two symmetric movements (Forward-Forward, Backward-Backward) and they were collapsed across the two asymmetric movements (Forward-Backward, Backward-Forward). Probabilities were normalised with the arcsine square-root transformation before statistical analysis; the data reported are probabilities. Control and startle trials were analysed separately with 3 Condition (simple, unilateral 2-choice, 2-choice) by 2 Symmetry (symmetric, asymmetric) repeated-measures ANOVAs. When local sphericity was violated (as indicated by Mauchly’s test, \( p < .10 \)), the Huynh-Feldt correction was used when the \( \varepsilon \) was greater than or equal to .75 and the Greenhouse-Geisser correction was used otherwise (Huynh and Feldt 1976). The uncorrected degrees of freedom and the \( \varepsilon \) values were reported (Huynh-Feldt \( \varepsilon_{HF} \), Greenhouse-Geisser \( \varepsilon_{GG} \)). Significant main effects were investigated with pairwise comparisons and significant interactions were analysed with simple main effects on Symmetry. This post-hoc analysis involved three paired-samples t-tests that compared symmetric movements to asymmetric movements in the three conditions (simple, unilateral 2-choice, 2-choice). These tests allowed us to probe for asymmetric costs in simple, unilateral 2-choice, and 2-choice conditions. The Sidak correction was used to control the familywise error rate of the analyses on main effects and interactions. The sizes of the bimanual asymmetric RT costs in unilateral 2-choice and 2-choice conditions were compared with a paired-samples t-test. Effect size for paired-samples t-tests are Cohen’s d, calculated with the pooled standard deviation.

Reported values (unless otherwise noted) are means and 95% within-participant confidence intervals (CIs; Cousineau 2005; Morey 2008).
4.3 Results

4.3.1 Smaller asymmetric cost in unilateral 2-choice than 2-choice

RTs on control trials had a significant main effect of Condition, $F(2,34) = 131, p < .001, \varepsilon_{HF} = .76, \eta_p^2 = .89$. Simple RTs were shorter than 2-choice RTs ($p < .001$), and RTs in unilateral 2-choice and 2-choice conditions were comparable ($p = .987$; Figure 4.3, left). Control RTs were also examined to determine which conditions had longer RTs for asymmetric movements compared to symmetric movements, or more specifically, a bimanual asymmetric RT cost. The interaction between Condition and Symmetry was investigated with simple main effects on Symmetry, $F(2,34) = 19, p < .001, \eta_p^2 = .53$. There was an asymmetric RT cost in 2-choice conditions (39.5 ms, CI [32.6, 46.5], $p < .001$), and this cost was eliminated when the movements were prepared in advance in simple conditions (0.4 ms, CI [-10.0, 10.8], $p = .934$). Both of these findings have also been shown for movements with symmetric and asymmetric amplitudes (Blinch et al. 2014). The unique results were that there was an RT cost in unilateral 2-choice (15.3 ms, CI [4.6, 26.0], $p = .013$) and that this cost was smaller than in 2-choice, $t(17) = 4.3, p = .001, d = 1.20$.

![Figure 4.3 Mean RTs for control trials (left) and startle trials (right). Error bars are 95% within-participant CIs (Cousineau 2005; Morey 2008)](image-url)
4.3.2 Precued arm was initiated before the other arm on startle trials

The differences in movement onsets and offsets between the arms (delta RTs and delta total response times) were compared to determine whether the precued arm was initiated and terminated before the other arm in unilateral 2-choice. Delta RTs on control trials were relatively small (0.8 ms, 95% between-participant CI [-1.2, 2.7]), and there were neither significant main effects nor interactions, Fs < 3.1, ps > .059. Delta total response times on control trials were also relatively small (5.1 ms, 95% between-participant CI [-1.2, 11.4]), and there were neither significant main effects nor interactions, Fs < 0.9, ps > .391. These results suggested that bimanual movements were initiated and terminated relatively synchronously on control trials.

For delta RTs on startle trials, there was a significant main effect of Condition, F(2,34) = 11, p < .001, ηp² = .39. Bimanual movements in simple conditions were initiated relatively synchronously (-0.2 ms, CI [-2.5, 2.1]). The left arm was initiated 3.3 ms (CI [-6.8, 0.1]) before the right arm in 2-choice conditions, but the delta RTs were not significantly different from simple conditions (p = .271). In unilateral 2-choice, the left, precued arm was initiated 10.0 ms (CI [-13.6, -6.3]) before the right arm, and this was significantly different from simple conditions (p < .001) but not significantly different from 2-choice conditions (p = .059). We also noted a time difference between the precued arm and the other arm during movement execution. The precued arm arrived at all kinematics landmarks (first peak acceleration, peak velocity, and second peak acceleration) approximately 20 ms before the other arm. For delta total response times, there was a significant main effect of Condition, F(2,34) = 4.0, p = .038, ηp² = .19. The left arm was terminated first by 4.3 ms (CI [-19.6, 10.9]) and 0.9 ms (CI [-10.0, 8.2]) in simple and 2-choice conditions, and the delta total response times in these conditions were not significantly different (p = .960). In unilateral 2-choice, the left, precued arm was terminated 24.9 ms (CI [-40.8, -9.0]) before the right arm, and this was significantly different from 2-choice conditions (p = .026) but not significantly different from simple conditions (p = .252).
4.3.3 Startle RTs and the probabilities of a startle reflex in unilateral 2-choice were comparable to 2-choice and not simple conditions

RTs on startle trials in all conditions were expected to be shorter than control trials due to the start-react effect (compare Figure 4.3 right to left). There was a significant main effect of Condition, $F(2,34) = 24, p < .001, \eta_p^2 = .59$, and RTs in simple conditions (178 ms, CI [156, 201]) were shorter than unilateral 2-choice (256 ms, CI [241, 271], $p = .002$) and 2-choice (253 ms, CI [234, 272], $p = .003$).\(^9\) RTs were not significantly different in unilateral 2-choice and 2-choice conditions, $p = .989$. There was also a significant main effect of Symmetry, $F(1,17) = 11, p = .004, \eta_p^2 = .40$, and a significant Condition by Symmetry interaction, $F(2,34) = 4.7, p < .029, \epsilon_{GG} = .69, \eta_p^2 = .22$. The Condition by Symmetry was investigated with simple main effects on Symmetry. There was an asymmetric RT cost in 2-choice conditions (22.0 ms, CI [8.7, 35.3], $p < .005$), and this cost was eliminated when the movements were prepared in advance in simple conditions (-5.4 ms, CI [-20.2, 9.4], $p = .330$). There was also an asymmetric RT cost in unilateral 2-choice condition (28.0 ms, CI [5.7, 50.3], $p = .019$) and this cost was not significantly different than the cost in 2-choice, $t(17) = 0.5, p = .651, d = 0.16$. It is interesting that these costs were not significantly different on startle trials, whereas the cost in unilateral 2-choice was smaller than 2-choice on control trials. Unfortunately, it is difficult to compare movement preparation on startle trials with choice (2-choice and unilateral 2-choice) to the control trials. This is because movement preparation after the imperative stimulus was disrupted by the startle tone. The disruption caused an increase in movement errors, which are analysed below.

\(^9\) Mean premotor RTs (interval from the imperative stimulus until EMG onset) on startle trials are typically less than 100 ms in simple conditions (Carlsen et al. 2011). Unfortunately, premotor RTs on startle trials could not be calculated in the present experiment. The challenge was that the startle reflex for some participants appeared in the deltoids and overlapped with the muscle activation for the movement. This made it difficult to determine whether the startle reflex or the motor command caused the EMG. Premotor RTs on startle trials were estimated by subtracting the motor RT (interval from EMG onset to initiation of the response) on control trials from the startle RTs (premotor RT = RT – motor RT). The motor RT on control trials was 83.8 ms, 95% between-participant CI [78.9, 88.7]. The estimated premotor startle RTs were 94 ms in simple (94 = 178 – 84), 172 ms in unilateral 2-choice (172 = 256 – 84), and 169 ms in 2-choice (169 = 253 – 84). Therefore, the premotor startle RT in simple conditions was comparable to previous experiments.
For the probabilities of a startle reflex on startle trials, there was a significant main effect of Condition, $F(2,34) = 3.5, p = .040, \eta^2_p = .17$, but all pairwise comparisons were not significant. The main effect was likely caused by a greater probability of a startle reflex in simple (86.6%, CI [75.6, 97.6]) compared to 2-choice (71.9%, CI [63.0, 80.7]) and unilateral 2-choice conditions (72.9%, CI [63.6, 82.3]). It has been shown that the probability of a startle reflex is initially comparable in simple and choice conditions. With exposure to more startle trials, however, the probability of a startle reflex in choice conditions decrease because of the inability to fully prepare movements in advance (Maslovat et al. 2012). It is possible the startle reflex began to decrease in this experiment, in 2-choice and unilateral 2-choice, but not enough for the pairwise comparisons to be statistically significant. The probabilities of a startle reflex were not significantly different in unilateral 2-choice and 2-choice conditions, $p = .981$.

### 4.3.4 Movement errors on startle trials in 2-choice and for the arm without the precue in unilateral 2-choice

Trajectories on control and startle trials for the left and right arms were visually examined to identify movement errors. We identified four types of movement errors after looking at the trajectories for each trial: 1) primary submovements (Khan et al. 2006) that were initiated to the wrong target without a subsequent correction, 2) movements that were initiated to the wrong target with a correction, 3) movements with a gradual change in displacement, and 4) freezes where no movement was made. Examples of movement errors and their occurrence in startle trials are shown in Figure 4.4. The probability of a movement error was calculated for each condition, movement, and arm. These were normalised with the arcsine square-root transformation before statistical analysis. Control and startle trials were analysed separately with Condition (simple, unilateral 2-choice, 2-choice) by Symmetry (symmetric, asymmetric) by Arm (left, right) repeated-measures ANOVAs. The values reported are percentages.
Initiated to the wrong target (without a correction)
Control movements: 0.1%, CI [0.0, 0.2]
Startle movements: 2.4%, CI [0.8, 4.1]

Initiated to the wrong target (with a correction)
Control: 0.9%, CI [0.4, 1.5]
Startle: 7.7%, CI [4.9, 10.4]

Gradual change in displacement
Control: 1.2%, CI [0.8, 1.7]
Startle: 5.1%, CI [1.0, 9.2]

Freeze
Control: 0.0%, CI [0, 0]
Startle: 0.7%, CI [-0.2, 1.6]

**Figure 4.4** Displacement by time plots of the four types of movement errors. In each plot, the left arm of a representative movement error on a startle trial is shown with a black, solid line and the right arm with a black, dashed line. The gray trials (left arm, solid line; right arm, dashed line) are control trials without errors from the same movement, condition, and participant. The percentages below each plot are the mean occurrences (and between-participant CIs) of that type of movement error for control and startle trials.

On control trials, there were relatively few movement errors (Figure 4.5, left). There was a significant main effect of Symmetry, $F(1,17) = 11, p = .004, \eta_p^2 = .40$, that showed there were more movement errors on asymmetric control trials (2.9%, CI [2.4, 3.4]) than symmetric control trials (1.6%, CI [1.1, 2.1]). There was also a significant Condition by Arm interaction, $F(2,34) = 14, p < .001, \eta_p^2 = .45$, that was analysed with simple main effects on Condition. This post-hoc analysis involved three paired-samples t-tests that compared the movement errors of the left arm in the three conditions.
(simple, unilateral 2-choice, 2-choice) and another three t-tests that compared the right arm in the three conditions. The probabilities of movement errors for the left arm were not significantly different in simple, unilateral 2-choice, and 2-choice conditions (ps > .216). For the right arm, simple conditions had the fewest movement errors (0.5%, CI [-0.5, 1.5]); there were significantly more in 2-choice (2.0%, CI [1.1, 2.9], p = .016) and significantly more than that in unilateral 2-choice (4.9%, CI [2.7, 7.0], p = .011). Despite these small but significant differences, there were relatively few movement errors on control trials; the grand mean was 2.3%, 95% between-participant CI [1.3, 3.2].

![Figure 4.5](image)

**Figure 4.5** Mean percentages of movement errors for control trials (left) and startle trials (right). Error bars are 95% within-participant CIs (Cousineau 2005; Morey 2008)

For startle trials (Figure 4.5, right), there was a significant Condition by Arm interaction, $F(2,34) = 5.1, p = .029, \varepsilon_{GG} = .62, \eta^2_p = .23$, that was investigated with simple main effects on Condition. Both the left and right arms had low probabilities of movement errors in simple conditions (2.8%, CI [-1.4, 6.9]; 3.5%, CI [-0.6, 7.6]) and significantly higher probabilities in 2-choice (26.5%, CI [21.6, 31.4], $p < .001$; 23.7%, CI [19.7, 31.4], $p < .001$). In the unilateral 2-choice condition, the left, precued arm had a probability of a movement error (11.8%, CI [3.1, 20.5]) that was significantly lower than 2-choice conditions, $p = .006$, and not significantly different than simple conditions, $p = .052$. The right arm had a probability of a movement error (26.4%, CI [17.6, 35.2]) that was significantly higher than simple, $p = .001$, and not significantly different than 2-choice, $p = .998$. 
4.4 Discussion

Movement preparation was longer for bimanual asymmetric movements than bimanual symmetric movements in 2-choice RT conditions. This bimanual asymmetric cost was eliminated in simple RT conditions. Both of these results replicated previous findings for bimanual movements in simple and choice conditions (Blinch et al. 2014). A vital condition in the present experiment was unilateral 2-choice, in which one target was precued. The asymmetric cost was smaller with a unilateral precue than in 2-choice conditions. This attenuation was presumably caused by the precue that encouraged movement preparation before the imperative stimulus. The question of interest was: What was prepared before the imperative stimulus when one target was precued?

4.4.1 Temporal separation of movement preparation

We began with two predictions of how movement preparation may change when one arm is precued (Figure 4.1). One prediction involved movement preparation of the precued arm before the imperative stimulus and preparation of the other arm after the imperative stimulus (Figure 4.1, left). This should eliminate the asymmetric cost, as the asymmetric movements are prepared at different times. The other prediction involved the preparation of both arms after the imperative stimulus (Figure 4.1, right). This is similar to 2-choice RT conditions, and so the asymmetric cost should be comparable in unilateral 2-choice and 2-choice conditions. The results in the unilateral 2-choice condition showed a significant asymmetric cost that was smaller than the cost in the 2-choice conditions. Therefore, the degree of movement preparation in the unilateral 2-choice condition was somewhere in between the possibilities we initially proposed. The asymmetric cost was not eliminated, suggesting that the precued arm was not fully prepared in advance. The cost, however, was smaller than the cost in 2-choice condition, and suggests that there must have been partial preparation of the stage that caused the asymmetric cost before the imperative stimulus.
4.4.2 Probing movement preparation

The attenuation of the asymmetric cost in the unilateral 2-choice condition suggested that the precued arm was partially prepared before the imperative stimulus. The pattern of movement errors on startle trials offered insight into how movement preparation was split before and after the imperative stimulus in the unilateral 2-choice condition. First off, there were relatively few movement errors on startle trials in simple conditions. The required movement was likely fully prepared in advance and then released by the startle tone. In 2-choice conditions, there were a higher percentage of movement errors. This was likely because the movements were selected after the imperative stimulus and the startle tone disrupted response selection during this time. The critical results are the movement errors on startle trials in unilateral 2-choice. In unilateral 2-choice, the arm without the precue had significantly more movement errors than the same arm in simple conditions. Therefore, the movement for the arm without the precue was likely selected after the imperative stimulus and this preparation was disrupted by the startle tone. Interestingly, there were fewer movement errors for the precued arm compared to the same arm in 2-choice conditions. This suggests the movement for the precued arm was selected before the imperative stimulus and avoided the disruption by the startle tone. If the precued movement was selected in advance, then the precued target must have also been discriminated before the imperative stimulus. The target for the other arm was discriminated and the movement was selected after the imperative stimulus.

The pattern of movement errors, therefore, suggests that target discrimination and response selection of each arm were temporally separated before and after the imperative stimulus. If the asymmetric cost was caused by either target discrimination or response selection, then the cost should have been eliminated in the unilateral 2-choice condition. As the asymmetric cost was not eliminated, it was likely caused by the remaining preparation processes – those related to response programming. Furthermore, the attenuation of the asymmetric cost suggests that response programming was partially divided before and after the imperative stimulus. The
precued movement was partially prepared before the imperative stimulus, and this partial preprogramming decreased the asymmetric cost. It may not have been possible to fully preprogram the precued movement because of the constraint of bimanual movements. That is, bimanual movements are not simply the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit (Kelso et al. 1979b; Swinnen and Wenderoth 2004). Therefore, both arms needed to be programmed into a single, bimanual movement after the imperative stimulus when the movement for each arm had been selected. Programming two different unimanual movements into a bimanual asymmetric movement caused the asymmetric cost. The cost in the unilateral 2-choice condition was decreased by the partial preprogramming of the precued arm.

The difference in movement initiation between the two arms on startle trials provides further evidence that the precued arm was partially programmed before the imperative stimulus. If the precued arm was fully pre-programmed (Figure 4.1, left), then the precued arm should have been initiated with startle RTs comparable to simple conditions and the other arm should have been initiated with longer startle RTs, comparable to 2-choice conditions. The mean difference in startle RTs between simple and 2-choice conditions was 75 ms. In comparison, the precued arm was initiated only 10 ms before the other arm. This small inter-limb difference RT can be explained by partial pre-programming of the precued arm. The partial pre-programming provided a slight advantage for the precued arm and even though it needed to be programmed into an integrated movement with the other, it was ready to be initiated slightly before the other arm.

One result of preparing bimanual movements as a unified structure is that movement initiation and termination of each arm occurs relatively synchronously (Kelso et al. 1979b; Marteniuk et al. 1984). This requirement for temporal coupling may be another reason that the precued arm was partially preprogrammed; programming of a temporally coupled bimanual movement could only be finished after the imperative stimulus when both targets were known. Movements with the left and right arms on control trials were temporally coupled, as they were initiated and terminated relatively
synchronously. This was the case even though participants were not explicitly instructed on how to coordinate the movements with their left and right arms; they were simply told to “react and hit the targets as quickly as possible.” Participants were told to initiate their movements more synchronously when the difference in movement initiation on control trials was larger than 60 ms. This, however, occurred on only 13 out of 4,032 control, test trials for all participants. Kelso et al. (1979b) found that bimanual reaching movements were initiated relatively synchronously whether or not participants were instructed to start the movements simultaneously. It is possible to make asynchronous bimanual movements (e.g. Maslovat et al. 2009), but temporal coupling seems to be a default characteristic of bimanual coordination.

To review, our hypothesis for movement preparation in the unilateral 2-choice condition is detailed in Figure 4.6. The precued target is discriminated and the movement is selected and partially programmed before the imperative stimulus. After the imperative stimulus, the target for the other arm is discriminated and the movement is selected. A single, bimanual movement is then programmed. It takes longer to program two different movements into a bimanual asymmetric movement than two of the same movements into a bimanual symmetric movement. Thus, the asymmetric cost is caused by increased processing demands on response programming.

**Figure 4.6** Movement preparation in the unilateral 2-choice condition when the left target is precued. The stages of information processing are target discrimination (TD), response selection (RS), and response programming (RP). The precued movement is partially programmed before the imperative stimulus (distinguished by the dotted box). The two unimanual movements are then programmed as a single, bimanual movement after the imperative stimulus. This is shown as a large box to emphasise that a single bimanual movement is programmed.
Other investigators have provided neurophysiological evidence of partial preparation before the imperative stimulus when a unimanual movement is partially precued (Cisek and Kalaska 2005; Leuthold et al. 1996; Ulrich et al. 1998). Leuthold et al. and Ulrich et al. investigated the cause of the decrease in RTs with the precuing of movement parameters [known as the precue effect (Rosenbaum 1980, 1983)]. They used the lateralised readiness potential to measure the duration of response programming to determine whether precuing some of the movement parameters caused motor preparation before the imperative stimulus. Both studies found that precuing the hand that would make the unimanual movement allowed some motor preparation before the imperative stimulus. They, therefore, argued that at least some of the precue effect occurred during motor preparation. In the present study, we refer to beginning motor preparation before the imperative stimulus as partial preprogramming. It is still unclear exactly what processing occurs during partial preprogramming; however, Leuthold et al. and Ulrich et al. argued that it involves muscle-specific preparation of the forthcoming response. Cisek and Kalaska showed that when primates were precued with two potential targets for one arm, neurons in the dorsal premotor cortex simultaneously represented the directions of both targets.

Another study that should be compared to our results was by Diedrichsen et al. (2001). They examined the asymmetric costs for symbolically- and directly-cued movements with and without one precue. Their experiments can also offer insight into movement preparation before the imperative stimulus. Similar to our logic, they reasoned that a decrease in a bimanual asymmetric cost with one precue would reveal interference during movement preparation of asymmetric movements. Diedrichsen et al. found a large asymmetric cost with symbolic cues (55 ms, Experiment 1) that was eliminated with one precue. They argued that the cost was caused by symbolic cues that placed increased processing demands on response selection, which has been confirmed by several studies (reviewed by Wenderoth and Weigelt 2009). Precuing one target likely temporally separated the response selection of each arm. The movement for the precued arm was selected before the imperative stimulus and the movement for the other arm was selected after. This avoided the bimanual interference during RT and
eliminated the asymmetric cost. In the present study, we also argue that there was pre-selection of the precued arm. With direct cues, Diedrichsen et al. (2001) found a 6 ms bimanual asymmetric cost that was not significant (Experiment 1). RTs were also not significantly different with or without one precue. Later studies, including one by Diedrichsen and colleagues, found that there is a small asymmetric cost (15-20 ms) with direct cues (Blinch et al. 2014; Diedrichsen et al. 2006; Heuer and Klein 2006b, Experiment 2). These studies, unfortunately, did not include a condition with one precue.

4.4.3 Unification of bimanual movements

Previous research has argued that asymmetric movements place increased processing demands on response programming (Blinch et al. 2014; Heuer 1986; Heuer and Klein 2006b; Stelmach et al. 1988). The explanations of how asymmetric movements are programmed have differed; for example, Heuer and colleagues argued that there is cross-talk between concurrent processes of parameter specification of asymmetric movements that causes transient interference (Heuer 1986; Heuer and Klein 2006b). It seems that the challenge with bimanual asymmetric movements comes down to programming two different movements at the same time. The results from the present experiment support that the asymmetric cost was caused by increased demands on response programming, but they also offer insight into how bimanual movements are programmed. We attempted to temporally separate the movement preparation of each arm by precuing one target. This allowed the precued movement to be selected before the imperative stimulus, but the precued movement was not fully programmed before the imperative stimulus. Complete programming of the precued movement waited until after the imperative stimulus when the response for the other arm was selected. Selecting the movements for each arm allowed them to be programmed as a single, bimanual movement. This reinforces the notion that bimanual movements are not simply the sum of two unimanual movements. Our results argue that the critical unification of a bimanual movement occurred during response
programming in the unilateral 2-choice condition. Responses for each arm could be selected at different time, but the movements could not be fully programmed separately. Response programming of a bimanual movement necessitates that the movement of each arm is combined into a single response rather than two independent ones.

The results in the unilateral 2-choice condition suggested that the bimanual movement was unified during response programming and not during response selection. Precuing the left target encouraged the left movement to be selected before the imperative stimulus and the right movement to be selected after the imperative stimulus. In most experiments, however, the movements for each arm of a bimanual movement are cued at the same time (e.g. Blinch et al. 2014; Heuer and Klein 2006b; Kelso et al. 1979b). Therefore, the two movements are likely selected at the same time. The atypical movement preparation with a precue in the present study may have caused the bimanual unification to occur during response programming instead of response selection. When the two targets of a bimanual movement are selected at the same time, as in the 2-choice conditions, the unification of the bimanual movement could occur during response selection or response programming. Our protocol and results cannot determine exactly when the bimanual unification occurred in the 2-choice conditions; this remains a fascinating area of investigation for future studies.

Regardless of when the bimanual integration occurs, the results suggest that there is a cost to unify two different unimanual movements into a bimanual asymmetric movement compared to two identical movements into a bimanual symmetric movement. Other studies have shown that changing how bimanual movements are conceptualised can eliminate various forms of bimanual asymmetric costs (reviewed by Swinnen and Wenderoth 2004). This has been done by having a single goal for both arms (Franz et al. 2001) or by having a single stimulus that represents the positions of each arm. The latter has been shown for continuous (e.g. Kovacs et al. 2009; Swinnen et al. 1997) as well as discrete bimanual movements (e.g. Franz and McCormick 2010; Shea et al. 2012; White and Diedrichsen 2010). Franz and McCormick suggested that unified conceptualisations can release attentional control from lower levels of the sensorimotor system and prevent interference from those levels. Shea et al. reasoned
that unified conceptualisations decrease or eliminate the interference caused by attentional and visual-perceptual factors.

It is possible that a unified conceptualisation might decrease the asymmetric cost in the present experiment. The asymmetric cost was caused by the need to unify two different unimanual movements into a bimanual asymmetric movement. The processing with a unified conceptualisation may always be on a single representation of the bimanual movement. This would bypass the unification of two unimanual movements into one bimanual movement and the asymmetric cost. Overall, changes in when bimanual unification occurs or whether bimanual unification is needed suggest that the preparation of bimanual movements is malleable.

In summary, the bimanual asymmetric cost was smaller in the unilateral 2-choice than the 2-choice conditions. This suggests that the precued movement was partially prepared before the imperative stimulus. Startle trials were included to determine what was prepared before the imperative stimulus in unilateral 2-choice. The probabilities of movement errors on startle trials suggested that the precued arm was selected before the imperative stimulus. The results from control and startle trials suggests that the precued movement was partially pre-programmed and that the partial pre-programming decreased the size of the asymmetric cost. This also implies that the asymmetric cost was caused by increased processing demands on response programming. Overall, the results support the notion that bimanual movements are not the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit. When one target is precued, this critical unification likely occurs during response programming.

4.5 Bridging summary

This study supports that the critical unification of bimanual movements occurs during response programming. However, this is the case in unilateral 2-choice where one target is precued. Bimanual unification may or may not occur during response programming when both targets of a bimanual movement are cued at the same time;
this was investigated in the next study (Chapter 5). We compared the RTs of bimanual symmetric and asymmetric movements when the target for each arm was cued at the same time. The additive factors method (AFM; Sternberg 1969) was used to determine which stages of movement preparation are longer for bimanual asymmetric movements compared to symmetric movements.
5 Preparation cost for bimanual asymmetric movements is caused by response selection\textsuperscript{10}

5.1 Introduction

Many studies have examined the coordination of bimanual reaching movements as an example of coordination in motor activities of daily life. These studies have compared the duration of movement preparation for various bimanual reaching movements (reviewed by Wenderoth and Weigelt 2009). Reaction time (RT) is used as a measure of how long it takes to prepare a movement, with the assumption that the more involved or difficult the preparation processes are, the longer the RTs. The common finding from these studies is that asymmetric bimanual reaches with different movement amplitudes for each arm have longer RTs than symmetric bimanual reaches with the same movement amplitudes, even with direct cues. A current goal is to determine how the information processing of bimanual asymmetric reaching movements is more complex than symmetric movements.

Spijkers et al. (1997) compared bimanual reversal movements with the same or different movement amplitudes. Importantly, the movement amplitudes for each arm were cued symbolically with the German words for short and long. Therefore, symmetric movements had the same cue for each arm (Long-Long or Short-Short) and asymmetric movements had a different cue for each arm (Long-Short or Short-Long).\textsuperscript{11} They found that RTs for asymmetric movements were 174 ms longer than symmetric movements (Experiment 1, no precue). Spijkers et al. reasoned that the RT cost for asymmetric movements was caused by cross-talk during response programming; specifically, there may be mutual interference between the two arms during concurrent

\textsuperscript{10} A version of Chapter 5 is under review: Blinch J, Franks IM, Carpenter MG, Chua R (under review) Preparation cost for bimanual asymmetric movements is caused by response selection

\textsuperscript{11} The target for the left arm is indicated before the hyphen and the right arm’s target is indicated after the hyphen. Long-Short, for example, means a long-amplitude movement with the left arm and a short-amplitude movement with the right arm.
programming of different movement amplitudes. This lengthened the paramaterisation process of each arm and caused longer RTs for asymmetric movements.

Diedrichsen et al. (2001) questioned whether the RT cost found by Spijkers et al. (1997) might be caused by the greater processing demands required to translate two different symbolic cues for asymmetric movements compared to two identical cues for symmetric movements. They reasoned that if the RT cost was caused by bimanual interference during response programming, then it should persist when the targets are directly cued by illuminating them. Direct cues place fewer processing demands on translation processes than symbolic cues and they should be more comparable for bimanual symmetric and asymmetric reaches. When movements were symbolically cued, they found large RT costs for bimanual movements with asymmetric amplitudes (55 ms, Experiment 1) or asymmetric directions (94 ms, Experiment 2). With direct cues, there were small, non-significant RT costs for bimanual movements with asymmetric amplitudes (6 ms, Experiment 1) or asymmetric directions (4 ms, Experiment 2). Diedrichsen et al. argued that bimanual asymmetric movements do not cause bimanual interference during response programming, as supported by the lack of RT costs with direct cues. The RT costs with symbolic cues were likely caused by increased processing demands on response selection.

More recently, Diedrichsen et al. (2006) found a small bimanual asymmetric cost (15 ms) with direct cues and a large cost (148 ms) with symbolic cues. They argued that the small cost with direct cues is caused by increased processing demands during the preparation of asymmetric movements. The large cost with symbolic cues is caused by two sources of increased processing demands: 1) during the preparation of asymmetric movements, which also occurs with direct cue, and 2) during the translation of two different symbolic cues. Several elegant studies have isolated the second source of processing demands to the translation of symbolic cues during response selection (e.g. Diedrichsen et al. 2001, 2003; Hazeltine et al. 2003). It has yet to be tested which stage or process of movement preparation causes the increased processing demands with direct cues. Two recent studies found small bimanual asymmetric costs (16-55 ms) with direct cues and suggested that they were caused by increased processing demands
during response programming (Blinch et al. 2014; Heuer and Klein 2006b). The RT costs in these studies supported that there was interference at some stage of movement preparation, and it was suggested that the interference might occur during response programming. Response programming may have been implicated because it was previously proposed as the source of bimanual interference in a theoretical framework by Heuer (1986, 1993). However, the studies by Blinch et al. (2014) and Heuer and Klein (2006b), as well as the studies that supported Heuer’s model, could not rule out possible contributions to the RT cost from other stages of information processing—namely, stimulus identification or response selection.

The purpose of the present study was to determine which stage (or stages) of movement preparation causes the bimanual asymmetric RT cost with direct cues. Movement preparation can be divided into three successive stages: stimulus identification, response selection, and response programming (e.g. Donders 1969; Sternberg 1969). Increased processing demands on one, or more, of these stages for bimanual asymmetric movements could cause the bimanual asymmetric cost. The challenge with bimanual asymmetric movements is simultaneously processing two different stimuli or responses; identifying two different stimuli at the same time, concurrently selecting two different responses, or simultaneously programming two different responses could cause the bimanual asymmetric cost. Stimulus identification may take longer because the illuminated targets for asymmetric movements are further apart than symmetric movements. When the targets are close together, they may be perceptually grouped as a gestalt, and this would create a processing advantage for symmetric movements (Han et al. 1999). Diedrichsen et al. (2001) argued that direct cues place fewer demands on translation processes; however, there could still be a cost to select two different responses compared to two identical responses.

We tested the contributions of stimulus identification, response selection, and response programming to the bimanual asymmetric cost by employing the additive factors method (AFM; Sternberg 1969; also reviewed by Sternberg 1998). This method requires selectively increasing the processing demands on each stage of movement preparation for bimanual reaching movements. Altering the stimulus contrast (bright
or dim), the response compatibility (compatible or incompatible), and the response complexity (reaches or reversals; the number of movement parts) modified the processing demands on stimulus identification, response selection, and response programming, respectively. For this illustration of the AFM, let us assume that the bimanual asymmetric cost is caused by increased processing demands on response programming (Figure 5.1a). Bimanual symmetric and asymmetric movements are retested with increased processing demands on stimulus identification (dim, compatible, reaches). The important point for this version of the task is that the processing demands have been increased in different stages: stimulus identification for dim stimuli and response programming for bimanual asymmetric movements. The AFM logic in this scenario is that “when factors influence no stages in common, their effects on mean RT will be independent and additive, because stage durations are additive. That is, the effect of one factor will not depend on the levels of the others” (Sternberg 1969, p 282). The result is longer RTs with dim stimuli for bimanual symmetric and asymmetric movements, and importantly, the size of the bimanual asymmetric cost remains the same as the control task (compare the size of the asymmetric cost in Figure 5.1b to 5.1a). The same additive logic applies when incompatible bimanual movements are tested (bright, incompatible, reaches); RTs will be longer for incompatible movements, but the size of the bimanual asymmetric cost will remain the same (compare Figure 5.1c to 5.1a).

A different effect on RTs is predicted when reversals and asymmetric movements both increase processing demands on response programming. The AFM logic is as follows, “When two factors influence at least one stage in common there is no reason to expect their effects on RT to add; the most likely relation is some sort of interaction” (Sternberg 1969, p 282). In other words, the processing demands for reversals and asymmetric movements will interact and be over-additive. This will cause a larger RT cost for asymmetric movements compared to the control task (compare the size of the asymmetric cost in Figure 5.1d to 5.1a).
In summary, we selectively increased processing demands on each stage of movement preparation. Manipulations with over-additive interactions would suggest that the asymmetric cost is caused by increased processing demands on that stage. In contrast, manipulations with additive effects on RT would suggest that the bimanual asymmetric cost is not caused by that stage. This is a common application of the AFM (reviewed by Sternberg 1998), and the manipulations of stimulus contrast, response compatibility, and response complexity have been previously combined to determine the stage responsible for a change in the duration of movement preparation (intersensory facilitation was found to enhance response programming; Schmidt, Gielen, van den Heuvel 1984). The AFM is based on the assumption of a serial sequence of stages whose durations are additive components of movement preparation. There can be parallel processing within a stage, but the stages must be sequential in the chosen task. The AFM can determine the selective influence of each stage on movement preparation, but it cannot determine the duration or the order of stages (Sternberg 1969, 1998). We predicted that bimanual asymmetric movements and response complexity would have an over-additive effect on RT in the present experiment. This would suggest that the bimanual asymmetric cost was caused by increased processing demands on response programming. This is consistent with previous research that has
suggested that response programming contributes to bimanual asymmetric cost (Blinch et al. 2014; Blinch et al. under review; Heuer 1986, 1993; Heuer and Klein 2006b).

5.2 Method

5.2.1 Participants

Twenty-four participants (mean age of 24.8 ± 4.9 years, 8 female) were tested from the university community. They were paid $15 CAD for their participation. All participants reported being right-handed and had normal or corrected-to-normal vision. Data from one additional participant were excluded, as the participant failed to follow the task instructions. The research ethics board at the University of British Columbia approved the study, and participants gave informed written consent before participation.

5.2.2 Apparatus

Participants were seated at a table in a dark room, and each participant rested their head in a chin rest. On the surface of the table were two linear slides (Low Profile Redi-Rail, PBC Linear) that were perpendicular to the front edge of the table. The linear slides were 15 cm apart, and participants were seated so that their midsagittal plane was in the middle of the slides. Participants held the handles of the left and right slides with their left and right hands. The slides allowed forward and backward movements of the arms with minimal friction and prevented movements in other directions. There was an Optotrak marker at the top of each handle. The positions of the handles were sampled at 500 Hz by an Optotrak system (3020; Northern Digital).

Virtual stimuli were projected on the surface of the table by an LCD monitor positioned over the table. Midway between the table and the monitor was a half-silvered mirror; it created the illusion that the stimuli appeared on the table. The stimuli created a three-row by two-column array of circle outlines (Figure 5.2a), and
the two columns were aligned with the linear slides. The circles in the closest row to the participants were the two backward targets, and the two forward targets were the circles in the farthest row; the targets had a radius of 15.3 mm. There was an inner circle inside the target circles that had a radius of 4.1 mm. The circles in the middle row were the home positions, and they had a radius of 3.4 mm. The distance from the center of the home positions to the center of the forward or backward targets was 100 mm. Filling any of the outer circles directly cued that target; this is subsequently referred to as illuminating a target.

![Figure 5.2](image)

**Figure 5.2** Visual stimuli at the time of the imperative stimuli in the four conditions: a) control, b) dim, c) incompatible, and d) reversal. The stimuli in each condition cue a forward movement with the right arm and a backward movement with the left arm (Forward-Backward). The magenta circles are the real-time positions of the handles. The home positions are missing because they disappeared at the time of the imperative stimuli.
Testing occurred in a dark room that prevented visual feedback of the participants' arms and the linear slides. The position of the handle for each slide was displayed on the surface of the table in real-time as a circle with a 1.7 mm radius. There was a 16.7 ms time lag between receiving the current positions of the Optotrak markers and displaying the feedback on the monitor that was determined by the 60 Hz refresh rate of the LCD monitor. To compensate for this lag, the positions of the markers in the next frame were predicted based on the current and previous positions.

5.2.3 Procedure

The procedure was slightly different for the four experimental conditions: control, dim, incompatible, and reversal. Control trials began with the outlines of the four potential targets and the two home positions appearing on the surface of the table. The home positions were illuminated as a cue for the participants to move the handles into the home positions. Participants could not see their arms for the entire trial. They could always see two small circles that were displayed on the table surface to represent the positions of the handles in real-time. A 1-2 s variable foreperiod began when the handles were in the home positions. A fixation cross appeared between the home positions during the foreperiod; participants were instructed to fixate on it while they waited for the imperative stimuli.

The imperative stimuli consisted of illuminating two targets (one on the left side and one on the right side) by filling the outer circles in with white. The home positions also disappeared when the imperative stimuli appeared. The positions of the handles were displayed in real-time during the trial. Participants were instructed to “react and hit the targets as quickly as possible.” After the trial, the positions of the handles at the end of the bimanual movement were displayed after the 2.0 s recording interval of the Optotrak as knowledge of results. These endpoints and the correct targets were displayed in green for a target hit and red for a target miss. Participants were encouraged to use this feedback to help them with subsequent trials.
The changes in the procedure in the different conditions were as follows. On dim trials, the imperative stimuli involved filling the small, inner circles instead of the large, outer circles. The fill colour was also a gray that was 50% as luminous as control trials. Participants were still instructed to make movements to anywhere within the large, outer circles. On incompatible trials, the same imperative stimuli as control trials were used but participants were instructed to reach for the targets that did not illuminate. On reversal trials, participants were instructed to perform reversal movements to the targets and back to the starting locations. Recall that the home positions disappeared with the imperative stimulus. This was done to promote a single reversal movement instead of two targeted movements: one out to the targets and one back to the home positions. Participants were trained on practice trials to make one smooth reversal movement without a pause at the targets.

Each trial was labeled as “good” or “bad,” with bad test trials being recycled to the end of the block. Types of bad trials included anticipation (RT < 100 ms), inattention (RT > 750 or movement time > 500 ms) asynchronous movement initiation (>60 ms RT difference between the arms), and target misses with either arm. In total, 12.6% of all test trials were recycled; the majority of recycled trials were target misses (11.2%). These were considered in the analysis on the proportion of target hits. If it was a bad trial, then a message explained the reason to the participant, but the participant was not told that these trials were recycled. Every trial ended with a blank screen for 1 s. An additional 1.2% and 0.2% of all test trials were removed after data collection and these were not recycled. The 1.2% represented movements when either arm was initiated in the opposite direction as the targets. These were considered in the analysis on the proportion of correctly initiated movements. The 0.2% represented trials when the participants were distracted.

A “speed score” was given to participants after every eight good trials. This score gave participants feedback on their total response time (RT + movement time) and was intended to motivate them to react and hit the targets as quickly as possible. It was calculated by comparing the mean total response time of the last eight good trials to the previous eight good trials. The percent change was calculated and multiplied by ten; for
example, if the total response time decreased from 300 ms to 270 ms (a 10% change), then the speed score would be $-100 \times 1000 \times (270/300 - 1)$. A multiple of ten was used to make the small changes in total response time (typically less than 5%) more salient to the participants.

### 5.2.4 Design

The experiment began with a familiarisation phase where the participants performed twenty trials in each condition. The order of familiarisation was control, dim, incompatible, and then reversal. There were four movement alternatives, two symmetric movements (Forward-Forward, Backward-Backward) and two asymmetric movements (Forward-Backward, Backward-Forward). If a participant had difficulty with any condition, then the twenty trials were repeated. Only one of the twenty-four participants repeated any part of the familiarisation phase; this participant performed the twenty dim trials twice.

Familiarisation was followed by the test phase. The order of the four conditions was determined by a balanced Latin square design. Each condition included two blocks: a symmetric block (Forward-Forward, Backward-Backward) and an asymmetric block (Forward-Backward, Backward-Forward). The order of these blocks was counterbalanced with half the participants completing the symmetric block first for all the conditions and the other half completing the asymmetric block first. Each block consisted of 12 practice trials followed by 32 test trials. There were two potential movements in these blocks, so each movement was used on half the trials. The order of these movements was randomised in each block.

An important aspect of the design was that the movements were either forwards or backwards. We have previously tested bimanual movements that were in the same direction to either short- or long-amplitude targets (Blinch et al. 2014). The problem with those movements is that default forward movements could be preprogrammed even in choice conditions, as all movements begin in the same direction (Forgaard et al.
2011). Forward and backward movements were used in this experiment to prevent preprogramming.

5.2.5 Data Analysis

RT for each arm was calculated as the time from the imperative stimuli until movement onset. The time from movement onset to movement offset was the movement time. Movement onset was determined by finding the first time after the imperative stimuli that forward or backward velocity exceeded 50 mm/s from the starting location. Movement offset for reaching movements was determined by finding the first time after peak velocity that forward or backward velocity was less than 50 mm/s. For reversal movements, movement offset was the time of peak displacement in the direction of the target. The position data from the Optotrak were filtered with a dual-pass, 2nd-order, low-pass, Butterworth filter with a cut-off frequency of 10 Hz. When an Optotrak marker was missing for 5 frames or fewer, the position was linearly interpolated. Velocity in the forward-backward direction was calculated with a 3-point central difference method. Velocity was used to calculate movement onset and the proportion of correctly initiated movements. A movement was correctly initiated if the velocity at movement initiation was in the direction of the target.

The dependent variables were RT, movement time, proportion of target hits, and proportion of correctly initiated movements. These variables were calculated for each arm and then collapsed across arm (left, right). We also collapsed across the two symmetric movements (Forward-Forward, Backward-Backward) and the two asymmetric movements (Forward-Backward, Backward-Forward). Proportions were normalised with the arcsine square-root transformation before statistical analysis; the data reported are proportions. The bimanual asymmetric RT cost for each participant in each condition was calculated by subtracting the mean RT for symmetric movements from the mean RT for asymmetric movements. The bimanual asymmetric costs were analysed with a priori comparisons to determine whether there were over-additive interactions between the control condition and the dim, incompatible, or reversal.
conditions. These comparisons were three one-tailed, repeated-measures t-tests that examined whether the bimanual asymmetric costs in dim, incompatible, or reversal conditions were larger than the bimanual asymmetric costs in the control condition (i.e. an over-additive interaction). Each of the three comparisons was statistically equivalent to testing for an interaction between control and experimental conditions and symmetric and asymmetric movements. The Šidák correction was used to control the familywise error rate of the a priori comparisons. Effect size for the repeated-measures t-tests are Cohen’s d, calculated with the pooled standard deviation. Movement time, proportion of target hits, and proportion of correctly initiated movements were statistically analysed with 2 Symmetry (symmetric, asymmetric) by 4 Condition (control, dim, incompatible, reversal) repeated-measures ANOVAs. When local sphericity was violated (as indicated by Mauchly’s test, α = .10), the Huynh-Feldt correction was used when the ε was greater than or equal to .75 and the Greenhouse-Geisser correction was used otherwise (Huynh, Feldt 1976). The uncorrected degrees of freedom and the ε values were reported (Huynh-Feldt ε_{HF}, Greenhouse-Geisser ε_{GG}). Significant main effects of Condition were investigated with pairwise comparisons, and significant interaction were analysed with simple main effects on Symmetry. The Šidák correction was used to control the familywise error rate of these post hoc comparisons. Reported values, unless otherwise noted, are means and 95% within-participant confidence intervals (CIs; Cousineau 2005; Morey 2008).

5.3 Results

5.3.1 Over-additive RT interaction between asymmetric movements and response compatibility

Mean RTs in the four conditions for bimanual symmetric and bimanual asymmetric movements are shown in Figure 5.3, left. The mean RT costs for asymmetric movements compared to symmetric movements are shown in Figure 5.3, right. The a priori comparisons showed that the RT cost of 37.8 ms (CI [28.1, 47.5]) for
asymmetric movements in the incompatible condition was significantly larger than the 21.6 ms (CI [11.9, 31.3]) cost in the control condition, \( t(23) = 2.4, p = .033, d = 0.65 \). The RT costs of 30.4 ms (CI [21.8, 39.1]) and 22.0 ms (CI [14.1, 29.9]) in the dim and reversal conditions, respectively, were not significantly different from the control condition, \( t(23) = 1.5, p = .217, d = 0.38; t(23) = 0.1, p = 1.000, d = 0.02 \). The a priori comparisons suggested that the relationship between control and incompatible conditions was over-additive and the relationships between control and either dim or reversal conditions were additive. Based on the AFM logic, an over-additive interaction for incompatible movements suggested that the bimanual asymmetric cost was caused by increased processing demands on response selection.

**Figure 5.3** The left graph illustrates the mean RTs in the four conditions (control, dim, incompatible, and reversal) for bimanual symmetric (gray) and bimanual asymmetric (white) movements. The right graph isolates the mean RT costs for asymmetric movements compared to symmetric movement in the four conditions. The RT cost in the incompatible condition was significantly larger than the cost in the control condition. Error bars are 95% within-participant CIs (Cousineau 2005; Morey 2008)

### 5.3.2 Performance characteristics across conditions

Movement times were shorter for symmetric movements (227 ms, CI [225, 230]) than asymmetric movements (245 ms, CI [242, 248]), \( F(1,23) = 75, p < .001, \eta^2_p = .77 \). There was also a significant Condition by Symmetry interaction, \( F(3,69) = 4.0, \varepsilon_{HH} = .94, p = .012, \eta^2_p = .15 \). Movement times were significantly longer for asymmetric movements than symmetric movements in all conditions. The difference in asymmetric
movement times compared to symmetric movement times were as follows: control 20.2 ms (CI [15.6, 24.9], \( p < .001 \)), dim 20.4 ms (CI [15.2, 25.5], \( p < .001 \)), incompatible 8.5 ms (CI [1.9, 15.0], \( p = .019 \)), and reversal 19.7 ms (CI [12.5, 26.9], \( p < .001 \)).

There was a lower proportion of target hits for asymmetric movements (.932, CI [.926, .937]) than symmetric movements (.951, CI [.946, .957]), \( F(1,23) = 21, p < .001 \), \( \eta^2_p = .48 \). There was also a significant main effect of Condition, \( F(3,69) = 6.3, p = .001 \), \( \eta^2_p = .21 \). Pairwise comparisons showed that reversal movements had a lower proportion of target hits (.919, CI [.905, .934]) compared to the other conditions that required reaching movements (control .949, CI [.939, .960]; dim .950, CI [.943, .956]; incompatible .948, CI [.939, .957]), \( p < .048 \). These results confirmed that it was harder to hit the targets for asymmetric movements than symmetric movements and for reversal movements than reaching movements. The Condition by Symmetry interaction was not significant, \( F(3,69) = 1.2, p = .320 \), \( \eta^2_p = .05 \).

For the proportion of correctly initiated movements, there was a significant main effect of Condition, \( F(3,69) = 16, \varepsilon_{GG} = .70, p < .001 \), \( \eta^2_p = .42 \). Pairwise comparisons revealed that the incompatible condition had a lower proportion of correctly initiated movements (.974, CI [.966, .983]) than the other conditions (control .997, CI [.993, 1.000]; dim .994, CI [.989, .998]; reversal .992, CI [.987, .997]), \( p < .003 \). This confirmed that selecting the correct target in the \emph{incompatible} condition was more challenging than the three, \emph{compatible} conditions. The Condition by Symmetry interaction was not significant, \( F(3,69) = 1.5, \varepsilon_{HF} = .83, p = .235 \), \( \eta^2_p = .06 \).

The displacements of representative reaching movements in the control condition are shown in Figure 4, left. Figure 4, right shows the displacements of reversal movements. Reversal movements consisted of two integrated segments: a reach towards the targets and a return to the home positions. Notice that the reaches are visibly similar to the first half of the reversal movements, the reach towards the targets. In fact, the movement time of a reach in the control condition (237 ms, CI [231, 242]) was not significantly different than the movement time of the reach to the targets in the reversal condition (230 ms, CI [219, 242]; \( t(23) = 1.1, p = .301 \), \( d = 0.16 \)). In the reversal condition, the time for the return to the home positions (286 ms, CI [276, 295])
was significantly longer than the initial reach to the targets (230 ms, CI [221, 240]; \( t(23) = 8.7, p < .001, d = 1.02 \)). The longer time for the return was not caused by a meaningful difference in the amplitudes of the two segments. The return to the home positions (103 mm, CI [102, 104]) was significantly longer than the reach to the targets (100 mm, CI [99, 101]; \( t(23) = 3.2, p = .004, d = 0.75 \)), but this 3 mm difference was not large enough to account for the 56 ms difference. Finally, we measured the duration of the transition at the reversal by determining the time at maximum displacement that was below the velocity threshold of 50 mm/s. The grand mean transition time was 16.3 ms (95\% between-participant CI [12.3, 20.0]).

**Figure 5.4** Trajectories of asymmetric movements from a representative participant in the control condition (left) and the reversal condition (right). The plotted trajectories are Forward-Backward movements: the left arm traveled forwards (positive displacement) and the right arm went backwards (negative displacement). The reaches to the targets in control (left) and reversal (right) conditions are visibly similar. For reversal movements (right), the return movements to the home positions appear more variable than the reaches to the targets. This is likely because the home positions disappeared with the imperative stimuli and so the movement was to a remembered location.

### 5.4 Discussion

In this experiment, we tested the contributions of stimulus identification, response selection, and response programming to the bimanual asymmetric RT cost by using the AFM (Sternberg 1969). This involved: altering the stimulus contrast (bright or dim), the response compatibility (compatible or incompatible), and the response complexity (reaches or reversals). These manipulations changed the processing
demands on stimulus identification, response selection, and response programming, respectively. Manipulations with over-additive interactions on RT suggest that the bimanual asymmetric RT cost is caused by increased processing demands on that stage, and manipulations with additive effects suggest that the asymmetric cost is not caused by that stage. The prediction was that asymmetric movements would have an over-additive interaction with response complexity. Unexpectedly, there was an over-additive interaction between only asymmetric movements and response compatibility. These results support that the bimanual asymmetric cost is caused by increased processing demands on response selection.

5.4.1 Response programming

Our prediction of an over-additive interaction between asymmetric and reversal movements was based on the propositions of previous studies. Many studies have suggested that RT costs for bimanual asymmetric movements are caused by increased processing demands on response programming, or more specifically, intermanual interactions during motor programming (e.g. Blinch et al. 2014; Heuer and Klein 2006). The RT costs in these studies supported that there was interference at some stage of movement preparation. Response programming may have been implicated because it was previously proposed as the source of bimanual interference in a theoretical framework by Heuer (1986, 1993). However, the studies by Blinch et al. (2014) and Heuer and Klein (2006), as well as the studies that supported Heuer’s model, could not rule out possible contributions to the RT cost from other stages of information processing – namely, stimulus identification or response selection. The present study is the first to test which stages of movement preparation contribute to the bimanual asymmetric cost with direct cues in choice RT tasks.

Movement preparation was longer for bimanual reversal movements than bimanual reaches. However, it was an additive change in RTs that did not affect the size of the bimanual asymmetric cost. It is important to consider whether some of the cost for reversal movements was deferred from the RT interval into the movement time and
prevented an over-additive interaction. We consider two ways that the preparation of a reversal movement could occur during the movement time instead of during the RT and offer evidence that these did not occur in the present experiment. First, the return to the home positions could be prepared online during the reach to the targets. This would likely increase the movement time of the initial reach to the targets compared to the movement time of the reach in the control condition (e.g. Adam et al. 1995; Ricker et al. 1999). The movement times of the reaches to the targets were comparable in control and reversal conditions, and so the return to the home positions was probably not prepared during the reach to the targets. Second, the return to the home positions could be prepared after the reach to the targets. This would likely introduce a long transition time between the reach to the targets and the return to the home positions. The mean transition time was only 16.3 ms, far shorter than the RT, and not long enough to prepare the return to the home positions. Overall, the reversal movement was likely prepared during the RT as two integrated segments, and deferred processing did not preclude an over-additive interaction between asymmetric and reversal movements.

5.4.2 Response selection

The results clearly suggest that the RT cost is caused by greater processing demands on response selection for bimanual asymmetric movements than symmetric movements. Response selection involves deciding what movement to make based on the imperative stimuli and the task instructions. Selection for bimanual asymmetric movements may take longer as a different unimanual movement is selected for each arm. In contrast, this process may be shorter for bimanual symmetric movements, as the same unimanual movement is selected for both arms. There is another process during response selection that could cause the bimanual asymmetric cost to select two different unimanual movements. A common finding from bimanual coordination research is that bimanual movements are not simply the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit (Kelso et al. 1979a, b; Swinnen and Wenderoth 2004). For example, there are
temporal and spatial constraints on bimanual movements that cause the two arms to have more similar timing and trajectories (Swinnen 2002). We have previously argued that the integration of two different unimanual movements into a bimanual asymmetric movement may take longer than the integration of two of the same unimanual movements (Blinch et al. under review; more on this study in section 5.4.3). This process may involve transforming the unimanual responses for each arm into a bimanual response for both arms. The temporal and spatial constraints for symmetric bimanual movements must be overcome when two different unimanual responses are integrated into a bimanual asymmetric movement, and this may cause greater processing demands for asymmetric movements than symmetric ones. The critical unification of a bimanual movement could occur during response selection and cause the bimanual asymmetric cost. The AFM logic supports that increased processing demands on response selection causes the asymmetric cost, but it cannot distinguish the processes that occur during response selection. Future experiments could investigate the contribution of selecting and integrating two different unimanual movements to the bimanual asymmetric cost.

The RT cost to select or integrate bimanual asymmetric movements with direct cues also occurs with symbolic cues (Diedrichsen et al. 2006). Two different unimanual movements must be selected and integrated regardless of the type of cue. With symbolic cues, however, there is also an RT cost to translate two different symbolic cues into target locations (Diedrichsen et al. 2001, 2006). This cost does not occur with direct cues, as the cues directly specify the target locations. It is important to differentiate between these two bimanual asymmetric costs that both occur during response selection. To review, the two bimanual asymmetric costs are as follows: 1) a cost to select or integrate two different unimanual movements, which occurs with direct and symbolic cues, and 2) a cost to translate two different symbolic cues.
5.4.3 Bimanual unification

At first glance, the results from Blinch et al. (under review) and the present experiment seem at odds. Blinch et al. suggested that response programming causes the asymmetric cost and the results of the present study suggest the cost is caused by response selection. This paradox can be explained by differences in how the tasks in the two studies were presented and conceptualised by the participants. The two targets for a bimanual movement were cued at the same time in the present experiment and in most bimanual studies (e.g. Blinch et al. 2014; Heuer and Klein 2006b; Kelso et al. 1979b). The AFM results suggest that integrating two different unimanual movements into a bimanual movement caused an asymmetric cost during response selection. In other words, the process of bimanual unification caused the asymmetric cost, and this process occurred during response selection. In the study by Blinch et al., one target was precued before the imperative stimulus. The precued target was selected before the imperative stimulus and the other movement was selected after the imperative stimulus. This temporal separation of response selection may have delayed the costly process of bimanual unification from response selection to response programming. That is, bimanual integration was likely deferred to response programming when the movement preparation of each arm was temporally separated with one precue.

The paradoxical results from Blinch at al. (under review) and the present study suggest that bimanual unification is a malleable process that, depending on the task, can occur during response selection or response programming. In the typical case, when both targets are cued at the same time, the integration of two unimanual movements into a bimanual movement likely occurs during response selection. Interestingly, other studies have shown that changing how bimanual movements are conceptualised can also eliminate various forms of asymmetric costs (reviewed by Swinnen and Wenderoth 2004). These conceptualisations may eliminate the need to unify two unimanual responses into a bimanual response. Instead, the processing during movement preparation may always be on a unified representation of the bimanual movement, bypassing the costly processes of bimanual unification. For example, Franz and McCormick (2010) showed that the RT cost for bimanual reaches with asymmetric
amplitudes was eliminated when the two targets were perceptually unified. This was accomplished by connecting the two circular targets with a bar. This may change movement preparation so that a single target is discriminated and then a single, bimanual response is selected. A specific process of bimanual integration is no longer needed and asymmetric costs are reduced or eliminated. [There are also examples of various conceptualisations reducing bimanual interference during continuous bimanual movements (reviewed by Swinnen and Wenderoth 2004).] Overall, the unification of unimanual movements is likely a malleable process. It can occur during response selection, response programming, or it can be bypassed entirely.

To summarise, the present results support that bimanual asymmetric movements that are directly cued place greater processing demands on response selection than bimanual symmetric movements. Selecting or integrating two different, asymmetric responses may cause this bimanual asymmetric RT cost. Stimulus identification and response programming did not contribute to the asymmetric cost. These novel findings, particularly the lack of cost for response programming, could be explored with further research; one possibility is to use the effect-propagation technique (theory by Pashler and Johnston 1998; an example study by Miller and Reynolds 2003) to confirm that increased processing demands on response selection, and not response programming, causes the bimanual asymmetric cost. Although response selection contributed to the asymmetric cost in this task, it is important to consider how movement preparation is altered with changes in how the task is presented and conceptualised by participants. In the typical scenario when the two targets of a bimanual movement are cued simultaneously, a response for each arm is simultaneously selected and then these responses are integrated into a bimanual response. Therefore, the process of bimanual unification occurs during response selection and causes the bimanual asymmetric cost.
6 General discussion

6.1 The road so far

The discussion of potential movement preparation costs for bimanual reaching movement led us to the first thesis study (Chapter 2). I tested whether movement preparation was longer for bimanual symmetric movements compared to unimanual movements (a potential bimanual symmetric cost) and whether preparation was longer for bimanual asymmetric movements compared to bimanual symmetric movements (a potential bimanual asymmetric cost). RTs were measured in simple and choice RT tasks. Donders’ subtraction method (1969) was used to isolate any bimanual costs to stages of movement preparation that are unique to simple RT tasks (imperative stimulus recognition and response initiation) or choice RT tasks (target discrimination, response selection, and response programming). The results showed that RTs were comparable for all types of movements in simple RT; that is, there was neither a bimanual symmetric cost nor an asymmetric cost. Therefore, unimanual, bimanual symmetric, and bimanual asymmetric movements have comparable complexity during imperative stimulus recognition and response initiation. In choice conditions, there was no bimanual symmetric cost but there was a bimanual asymmetric cost, indicating the preparation of asymmetric movements is more complex than symmetric movements.

12 “This concept [task complexity], which is prominent in comparing various RT paradigms, does not have a univocal definition or a single objective unit of measurement independently of RT. It may even be premature to impose a too restrictive criterion for its scientifically useful meaning. In the present context, the term complexity refers to the information load of the given task, which is usually described in terms of (1) the number of task elements the subject must attend to; (2) the degree of prior uncertainty about the requires response; (3) the degree of essential stimulus or response discrimination involved in the task; (4) the degree of stimulus-response compatibility; (5) the number of decisions that have to be made to achieve a correct response; or (6) the amount of prior-learned information that must be retrieved from short- or long-term memory to make the correct response. Reliable measures of RT are highly sensitive to remarkably slight variations in any of these conditions or complexity. In groups of college students, for example, there is an average difference of 40-50 ms even between [simple] RT and two-[choice] RT, when there is an optimal preparatory signal and the RT in each case is simply a bright green light going ‘on,’ always in the same location ([simple] RT), or randomly in one of two locations ([choice] RT)” (Jensen, 2006, p 205).
This bimanual asymmetric cost could be caused by increased processing demands on target discrimination, response selection, or response programming.

The goals of the second study (Chapter 3) were to determine which symmetric movement parameters facilitate the preparation of bimanual movements and to compare the size of the facilitation for different parameters. Participants performed bimanual reaching movements that varied in terms of the symmetry/asymmetry of starting locations, movement amplitudes, and target locations. RT savings were examined by comparing movements that had one symmetric parameter (and two asymmetric parameters) to movements with all asymmetric parameters. I observed significant savings for movements with symmetric amplitudes and movements with symmetric target locations. RT costs were examined by comparing movements that had two asymmetric parameters (and one symmetric parameter) to movements with all symmetric parameters. I observed significant RT costs for all movements with asymmetric amplitudes. These results suggest that movement preparation is facilitated when amplitudes or target locations are symmetric and that movement preparation suffers interference when amplitudes are asymmetric. The relative importance of the three parameters to movement preparation, from most to least important, is movement amplitudes, target locations, and then starting locations.

The third study (Chapter 4) tested the demands on the movement preparation of bimanual movements by temporally separating the preparation of each arm. This was achieved by precuing the target of one arm before the imperative stimulus. We asked: What was prepared in advance when one arm was precued? The answer to this question suggested which process caused the bimanual asymmetric cost. Movement preparation before the imperative stimulus was examined by comparing RTs with and without a precue for the left target and by using the start-react effect. Participants made bimanual symmetric and asymmetric reaching movements in simple and 2-choice RT conditions and a condition with a precue for the left target. I found a bimanual asymmetric cost in 2-choice conditions, and the asymmetric cost was significantly smaller when the left target was precued. These results suggested: 1) that the precued movement was not fully programmed but partially programmed before the imperative
stimulus, and 2) that the asymmetric cost was caused by increased processing demands on response programming. The results of the startle trials also supported these two conclusions. Overall, the results support the notion that bimanual movements are not the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit. When one target is precued, this critical unification likely occurs during response programming.

In the final study (Chapter 5), I asked: Which stages of movement preparation contribute to the bimanual asymmetric cost with direct cues? The bimanual asymmetric cost may be caused by increased processing demands on any stage (or stages) of movement preparation that are unique to choice RT: specifically, target discrimination, response selection, or response programming. The additive factors method (Sternberg 1969) was used to test the contributions of each stage. This involved: altering the stimulus contrast (bright or dim), the response compatibility (compatible or incompatible), and the response complexity (reaches or reversals). These manipulations changed the processing demands on target discrimination, response selection, and response programming, respectively. Incompatible bimanual asymmetric movements were the only movements that had an over-additive RT interaction. This suggested that the bimanual asymmetric cost was caused by increased processing demands on response selection and that target discrimination and response programming did not contribute to the cost. The asymmetric cost was caused by response selection despite the use of direct cues that place fewer processing demands on translation processes compared to symbolic cues. Selecting or integrating two different, asymmetric responses could have increased the processing demands on response selection. Although response selection contributed to the asymmetric cost in this task, altering movement preparation may change when the bimanual asymmetric cost occurs or the magnitude of the cost.
6.2 Interpretations and reinterpretations

The combination of these thesis studies allows for interpretations, and reinterpretations, of the separate results. Let us begin with which stage of information processing causes the bimanual asymmetric RT cost. In the first study, I hypothesised that response programming was the most likely source of the asymmetric cost. Study four sought to determine which stage of movement preparation caused the asymmetric cost. Interestingly, the results supported that response selection and neither target discrimination nor response programming caused the asymmetric cost. The results from studies one and four are in agreement that there is a movement preparation cost for bimanual asymmetric movement in choice RT tasks. However, the evidence from study four that response selection causes the asymmetric cost is stronger than my hypothesis in favour of response programming in study one. My argument in favour of response programming in study one was supported by the theoretical framework by Heuer (1986, 1993); it proposed that response programming is a source of bimanual interference. However, study one (as well as the studies that supported Heuer’s model) could not rule out possible contributions to the RT cost from response selection. The potential contribution from response selection was discounted because my thesis experiments used direct cues that, compared to symbolic cues, place fewer processing demands on response selection (Diedrichsen et al. 2001). Even with direct cues, however, two targets must be translated into a bimanual response, and we now know that this takes longer for two different targets than two identical targets (a bimanual asymmetric response vs. a symmetric response).

The asymmetric bimanual reaches in the first study involved reaching different amplitudes to different target locations. The second study (Chapter 3) was designed to determine how these parameters, as well as starting locations, contributed to asymmetric costs. The results suggest that the relative contribution of the three parameters to the asymmetric costs, from most to least important, was movement amplitudes, target locations, and then starting locations. Starting locations may have had the smallest contribution to the asymmetric costs as they were known before the imperative stimulus and could be accounted for before the RT. This may be similar to
the lack of asymmetric cost in the first study when the asymmetric parameters were known in advance; specifically, there was no cost for movements with asymmetric amplitudes and target locations in a simple RT task.

There were costs for asymmetric amplitudes and target locations in the second study, with asymmetric amplitudes having the largest contribution to the costs. Interestingly, the costs for asymmetric amplitudes and target locations may have been additive. Based on the AFM (Sternberg 1969), this suggests that the costs for these parameters occur during separate preparation processes. This can be integrated with the finding that the asymmetric cost was caused by response selection (study four). Therefore, the results from studies two and four suggest that when bimanual movements are cued by the imperative stimulus, the selection of movement amplitudes and target locations are serial processes during the response selection stage. The AFM, unfortunately, cannot determine the order of these processes. The caveat is that the fourth study tested movements with asymmetric directions and not movements with asymmetric amplitudes and target locations. It is most likely that all parameters place increased processing demands on the same stage of movement preparation, namely, response selection. There is a slight possibility that asymmetric amplitudes and target locations increase processing demands on a different stage than asymmetric directions. This possibility is unlikely because all movement parameters (amplitudes, targets, directions, etc.) contribute to the selection and programming of a response. In other words, the asymmetric cost is unlikely to be specific to movement directions, but rather a cost to select any different movement parameter for each arm.

If we entertain the possibility that the cost for movement with asymmetric amplitudes and target locations might be caused by a process other than response selection, then there are some studies that argue against a contribution from target discrimination. First, Han et al. (1999) argued that there could be a cost when targets are physically apart if they are no longer conceptually processed as a gestalt. However, Albert et al. (2007) found that the perceptual similarity or dissimilarity of the bimanual targets did not affect RT. If perceptually similar targets were grouped as a gestalt, then RTs for perceptual similar targets should be shorter than dissimilar targets that are
unlikely to be grouped. The comparable RTs for similar and dissimilar targets suggest that perceptually similar targets are not processed as a gestalt. Therefore, there should be no cost during target discrimination for movements with asymmetric amplitudes and target locations. The second result that refutes the possibility of a cost during target discrimination is from the fourth study of this thesis. In that study, symmetric targets were 15 cm apart and asymmetric target were 25 cm apart, with a difference between asymmetric and symmetric movements of 10 cm \((25 - 15 = 10)\). The results showed that a 10 cm difference was not large enough to cause a cost during target discrimination. The difference between asymmetric movements with different amplitudes and target locations and symmetric movements in studies one and two was only 3 cm \((18 - 15 = 3)\). If a difference of 10 cm did not cause a cost during target discrimination, then it is unlikely that a smaller difference of 3 cm would cause a cost. Therefore, when two different targets are cued at the same time, the asymmetric cost is likely caused by increased processing demands on response selection for any movement parameters that differ between the two arms. I will address in sections 6.4 and 6.5 how the asymmetric cost can be deferred to response programming or eliminated when there is one target for both hands or when one target is precued.

### 6.3 Bimanual unification and the stages of movement preparation

A common finding from bimanual coordination research is that bimanual movements are not simply the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit (Kelso et al. 1979a, b; Swinnen and Wenderoth 2004). For example, there are temporal and spatial constraints on bimanual movements that cause the two arms to have more similar timing and trajectories (Swinnen 2002). The findings from this thesis adds that the integration of two different unimanual movements into a bimanual asymmetric movement may take longer than the integration of two of the same unimanual movements. Bimanual integration may involve transforming the unimanual responses for each arm into a bimanual response for both arms. The temporal and spatial
constraints for symmetric bimanual movements must be overcome when two different unimanual responses are integrated for a bimanual asymmetric movement, and this may cause greater processing demands for asymmetric movements than symmetric ones. The AFM study supports that if the critical unification of a bimanual movement causes the asymmetric cost when two targets are cued at the same time, then it occurs during response selection.

Figure 6.1 depicts the addition of the process of bimanual unification to the stages of movement preparation for symmetric and asymmetric movements. Discrimination of the target and selection of the response occurs separately for the left and right arms. The first thesis study supported that these two processes within each stage occur in parallel – recall that movement preparation was comparable for unimanual and bimanual symmetric movements in choice RT tasks. Let us interpret this finding by considering one stage, say target discrimination. How can the duration of target discrimination of two targets for a symmetric movement be comparable to the discrimination of one target for a unimanual movement? The most likely explanation is that the left and right targets are discriminated in parallel. The same logic applies to selecting the response, but we must also consider the process of bimanual unification that also occurs during the response selection stage. After selecting two unimanual responses, these must be integrated into a single bimanual response. Bimanual unification likely takes longer for two different responses than two identical responses, because the temporal and spatial constraints in favour of bimanual symmetric movements must be overcome for a bimanual asymmetric movement (Figure 6.1, bottom vs. top). This integration changes the conceptualisation of the movement from two unimanual movements into one bimanual movement. Now that the response is unified, it can be programmed with a comparable duration for either a symmetric or an asymmetric movement.
6.4 Unification during response selection or programming

It is time to address the seemingly contradictory results from this thesis: Is the bimanual asymmetric cost caused by increased processing demands on response selection, as suggested by the AFM study, or by response programming, as suggested by the startle study? The asymmetry in both of these studies involved movements in different directions, so that was a fair comparison. An important difference was that the AFM study tested bimanual movements in 2-choice RT tasks and the critical condition in the startle study was a unilateral 2-choice task (where the target for one arm was precued). The precue in unilateral 2-choice allowed some movement preparation to occur before the imperative stimulus, and this is vital to understanding these seemingly contradictory results. Movement preparation before the imperative stimulus will also be referred to as advanced preparation. Advanced preparation does not contribute to the RT and can prevent RT costs; this was already seen for bimanual asymmetric movements in a simple RT task (study 1). I will add the prefix “pre” when a specific stage of movement preparation occurs before the imperative stimulus, for example pre-selection or preprogramming. One further complication is that processing from any stage may be split before and after the imperative stimulus. If only some response
selection occurs in advance, for example, then this will be referred to as partial pre-selection.

The results of the AFM study that implicated response selection in the bimanual asymmetric cost are straightforward, so let us discuss the more complicated results from the startle study. In the 2-choice RT tasks, bimanual asymmetric movements on startle trials had RTs that were longer than simple RT tasks. This suggested that asymmetric movements in 2-choice were not fully prepared before the imperative stimulus. This was expected, as the required response was unknown before the imperative stimulus. Startle RTs in unilateral 2-choice were longer than simple and comparable to 2-choice task, so a movement was not fully prepared in advance. However, the precue allowed some movement preparation to occur before the imperative stimulus and, importantly, this advance preparation reduced the size of the asymmetric cost. I will now detail two ways that movement preparation could have been divided before and after the imperative stimulus in the unilateral 2-choice task. The first involves bimanual unification occurring during response selection, as suggested by the AFM study, and we shall see that this cannot account for the reduction of the asymmetric cost. The second involves bimanual unification occurring during response programming, and it can account for the attenuation of the asymmetric cost.

In the first explanation, the precue allowed the target for the left arm to be discriminated and a response to be selected in advance (Figure 6.2). The evidence in favour of pre-selection was that the probability of a disrupted movement for the precued arm on startle trials was reduced when there was a precue. The target for the other arm was discriminated and a response was selected after the imperative stimulus. These two unimanual responses could then be unified into a bimanual response and then this response was programmed. The problem with this explanation is that bimanual unification – the process that causes the asymmetric cost – occurs after the imperative stimulus. Therefore, the size of the asymmetric cost should be comparable to 2-choice tasks (compared Figure 6.2 to Figure 6.1). As the asymmetric cost was reduced in unilateral 2-choice, I reject this explanation in favour of the next one.
Figure 6.2 Depictions of movement preparation in unilateral 2-choice for bimanual symmetric movements (top) and bimanual asymmetric movements (bottom). This division of preparation before and after the imperative stimulus (the vertical line) is based on bimanual unification occurring during response selection. The three stages of movement preparation are target discrimination (TD), response selection (RS), and response programming (RP).

The second explanation can account for the attenuation of the asymmetric cost. In this explanation, the precue also allowed the target for the left arm to be discriminated and a response to be selected in advance (Fig 6.4). In addition, a bimanual response was partially preprogrammed. A bimanual response was not fully pre-programmed because only the left response was known at this point. If a bimanual response was fully preprogrammed, then it should have been released by the startle tone with RTs comparable to simple RT tasks, and this was not the case. By the same logic, a unimanual response for just the precued arm was not fully preprogrammed or it would have been released by the startle tone with RTs comparable to simple tasks. Instead, the partially preprogrammed bimanual response may have included the response for the precued arm and both potential responses for the other arm. After the imperative stimulus, the target for the right arm was discriminated and the response was selected. The partially preprogrammed movement was then updated with the exact response for the right arm.

The key difference in the second explanation is that bimanual unification was deferred from response selection to response programming. The atypical scenario of
Precuing the target for one arm likely caused this change in bimanual unification. Bimanual unification during response programming was now divided before and after the imperative stimulus, and this caused the decrease in the size of the asymmetric cost (compare Figure 6.3 to Figure 6.1). I believe the unification of bimanual movements occurs during response selection in the typical scenario when the target for each arm is cued at the same time, and this was the case for 2-choice RT tasks in the AFM study. However, the critical process of bimanual integrating appears to be a malleable process that can occur during response selection or response programming.

Figure 6.3 Depictions of movement preparation in unilateral 2-choice for bimanual symmetric movements (top) and bimanual asymmetric movements (bottom). This division of preparation before and after the imperative stimulus (the vertical line) is based on bimanual unification occurring during response programming. The three stages of movement preparation are target discrimination (TD), response selection (RS), and response programming (RP).

There are a few potential ways to test which stages of movement preparation contribute to the asymmetric cost in unilateral 2-choice. One possibility is to re-run the AFM study with the unilateral 2-choice task instead of 2-choice tasks. If bimanual asymmetric movements have increased processing demands on response programming in the unilateral 2-choice task, then there should be an over-additive interaction between asymmetric movements and response complexity (reversal movement). Another possibility is to look for a lateralised readiness potential in unilateral 2-choice.
between the precue and the imperative stimulus. A lateralised readiness potential during the foreperiod would support partial preprogramming of the precued movement and bimanual unification during response programming. If a lateralised readiness potential is not seen, then there are two conclusions: 1) partial preprogramming did not occur or 2) the partial preprogramming occurred in both hemispheres and was not lateralised. The second conclusion could be tested with a dipole source analysis during the foreperiod (c.f. Leuthold and Jentzsch 2002). Non-lateralised preprogramming would be supported by a dipole in the motor areas of both hemispheres.

### 6.5 Relationship between unification and conceptualisation

The process of bimanual unification may depend on how the task is presented and conceptualised. Two targets were directly cued in my thesis studies: one target for the left arm and one for the right arm. This task was likely conceptualised as two unimanual movements until the responses were integrated into a single bimanual response at the end of response selection (Figure 6.1). This integration took longer for bimanual asymmetric movements and caused the asymmetric cost. Interestingly, other studies have shown that changing how movements are conceptualised can eliminate various forms of bimanual asymmetric costs (reviewed by Swinnen and Wenderoth 2004). These conceptualisations may eliminate the need to unify two unimanual responses into a bimanual response. Instead, the processing during movement preparation may always be on a unified representation of the bimanual movement. This would bypass the unification during response selection and eliminate the cost for creating a bimanual asymmetric response.

Let us discuss two examples of conceptualisation that eliminate bimanual asymmetric costs. First, Franz and McCormick (2010) showed that the RT cost for bimanual reaches with asymmetric amplitudes was eliminated when the two targets were perceptually unified. This was accomplished by connecting the two circular targets with a bar. This may change movement preparation so that a single target is
discriminated and then a single, bimanual response is selected (Figure 6.4). A specific process of bimanual integration is no longer needed and asymmetric costs are eliminated. Second, White and Diedrichsen (2010) had participants move a cursor into a target by making reaching movements with the left arm, the right arm, or both arms. The position of the cursor was determined by the mean location of both arms for the bimanual movements. A visible error was introduced at movement initiation and the subsequent online corrections were compared. The dominant arm initiated an online correction before the nondominant arm in the unimanual conditions. In the bimanual condition, the dominant arm initiated a correction after the nondominant arm. It was interesting that a bimanual asymmetric correction was used instead of a symmetric one and that the opposite initiation pattern was seen for bimanual movement (nondominant then dominant) than unimanual ones (dominant then nondominant). White and Diedrichsen reasoned that the error in the cursor's locations was unequally assigned to the two arms in bimanual conditions and this caused a bimanual asymmetric correction. I would argue that bimanual asymmetric corrections were initiated as quickly as unimanual correction (i.e. no bimanual asymmetric cost) because the single cursor for the two arms allowed the two unimanual movements to be represented as a single bimanual movement. The unified goal of reaching the target was accomplished, and it was irrelevant to this bimanual task that each arm contributed differently to the online correction. There are also examples of various conceptualisations reducing bimanual interference during continuous bimanual movements (reviewed by Swinnen and Wenderoth 2004). Several studies have shown that difficult relative phase patterns are much easier when a single stimulus represents the position of both arms (e.g. Kovacs et al. 2009; Swinnen et al. 1997). Continuous bimanual asymmetric movements are also facilitated when the two arms share a single goal (Franz et al. 2001).
Figure 6.4 Depiction of movement preparation for bimanual movements that are facilitated with conceptualisations. A single target is discriminated and then a single, bimanual movement is selected and programmed. This bypasses the costly process of integrate two unimanual movements into a single bimanual movement. The vertical line depicts the imperative stimulus. The three stages of movement preparation are target discrimination (TD), response selection (RS), and response programming (RP).

It is possible to further test the hypothesis that bimanual conceptualisations can eliminate bimanual asymmetric costs. Franz and McCormick (2010) have shown that connecting the targets of bimanual asymmetric movements eliminated the asymmetric RT cost. The AFM study could be re-run with connected targets instead of separate targets. If connected targets eliminate the need to integrate the two unimanual responses into a single bimanual response, then the over-additive interaction between asymmetric movements and response compatibility should also be eliminated.

Overall, changes in when bimanual integration occurs or whether bimanual integration is needed suggest that the preparation of bimanual movements is flexible. Bimanual integration can occur during response selection, response programming, or it can be bypassed entirely. Deferring the asymmetric cost from response selection to response programming when one target is precued may also be an example of a conceptualisation. Precuing one target has a large affect on movement preparation, and it may also affect how the task is conceptualised. As conceptualisations can eliminate asymmetric cost, it should not be surprising that the process of bimanual integration was altered by a precue.
6.6 Future directions

There are many potential extensions to these thesis studies, but I will limit the discussion in this section to two important research questions that I am investigating. The first potential extension is to the findings from study two on the contributions of staring locations, movement amplitudes, and target locations to asymmetric costs. Recall that movement amplitudes had the largest contribution to the asymmetric costs. Another movement parameter that has an asymmetric RT cost is movement directions (studies three and four). Moving in different directions requires the activation of antagonistic (or nonhomologous) muscles in opposite arms. It has been shown with continuous bimanual movements that coordination is less stable and requires more attention for movements that require simultaneous activation of antagonistic muscles compared to agonist muscles (Monno et al. 2002; Swinnen 2002). The first proposed study would ask: What is the relative contribution of movement directions and movement amplitudes to the asymmetric cost of bimanual reaching movements?

Three experiments will test the relative contributions of movement directions and movement amplitudes to movement preparation. All three experiments will use a button box with five rows and two columns of buttons, similar to the button box in study two. The participants will begin by pressing and holding down the left and right buttons in the middle row. In the first study, a bimanual movement will be cued after a variable foreperiod by cueing two targets. The participants will be instructed to react and hit the targets as quickly as possible. The four potential targets for the right hand combined with the four potential targets for the left hand for a total of sixteen potential bimanual movements. These will be divided into four categories based on the symmetry and asymmetry of the movement directions and amplitudes:

1. Symmetric directions and amplitudes
2. Symmetric directions and asymmetric amplitudes
3. Asymmetric directions and symmetric amplitudes
4. Asymmetric directions and amplitudes
I hypothesize that there will be RT costs for asymmetric directions and for asymmetric amplitudes and that the cost for asymmetric directions will be larger than the cost for asymmetric amplitudes. This would support a hierarchy of movement parameters that affect the preparation of bimanual movements, which was suggested by study two. The relative importance of the three parameters in study two to movement preparation, from most to least important, was movement amplitudes, target locations, and then starting locations. The hypothesised results for this study would suggest that movement directions should be added to the front of the list as the most important parameter for movement preparation. It would also suggest that preparing antagonistic muscles for different directions takes longer than preparing different levels of activation of agonistic muscles for different amplitudes. I also predict an RT interaction between asymmetric directions and amplitudes. Based on the AFM logic, this would support that asymmetric directions and amplitudes increase processing demands on the same stage of information processing, specifically, response selection. An over-additive interaction would suggest that both parameters are prepared simultaneously, and an under-additive interaction would suggest they are prepared serially with some overlap.

The second study involves precuing four targets during the foreperiod. The precues will specify movements with:

1. Symmetric directions
2. Asymmetric directions
3. Symmetric amplitudes
4. Asymmetric amplitudes
5. Ambiguous information about the amplitudes and directions

(This study is a bimanual version of Goodman and Kelso 1980.) If directions make a larger contribution to movement preparation than amplitudes, then movements with direction precues should have shorter RTs than movements with amplitude precues. I also predict that RTs should be comparable when either symmetric directions or asymmetric directions are precued. In both cases the directions can be prepared in advanced. This is similar to how RTs were comparable in study one for bimanual
symmetric and asymmetric movements when they were prepared in advance in simple RT tasks. The third study is a control for the second study. Differences in RTs could be caused by attentional factors; for example, stimulus identification could be shorter for some types of precues. To test this, the precue task will be changed into an imperative stimulus recognition task. The same precues will be used but only one target will be cued as the imperative stimulus. Participants will be instructed to respond to the imperative stimulus as quickly as possible by lifting both fingers off the home buttons. Differences in RTs will reveal attentional cost for the precue conditions. Potential costs can be subtracted from the costs in the second study to isolate bimanual costs attributed to response selection or programming. The second and third studies will be used to confirm the result and the theoretical predictions of the first study. I predict that the RT costs from the first study will be seen even when attentional costs are controlled. It will be revealing to see whether there will be attentional costs for bright stimuli that do not require eye movements; this would be something like a Hick's law for stimulus alternatives.

The second potential extension is to test the putative process of bimanual unification. Two experiments will address the following question: How are bimanual movements integrated and de-integrated? The idea is to isolate and investigate the process of bimanual unification from the other processes of movement preparation. This will be done with two applications of the reprogramming technique (Rosenbaum and Kornblum 1982): a unimanual condition and a bimanual condition. In the unimanual condition, participants will be precued with two potential unimanual movements: one for the left arm and one for the right arm. On 80% of the trials, one of these two movements will be cued by the imperative stimulus. The participant will need to discriminate the imperative stimulus, inhibit the prepared response for one arm and excite the prepared response for the other arm (Hasbroucq et al. 2000). On 20% of the trials, a bimanual movement will be cued that consists of the precued unimanual movements. These two unimanual movements were prepared in advance, but now a bimanual movement is required. If two unimanual movements must be integrated into a single bimanual movement, then this process will be isolated to the RT of bimanual
trials. If unimanual movements are integrated into a bimanual movement, then reprogramming will be required to unify the two unimanual movements into a single bimanual movement. If bimanual unification does occur, then I predict that bimanual asymmetric movements will have longer RTs than bimanual symmetric movements. This prediction follows from my explanation of the bimanual asymmetric cost in the AFM study; bimanual asymmetric movements require increased processing to overcome spatial and temporal coupling that favours bimanual symmetric movements. It is also possible that bimanual unification does not occur. If that is the case, then reprogramming unimanual movements into bimanual symmetric or asymmetric movements should have comparable RTs.

In the bimanual condition, participants will be precued with a bimanual movement. This movement will be cued on 80% of the trials, and on 20% of the trials a unimanual movement will be cued. If bimanual movements are integrated, then cuing a unimanual movement will require the bimanual movement to be de-integrated into two unimanual movements. This process of de-integration might take longer for bimanual asymmetric movements compared to symmetric ones. One reason is that the temporal coupling of bimanual movements may need to be reversed when a unimanual movement is required. The timing of each arm of a bimanual symmetric movement is similar, and so the de-integration into a unimanual movement should have short RTs. The timing of each arm of a bimanual asymmetric movement is also similar, but they are unlike the timing of their unimanual counterparts. When a long-distance movement is paired with a short-distance movement, for example, the movement time of the short movement is extended to be more like the long movement (Kelso et al. 1979b). The de-integration of a bimanual asymmetric movement might require that the temporal coupling be reversed. This would cause longer RTs to de-unify bimanual asymmetric movements compared to symmetric ones. Alternatively, the temporal coupling of bimanual asymmetric movements may persist when a unimanual movement is required. If this is the case, then a unimanual short-distance movement that was originally prepared as a bimanual asymmetric movement will have a longer movement time than a control unimanual movement that was not reprogrammed. This would entail that
bimanual movement are not completely de-integrated into unimanual movements, a form of hysteresis in reprogramming. It should also follow that this partial de-integration of bimanual movements has comparable RTs for symmetric and asymmetric movements. In summary, the results from this thesis suggest that the unification of unimanual movements into bimanual movements may cause the bimanual asymmetric costs. The reprogramming study is a potential way to isolate and investigate this process of bimanual unification.

6.7 Summary

In conclusion, bimanual asymmetric movements in choice RT tasks take longer to prepare than bimanual symmetric movements (study one). Many different movement parameters can cause bimanual asymmetric costs. The result from study two suggested that the relative contribution of three parameters to the asymmetric cost, from most to least important, was movement amplitudes, target locations, and then startling locations. Studies three and four investigated the preparation of movements with symmetric and asymmetric movement directions. Study four used the AFM and found that the asymmetric cost was caused by increased processing demands on response selection. Target discrimination and response programming – contrary to previous hypotheses – did not contribute to the asymmetric cost. The bimanual asymmetric RT costs in all of these studies were likely caused by the need to unify both arms into a single bimanual movement. Bimanual unification may take longer for bimanual asymmetric movements than symmetric ones because asymmetric movements must overcome spatial and temporal coupling that favour symmetric movements. This processes of bimanual integration occurs during response selection when both targets are cued at the same time (study 4), during response programming when one target is precued (study 3), and it may be bypassed entirely when the movement is presented or conceptualised as a single bimanual movement and not as two unimanual movements. Overall it seems that the information processing of bimanual reaching movements must ultimately lead to the execution of a unified
bimanual movement. Future studies will investigate this putative process of bimanual integration. It may be possible to de-integrate bimanual movements into independent unimanual movements with expertise from extended practice. It could be revealing to investigate the asynchronous and asymmetric bimanual movements made by athletes, dancers, and musicians to see how their movements range from being complex integrations to completely independent. However, bimanual integration – and bimanually interference for asymmetric movements – defines the default mode of coordination that typifies coordinated actions in daily life.
References


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Appendices

Appendix A: literature review

A.1 In the beginning

One of the foundational investigations into bimanual coordination was done by Kelso et al. (1979a, b).¹³ They reasoned that the principles governing coordination could be discovered by determining the units that the nervous system controls; specifically, the nervous system may constrain certain elements of a coordinated movement to act as a single unit. This coordinative structure would emerge as a common parameter to multiple types of movements. They tested bimanual reaching movements with different movement amplitudes and target widths for common elements.

Reaching movements were made to either an “easy” target that had a short movement amplitude (6 cm) and a large target width (7.2 cm) or a “hard” target that had a large movement amplitude (24 cm) and a small target width (3.6 cm). It is well documented that movement times are longer for unimanual movements with larger movement amplitudes and smaller target widths (Fitts, 1954; Fitts and Peterson, 1964). Kelso et al. were curious about what would happen to the movement times when an easy target with one arm was combined with a hard target for the other arm into a single, bimanual reaching movement. Several different types of unimanual and bimanual movements were tested. Unimanual movements with the left and right arms were made to the easy and hard targets. This was done to confirm that Fitts’ law can describe the movement times in this task. Some of the bimanual movements were made to targets with equivalent difficulty; this could be either easy or hard targets with both arms. These are referred to as bimanual symmetric reaching movements. Asymmetrical

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¹³ There were earlier investigations on bimanual movements; for example, Woodworth commented on the coupling of bimanual movements, but a cascade of research followed the study by Kelso et al. (1979b).
reaching movements involved different difficulty targets with each arm (a hard target for the left arm and an easy target with for right or vice versa).

The three types of movements (unimanual, bimanual symmetric, bimanual asymmetric) resulted in eight movement conditions (unimanual: left long, left short, right long, right short, bimanual symmetric: long-long, short-short, bimanual asymmetric: long-short, short-long) that were tested in different blocks. Each condition had only one type of movement, so it was a simple reaction time (RT) task. Anticipation of the imperative stimulus was minimised by using a variable 1-3 s foreperiod. In simple RT, the RT measures the duration of imperative stimulus identification, response initiation, and motor time; target discrimination, response selection, and response programming can occur before the imperative stimulus (Summers and Anson 2009). Participants were instructed to hit the target(s) as fast and accurately as possible. No instructions were given on the simultaneity of movement initiation in bimanual blocks to prevent instructional bias.

The studies by Kelso et al. (1979a, b, 1983) included similar experiments that altered the orientation of the movements. They tested lateral movements away from the midline of the body, lateral movements towards the midline, forward movements, and lateral movements to the right. This was done to ensure that their findings were replicable across movement with different biomechanical factors. The results in the five experiments were consistent, so we will present mean data collapsed across the experiments.

In accordance with Fitts' law, unimanual movements to hard targets had longer movement times (171 ms) than unimanual movements to easy targets (104 ms; Figure A.1). Bimanual symmetric movements showed the same trend, with longer movement times to hard targets (182 ms) than to easy targets (116 ms). Asymmetric movements to hard targets (176 ms) had comparable movement times to symmetric hard targets (182 ms). The interesting result was related to the movement times of the other half of the asymmetric movements, specifically, the arm that moved to the easy target. The movement times of easy asymmetric movements (156 ms) were significantly longer than easy symmetric movements (116 ms). The extended movement times of easy
asymmetric movements (156 ms) were still significantly shorter than *hard* asymmetric movements (176 ms).

Why would the movement time of the *easy* asymmetric movement be drawn to the movement time of the other arm (the *hard* asymmetric movement)? Kelso et al. argued that the arms were constrained to function as a single unit. More specifically, a central command sets the destination for each arm (the hard or easy target), and the specifics of the bimanual coordination are left to low-level automatisms that cause similar movement times for asymmetric movements. The attraction of the easy movement time to the hard movement time is known as temporal coupling. Kelso et al. interpreted temporal coupling as evidence for a coordinative structure. Kinematic data was also analysed to show that the temporal kinematic landmarks (e.g. time to positive peak acceleration and time to peak velocity) of asymmetric movements, like movement time, showed temporal coupling (Figure A.2). The easy asymmetric movement, for example, slowed down to have temporal landmarks that were similar to the hard movement. Equating movement times and temporal landmarks for asymmetric movements may simplify coordination by reducing the degrees of freedom.
Kelso et al. (1983) reasoned that the coordinative structure might also constrain the spatial elements of bimanual movements to act as a single unit. To test this, an obstacle was added to the path of one arm to see whether it would exert an influence on the other arm. The kinematic profiles of four of the seven participants showed that spatial elements could be constrained to act as a single unit (Figure A.3, left). Notice that the right arm increased its trajectory height to match the left arm even though there was an obstacle on only the left side. This spatial coupling was not seen in every participant; three out of the seven participants did not increase the trajectory height of the right, unobstructed arm (Figure A.3, right). It has subsequently been shown that temporal coupling is typically stronger than spatial coupling (Swinnen 2002). This may explain why temporal coupling was seen in all participants and spatial coupling was seen in most participants.
Figure A.3 A Trajectory from two participants as they make a bimanual movement with a hurdle for the left arm. The participant on the left has strong spatial coupling, with the trajectory height of the right arm increasing to be comparable to the left arm. The participant on the right, in contrast, has weak or no spatial coupling. Adapted from Kelso et al. (1983)

Kelso et al. (1979a, b, 1983) also showed that RTs were not significantly different for each arm in a bimanual movement. They argued that simultaneous movement initiation was another example of temporal coupling and the underlying coordinative structure. RTs of unimanual and bimanual movements are important for my thesis, so I will briefly summarise the RT results. Easy bimanual asymmetric movements had longer RTs (243 ms) than easy symmetric movements (228 ms). Hard asymmetric RTs (239 ms) were not statistically compared to hard symmetric RTs (238 ms) but they are visibly similar, so we cannot conclude that all asymmetric movements have longer simple RTs than symmetric movements. RTs of easy (218 ms) and hard (224 ms) unimanual movements were shorter than easy (236 ms) and hard (238 ms) bimanual movements, but these bimanual movements included symmetric and asymmetric movements. It would be more interesting to compare the RTs of unimanual movements to only bimanual symmetric movements. The last thing to note is that these are simple RTs, so they reflect changes in the durations of imperative stimulus identification, response initiation, and/or motor time but neither response selection nor response programming. A choice RT task could be used to include response selection and programming in the RT.

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14 We will later show more powerful analysis of differences in response initiation that have small (~8 ms) but significant difference in reaction time for asymmetric movements. The movements still exhibit “almost perfect synchrony,” (Kelso et al. 1979a, pp 236) so these differences do not undermine the existence of temporal coupling.

15 Most of the reaction time analysis appeared in Kelso et al. 1979a and neither 1979b nor 1983.
A.2 Theories of bimanual coordination

Some researchers (notably Marteniuk and MacKenzie 1980; Marteniuk et al. 1984) felt that a coordinative structure was an improper explanation for movements that were not perfectly synchronous. Marteniuk et al. proposed an alternative theory that involved neural crosstalk between the two movements. In retrospect, both the neural crosstalk and coordinative structure theories are well founded and have resulted in two fruitful ways to frame coordination research. Coordinate structures have evolved into dynamic pattern theory; it is a bottom-up perspective that posits that stable coordination patterns emerge from the dynamic process of self-organising subsystems (reviewed by Swinnen 2002; Swinnen and Wenderoth 2004). It has mainly been used to study continuous movements, but it can be applied to discrete movements (e.g. Kelso et al. 1979a, b, 1983).

Neural crosstalk is associated with the information processing theory. This top-down perspective states that information processing in the central nervous system results in the creation of a motor command (also reviewed by Swinnen 2002; Swinnen and Wenderoth 2004). It is an unanswered question whether bimanual movements require a motor command for each limb or an integrated command for both limbs.
Coordination is typically examined from either the information processing or the dynamical systems perspective, but they may be describing two sides of the same coin (e.g., Amazeen 2002). Independent of the bimanual theories, neurophysiologists have identified several neural pathways that may result in spatial or temporal coupling, or, more generally, bimanual interference (reviewed by Carson 2005).

### A.3 Bimanual interference and neural pathways

Bimanual interference may result from neural interactions at multiple levels of the central nervous system (Swinnen 2002). I will briefly discuss three interactions that are commonly cited in bimanual research: uncrossed corticospinal fibers, bilateral corticospinal projections, and the corpus callosum. Almost all of the corticospinal fibers cross to the contralateral side of the nervous system in the pyramidal decussation. This causes the contralateral control of the left arm by the motor areas in the right hemisphere (Kandel et al. 2000). The contralateral hemisphere, therefore, controls each arm of a bimanual movement. Some of the corticospinal fibers, typically 10 to 15%, do not cross in the pyramidal decussation and innervate ipsilateral motor neurons (Carson 2005). These ipsilateral paths may cause bimanual inference (Figure A.5).

*Figure A.5* Depiction of corticospinal fibers from one hemisphere that either cross or do not cross at the pyramidal decussation.
Imagine that you are going to make a long-distance movement with your left arm and a short-distance movement with your right arm, a bimanual asymmetric movement. A motor command that causes a lot of force – what I will call a “large” motor command – will travel from your right hemisphere to your left arm in order to produce a long-distance movement. A short-distance movement in your right arm is caused by a “small” motor command from the left hemisphere. These commands travel the contralateral pathways, but we also need to consider the small percentage of fibers in the ipsilateral pathways. The ipsilateral pathways will transmit the large motor command from your right hemisphere to your right arm, the arm that should do a short-distance movement. This interference from the ipsilateral pathways may increase the motor command of the short-distance movement, causing it to travel too far.

The opposite pattern of interference in the other arm is possible: the small motor command from the ipsilateral pathways may cause the long-distance movement to undershoot. In bimanual experiments, it is more common to see the long-distance movement influence the short-distance movement (or, more generally, for the hard movement to influence the easy movement). It has been suggested that the interference may be proportional to the size of the motor command (Marteniuk and MacKenzie 1980). The long-distance movement has a “larger” motor command, so it has a greater influence on the short-distance movement than vice versa. The dominant arm may also result in larger interference on the non-dominant arm than the other way around (Cardoso de Oliveira 2002).

Another pathway for bimanual interference during the output of the motor command is the bilateral corticospinal projections. Typically, a corticospinal axon innervates a single motor neuron pool (Kandel et al. 2000). There are some corticospinal axons that branch in the spinal cord and innervate motor neurons for the same muscle on both sides of the body (homologous muscles; Figure A.6). The bilateral fibers may facilitate the coactivation of homologous muscles with a single motor
These fibers may also cause bimanual interference when the movement requires simultaneous activation of heterologous muscles; for example, activation of the biceps in one arm and the triceps in the other arm.

Figure A.6 Depiction of the contralateral corticospinal axons (CCSA) that cross in the pyramidal decussation and then branch in the spinal cord to innervate ipsilateral and contralateral motor neurons. Adapted from Carson (2005)

Bimanual interference may also occur during the preparation of the motor command in the brain. This preparation involves a distributed network of cortical and subcortical areas in both hemispheres (Debaere et al. 2001; reviewed by Swinnen and Wenderoth, 2004). Communication between the hemispheres, via the corpus callosum, has been shown to be a source of bimanual interference. There are several lines of evidence that implicate the corpus callosum in bimanual interference. Mirror movements, the accidental activation of a homologous muscle when performing a unimanual movement, are seen in children until the corpus callosum has finished myelination (~9 years old; Franz 2003). There is a rare condition called congenital mirroring that involves hypertrophy of the corpus callosum. This causes augmented mirror movements that persist past childhood (Franz 2003).

Bernstein (1967) defined coactivation of homologous muscles by a single motor command as a muscle synergy. Kelso et al. (1979a, b) generalised this idea of synergies to a coordinative structure: a coordinated movement constrained by the nervous system to act as a single unit.
The most intriguing evidence linking the corpus callosum to bimanual interference comes from people who do not have a corpus callosum. People who are acallosal are often referred to as split-brain as their interhemisphere communication has been drastically reduced. This interesting population has decreased spatial coupling and can trace different shapes with each arm much better than control participants (Figure A.7; Franz et al. 1996). Interestingly, attenuated spatial coupling only occurs with the removal of the posterior third of the corpus callosum. Spatial coupling is still intact when the anterior two-thirds of the corpus callosum are severed.

The posterior aspect (splenium) of the corpus callosum links the parietal cortex, so it may be the source of spatial interference (Eliassen et al. 1999). Temporal coupling is also reduced for people who are acallosal, but only for continuous movements and not for discrete movements. One explanation is that temporal coupling in continuous movements involves interhemispheric communication across the corpus callosum, while subcortical structures are involved in temporal coupling during discrete movements (Kennerley, Diedrichsen, Hazeltine, Semjen, Ivry, 2002).

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17 The typical cause is corpus callosotomy, the surgical cutting of the corpus callosum to prevent intractable epileptic seizures from spreading across the hemispheres. It is also possible to be born without a corpus callosum or with a partial corpus callosum, collectively referred to as agenesis of the corpus callosum.

18 Some interhemispheric communication can still occur through the anterior, posterior, and hippocampal commissures as well as through subcortical connections (Kandel et al. 2000).

19 Another fascinating fact about people who are acallosal is that they can perform previously learned bimanual movements but have great difficulty learning new bimanual movements (Franz et al. 2002). This, however, is best explained by another thesis.
Figure A.7 The ability of control participants (left column) and people who are acallosal (right column) to trace either two identical shapes (with reflection symmetry about the midsagittal plane; top row) or two different shapes (bottom row). Identical shapes require symmetric movements and they are easily traced by control and acallosal participants. Different shapes, however, require asymmetric movements. These are relatively easy for acallosal participants and hard for control participants. Adapted from Franz et al. (1996)

A.4 Bimanual interference during preparation and execution

These three neural pathways are examples of how neural interactions may result in bimanual interference. This can occur during information processing (via the corpus callosum) or during transmission of the motor command (via ipsilateral or bilateral corticospinal axons). Is it possible to differentiate interference from movement preparation from movement transmission? Interference during movement transmission may cause temporal or spatial coupling during execution of the movement. Interference during movement preparation can also cause temporal or spatial coupling, so movement execution reflects interference from preparation and execution.

Bimanual interference during movement preparation should also affect the duration of information processing (Heuer 1993). The interference that occurs during the preparation of an asymmetric movement compared to a symmetric movement may increase the duration of any or all of the stage of information processing. RT has been used to quantify the duration of information processing, so it should be able to quantify bimanual interference during movement preparation. RT also includes the time for
transmission from the cortex to the muscles. This is when interference related to movement transmission occurs, but it should not influence the speed of the neural commands. It may result in temporal or spatial coupling, but it should not affect the RT. Thus, RT can isolate bimanual interference cause by movement preparation.

**A.5 An RT cost for bimanual asymmetric movements**

Spijkers et al. (1997) examined RTs of bimanual movements for interference during movement preparation. They reasoned that bimanual interference during the preparation of bimanual asymmetric movements would cause longer RTs than bimanual symmetric movements. They also argued that precuing the movements would eliminate this bimanual RT cost. Say, for example, that asymmetric movements without a precue take 700 ms to prepare and symmetric movements take 600 ms to prepare. If a 1000 ms precue is given, then programming of symmetric or asymmetric movements can be completed before the imperative stimulus. Asymmetric movements take longer to preprogram, but this difference occurs before the imperative stimulus and so it is not reflected in the RT. An analogy is giving a slow runner (asymmetric preparation) and a fast runner (symmetric preparation) 60 s to run 100 m. They can both easily finish the race with this abundance of time, similar to the abundance of time for preparation with a precue.

The experiment involved lateral movements away from the midline of the body, similar to Kelso et al. (1979a). The movements were reversals, made to either a short (10 cm) or long (20 cm) target line and back to the home position as fast as possible, with no emphasis on accuracy. An important distinction from the studies by Kelso (1979a, b, 1983) was that the four types of bimanual movements (symmetric: long-long, short-short; asymmetric: long-short, short-long) were tested in choice RT and not simple RT. The required movement on each trial was indicated by the imperative stimuli. These were one of two words – either “Short” or “Long” – for the left and right arms. As an example, “Long Short” cued an asymmetric movement where the left arm should go to the long-distance target and the right arm should go to the short target.
These types of cues are referred to as symbolic as a word (or any other abstract symbol) is used to represent a movement.

How does the time courses of movement preparation compare with or without a precue (Figure A.8)? Without a precue, in choice RT, all preparation occurs after the imperative stimulus. RT, therefore, reflects all the stages of information processing: imperative stimulus recognition, target discrimination, response selection, response programming, and response initiation. When the movement is precued, some preparation can occur before the imperative stimulus. This preprogramming reduces the information processing during the RT and therefore decreases the RT. Which stages of information processing can be preprogrammed (assuming enough time is given between the precue and the imperative stimulus)? Long duration precues in this experiment potentially allowed target discrimination, response selection, and response programming to be preprogrammed. As an example, say that “Long Short” was displayed as the precue. Target discrimination would occur to identify the words Long and Short. (It may be more accurate to refer to this process as identification of the target stimuli with symbolic cues.) Response selection would then involve selecting a long distance movement for the left arm and a short movement for the right arm. Response programming would prepare the motor command for a Long-Short movement. The movement would be stored until the imperative stimulus is recognised and then the stored motor command would be initiated. The RT therefore reflects identification of the imperative stimulus and response initiation.

To be precise, the reaction time interval includes the stages of information processing, the transmission of the motor command from the brain to the muscles (transmission time), and the delay between the motor command arriving at the muscles and the initiation of the movement (motor time).

Preprogramming is similar in simple reaction time to choice reaction time with a precue (Fig. A.8). In both cases, knowing the response before the imperative stimulus allows preprogramming that decreases the reaction time. The one difference in simple reaction time is that target discrimination is not required during preprogramming; the response is known by the participant and not indicated by a precue.
The RTs of bimanual asymmetric movements were 174 ms longer than symmetric movements without precues (0 ms precue interval; Figure A.9, left). This asymmetric RT cost decreased with longer precue durations. When the movement was precued 750 ms before the imperative stimulus, there was still a significant asymmetric cost of 40 ms. A second experiment included a 1000 ms precue that eliminated this cost. These results support that bimanual interference can occur during movement preparation. Spijkers et al. (1997) made two other conclusions; first, interference during preparation is transient as it can be eliminated by a long, 1000 ms precue. This is in contrast to a static form of bimanual interference that occurs regardless of the time for movement preparation. An example of static interference is temporal coupling, which we will discuss shortly. Second, Spijkers et al. concluded that the asymmetric RT cost was caused by interference during response programming. The asymmetric cost must be related to a stage or stages of information processing that are influenced by precues. Response programming is one such stage but so are target discrimination and
response selection. Other researchers have argued that the bimanual RT cost observed in this experiment could be caused by interference during response selection (Diedrichsen et al. 2001). This is relevant to my thesis, so I will return to this in the next section.

Figure A.9 Mean RTs (left) and movement times (right) for the precue intervals. Notice that the asymmetric cost decreased with longer precue intervals (left), and that the temporal coupling of asymmetric movements was comparable across precue intervals (right). Adapted from Spijkers et al. (1997)

Bimanual asymmetric movement exhibited temporal coupling in their movement times. The movement times of short asymmetric movements were longer than short symmetric movements, and they were almost as long as long-distance movements (Figure A.9, right). Temporal coupling was independent of the precue duration, so it is an example of static bimanual interference. Temporal coupling could be caused by interference during movement preparation or movement transmission, but it is not caused by limited time for information processing.

A.6 Berkeley sounds off

As I mentioned earlier, target discrimination, response selection, and/or response programming could cause the asymmetric RT cost. Spijkers et al. (1997) concluded that response programming caused the cost, but they did not give any evidence against the other stages. A group from Berkeley decided to test which stage
caused the bimanual RT cost. Diedrichsen et al. (2001) argued that symbolic movement cues, like the words Short and Long, place unusual processing demands on response selection. Direct cues – simply illuminating the required targets for each trial – are a more direct representation of the movement and should decrease the processing demands on response selection. It is possible that the use of symbolic cues caused the bimanual RT cost for asymmetric movements. This would suggest that response selection, and not response programming, caused the asymmetric cost.

Diedrichsen et al. (2001) tested this hypothesis with a similar experiment, but they included blocks with symbolic cues and blocks with direct cues. If response programming causes the asymmetric cost, then it should occur with direct and symbolic cues, as the type of cue does not affect the required movement; a long-short movement with direct or symbolic cues should require the same programming. If response selection causes the asymmetric cost, then the cost should only occur when the processing demands on selection are increased with symbolic cues. The distinction between direct and symbolic cues in motor control research goes back to the debate between Rosenbaum (1980) and Goodman and Kelso (1980). Rosenbaum showed that there was a serial order to the specification of parameters for motor commands: arm, direction, and then the extent of the movement were parameterised. Goodman and Kelso showed that this only occurred with symbolic cues and not with the more naturalised use of direct cues. Perhaps the asymmetric RT cost is also specific to symbolic cues.

The first experiment by Diedrichsen et al. (2001) involved forward reaching movements to short-distance (10 cm) and long-distance (20 cm) circular targets (3.6 cm diameter). The participants were instructed to move their index fingers from the home positions to the required targets as quickly and accurately as possible. Symbolic blocks used the letters “S” and “L” to cue short- and long-distance movements. The targets were illuminated in the blocks with direct cues. Blocks were also included.

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22 I'm still curious how these two articles ended up being back-to-back in the same issue of the Journal of Experimental Psychology. The article by Goodman and Kelso even included a replication of Rosenbaum's first experiment.
where the movement for one arm was precued before the imperative stimulus. This resulted in the precued arm being a simple RT task and the other arm being a 2-choice RT task; we will refer to these blocks as unilateral 2-choice.

**A.6.1 Aside about unilateral 2-choice**

Diedrichsen et al. (2001) proposed that there might be an asymmetric cost associated with simultaneously specifying two movements with different amplitudes. This cost may be revealed by RT or movement time differences between 4-choice and unilateral 2-choice conditions. I am intrigued by how a precue for one arm will change the preparation of a bimanual movement. One might assume that when you precue one arm, a unimanual response can be preprogramed. Movement preparation for the other, non-precued arm will then occur after the imperative stimulus. This assumes that bimanual movements are simply the combination of two unimanual movements, which is not true. It has been shown that the principles of bimanual coordination are unique from unimanual control (reviewed by Swinnen 2002). One example is temporal coupling in asymmetric movements; the movement time of the short-distance movement is extended to be more like the movement time of the long movement (Kelso et al. 1979a, b).

There are several possibilities for how bimanual movements could be prepared in the unilateral 2-choice condition. One possibility is that the precue will allow the movement for one arm to be preprogramed. This could allow the other movement to be prepared after the imperative stimulus without interference from the previous movement. In this case, the bimanual movement may be more like the combination of two unimanual movements. This could attenuate the temporal coupling that is seen in asymmetric movements. One complication is that temporal coupling may be caused by interference during transmission of the motor command. If so, temporal coupling will still occur with a precue, as the independently prepared movements are still executed simultaneously.
Another possibility is that the unilateral precue will allow the movement for one arm to be selected in advance, but programming of the movement will wait until both movements are known. In other words, it is not possible to preprogram half of a bimanual movement. The bimanual movement can only be programmed after the imperative stimulus, when both movements are known. This will allow distinctive bimanual features, such as temporal coupling, to be included in the motor command. There are, of course, other possibilities for movement preparation; for example, perhaps some response programming can occur after the precue, but more programming occurs after the imperative stimulus to temporally couple the movements. The unilateral 2-choice condition in the study by Diedrichsen et al (2001) will offer some insight into the preparation of bimanual movements. This is a fascinating manipulation that was used in study 3 (Chapter 4).

A.7 Back to the (bimanual) task at hand

Let us return to the results of Experiment 1 by Diedrichsen et al. (2001). In the symbolic 4-choice condition, there was a 55 ms RT cost for asymmetric movements compared to symmetric movements (Figure A.10). There was a 6 ms RT cost in the direct 4-choice condition, but it was not significant. This supported the notion that the asymmetric cost is mostly (save for those 6 ms) related to response selection. But why are processing demands on response selection increased when two different symbolic cues need to be translated for an asymmetric movement? How about a simile: translating two different symbolic cues is like answering two different math problems. Translating the same cue twice for a symmetric movement is like answering the same math question twice in a row. Once you have solved it the first time, you will have the solution at hand when the question is repeated.

Diedrichsen et al. (2001) concluded that the asymmetric cost is related to increased processing demands on response selection with symbolic cues. As there was no significant bimanual cost with direct cues, they also concluded that two different distance movements (an asymmetric movement) could be prepared simultaneously
without interference expressed in RT. Further experiments by Diedrichsen et al. have supported that the majority of the bimanual RT cost is caused by the translation of symbolic cues and neither stimulus identification nor response programming (Diedrichsen et al. 2003; Hazeltine et al. 2003). Recent research – which I will detail in the next section – has shown that there is a small, bimanual RT cost (10-20 ms) with direct cues (Diedrichsen et al. 2006; Heuer and Klein 2006b). Before I get ahead of myself, let us return to some other interesting results from the Diedrichsen et al. (2001).

**Figure A.10** Mean RTs for symmetric and asymmetric movements in the four conditions (4C = 4-Choice, U2C = Unilateral 2-choice). The asymmetric cost was significant in only the symbolic 4-choice condition. Adapted from Diedrichsen et al. (2001)

RTs with direct cues were not significantly different in 4-choice and unilateral 2-choice (Figure A.10). Symbolic RTs were 92 ms faster in unilateral 2-choice than 4-choice, and the asymmetric cost was eliminated. The elimination of this cost suggested that the precue did allow some response selection to occur before the imperative stimulus. If response selection had to wait for the imperative stimulus, then the asymmetric cost should still occur. It is difficult from just these results to determine whether the precue also allowed some response programming to occur before the imperative stimulus. Interestingly, the movement times exhibited similar temporal coupling with and without precues (Figure A.11), so a precue did not attenuate the
temporal coupling. This agreed with the conclusion by Spijkers et al. (1997) that
temporal coupling is not caused by limited time for movement preparation.

![Figure A.11](image.png) Mean movement times for symmetric and asymmetric movements in the four conditions. The temporal coupling of asymmetric movements was comparable across conditions. Adapted from Diedrichsen et al. (2001)

A second experiment was conducted to see whether the asymmetric cost would
generalise to a different type of asymmetric movement. The asymmetric movements in
the first experiment had different amplitudes and in the second experiment they had
different directions. The target for each arm was either forward or sideways (with
equivalent amplitudes of 10 cm). Symmetric movements involved both arms going
forwards or both arms going sideways, and asymmetric movements involved one arm
going forwards and the other going sideways. These movements were cued with either
direct or symbolic cues (the letters “F” and “S” for forwards and sideways movements).
The results replicated the first experiment; there was a 106 ms asymmetric cost with
symbolic cues and a non-significant 4 ms cost with direct cues. This generalisation
exposed a confound in the symbolic conditions; asymmetric movements were always
indicated with two different symbolic cues (Long-Short or Short-Long) and two
identical symbolic cues indicated symmetric movements (Long-Long or Short-Short).
The lack of bimanual cost with direct cues suggested that the cost with symbolic cues is
related to translating two different symbolic cues. Therefore, there should also be an RT cost for symmetric movements if they are indicated by two different symbolic cues.

Movement symmetry and cue similarity were dissociated by Diedrichsen et al. (2003; see also Weigelt et al. 2007). In one block, two identical symbolic cues indicated symmetric movements and two different cues indicated asymmetric movements; this served as a replication of Diedrichsen et al. (2001). In the other block, two identical symbolic cues indicated asymmetric movements (and two different cues indicated symmetric movements). The results were clear; there was an identical 185 ms RT cost for two different symbolic cues that was independent of the symmetry of the movement (Figure A.12). Therefore, translating two different symbolic cues causes the RT cost.

![Figure A.12](image)

**Figure A.12** Mean RTs for symmetric and asymmetric movements in two conditions. The RT cost in both conditions occurred when the movement was cued by two different symbolic cues, regardless of whether the subsequent movement was symmetric or asymmetric. Adapted from Diedrichsen et al. (2003)

### A.8 Translating symbolic cues may be similar to translating movement goals

Where does this leave our interpretation of the bimanual RT cost? It is tempting to drop the word bimanual and just call it an RT cost. It does not seem surprising that translating two different cues takes longer than translating two identical cues (the math problem analogy is really quite accurate). I already mentioned that part of the bimanual RT cost is related to preparing asymmetric movements, and I promise to discuss the experimental support soon (Diedrichsen et al. 2006; Heuer and Klein 2006b). First, I
would like to show how the translation of symbolic cues is similar to the translation of bimanual movement goals.

In previous studies by Diedrichsen et al. (2001, 2003), the symbolic cues indicated target locations and these target locations were the goals of the bimanual movements. In other words, the symbolic cues were translated into bimanual goals. Kunde and Weigelt (2005) argued that selecting different goals for each arm, and not simply the translation of two different cues causes the bimanual RT cost. This was tested with an object manipulation task that involved rotating a block with each arm into a right side up or upside down position. Imagine two glasses lying on their sides. An image appeared of the glasses with each glass either right side up or upside down and the participant had to rotate the glasses to match the image as fast as possible. Each hand performed an overhand grasp on the glass and than supinated or pronated to rotate the glass into the required position. The required goal for each hand could be the same (both glasses up, both glass down) or different (one glass up and one glass down), which were referred to as congruent or incongruent. Congruent or incongruent goals could be accomplished by symmetric movements (both arms pronate, both supinate) or asymmetric movements (one arm pronate the other supinate). The full-factorial combination of goal congruency and movement symmetry is shown in Figure A.13.

![Figure A.13](image-url) The starting positions of the blocks and the goal end positions. The required movements were either symmetric or asymmetric, and the goals were either congruent or incongruent. Adapted from
Kunde and Weigelt (2005)

The main dependent variable was RT. There was no significant different in RTs for symmetric and asymmetric movements. RTs for incongruent goals were 62 ms longer then congruent goals (Figure A.14). Thus, there is a bimanual RT cost for selecting different goals for each arm. It is clear in this task that the bimanual RT cost is related to incongruent goals and not the translation of two different symbolic cues. Perhaps the cost with symbolic cues is also related to translating incongruent goals. This is harder to see in the reaching task, as the goals (the target locations) and the symbolic cues are intertwined. The connection between goals and bimanual interference was shown by Kunde and Weigelt (2005), so it is possible that bimanual interference with symbolic cues is also related to the movement goals. Let us put the conversation about symbolic cues aside and return to the bimanual interference associated with preparing asymmetric movements with direct cues.

![Figure A.14](image)

**Figure A.14** Mean RTs for symmetric and asymmetric movements with congruent and incongruent goals. Importantly, asymmetric movements had RTs that were comparable to symmetric movements (no asymmetric cost), but there was a cost for incongruent movements. Adapted from Kunde and Weigelt (2005)

A.9 Both are correct

So far we have seen Spijkers et al. (1997) argue that the bimanual RT cost for asymmetric movements is caused by interference during response programming.
Diedrichsen et al. (2001) argued that the cost is caused by interference during response selection. There is plenty of evidence in favour of the selection hypothesis (e.g. Diedrichsen et al. 2003; Hazeltine et al. 2003; Weigelt et al. 2007), but is it possible that there is a small RT cost with direct cues? Heuer and Klein (2006b) tackled this question by replicating the study by Diedrichsen et al. (2001). They tested reversal movements and forward reaching movements. The results were similar in each condition; we will focus on the reaching movements as they more closely replicated the study by Diedrichsen. Bimanual reaches to short (10 cm) and long (20 cm) distance targets (2.2 cm diameter) were cued by direct and symbolic cues. The main question was whether there would be a small bimanual RT cost for asymmetric movements with direct cues.

There was a 91 ms RT cost for asymmetric movements compared to symmetric movements with symbolic cues, which replicated the study by Diedrichsen et al. (2001). The novel finding was that there was also an RT cost with direct cues; the RTs of asymmetric movements were 20 ms longer than symmetric movements. Heuer and Klein concluded that there is a large cost associated with interference during response selection that is seen with only symbolic cues. There is also a small cost with symbolic and direct cues that is caused by increased processing demands on response programming. Small RT costs with direct cues have been seen in other experiments (reviewed by Wenderoth and Weigelt 2009) and even one by Diedrichsen (Diedrichsen et al. 2006). That study had an RT cost of 15 ms with direct cues and a symbolic RT cost of 148 ms.

RTs and movement times of bimanual movements are one way to examine intermanual interactions. Heuer and Klein (2006b) also correlated various variables of the left arm with the right arm across a series of trials. These intermanual correlations may reveal how coupled or decoupled the movements are in symmetric and asymmetric movements. They found that intermanual correlations of RT, movement time, and amplitude were significantly smaller for asymmetric movements than symmetric movements. It makes sense that symmetric movements are more coupled than asymmetric movements, as the temporal coupling is stronger for symmetric
movements (Kelso et al. 1979a, b). I’ve introduced intermanual correlations because they are a measure of bimanual coupling that are occasionally used in my thesis.

To summarise, there is some evidence that bimanual asymmetric movements take longer to prepare than symmetric movements, even with direct cues (e.g. Diedrichsen et al 2006; Heuer and Klein 2006b). This RT cost with direct cues could be caused by increased processing demands on any stage (or stages) of movement preparation. There are other questions that are still unanswered: for example, how does the preparation of bimanual symmetric movements compare to unimanual movements? In the next section, I will detail the studies that have measured the RTs of unimanual, bimanual symmetric, and/or bimanual asymmetric movements.

**A.10 The preparation of bimanual movements**

In the previous sections, I highlighted some of the research on the movement preparation of bimanual reaching movements. Many studies have measured the preparation, via RT, of unimanual, bimanual symmetric, and bimanual asymmetric movements. Some of these studies were designed to compare the preparation of unimanual to bimanual symmetric movements and/or the preparation of bimanual symmetric to asymmetric movements, but all offer insight into the information processing of bimanual reaching movements. I will now discuss the themes from fifty years of research; specifically, what do we know about the preparation of bimanual movements, what do we not know, and what are the inconsistencies?

**A.10.1 Simple RT tasks**

Most of the early studies into the preparation of bimanual movements tested unimanual and bimanual symmetric movements in simple RT tasks. The majority of these studies found that the RTs of unimanual movements are shorter than bimanual symmetric movements. This RT cost for bimanual symmetric movements compared to unimanual movements ranged from 2 ms (Di Stefano et al. 1980, key press) to 16 ms
Three studies (Anson and Bird 1993, elbow flexion; Taniguchi 1999a; Negelkerke 2002) have shown non-significant simple RT costs that ranged from 1 to 4 ms.

Recall that simple RT measures the durations of imperative stimulus recognition and response initiation (Figure A.8). The same imperative stimulus was used in unimanual and bimanual conditions, so the duration of stimulus identification was likely comparable. The only remaining stage is response initiation, so a simple RT cost suggests that the initiation of a bimanual symmetric movement takes longer than a unimanual movement. Perhaps the initiation of a bimanual symmetric movement takes longer because of direct and temporal coupling that acts to coordinate the arms.

Few of the studies that employed simple RT tasks statistically compared the RTs of bimanual symmetric and asymmetric movements. This raises the question of whether there is a simple RT cost for bimanual asymmetric compared to symmetric movements, or more specifically, does the response initiation of bimanual asymmetric movements take longer than symmetric movements? This question was investigated in chapter 2.

**A.10.2 Choice RT tasks**

Most of the studies that have used choice RT tasks have compared the preparation of bimanual symmetric movement to asymmetric movements. I previously discussed the large RT cost for asymmetric movements compared to symmetric movements with symbolic cues, which has been attributed to increased processing demands on response selection (e.g. Diedrichsen et al. 2001, 2003; Hazeltine et al. 2003). A few recent studies have also suggested that part of the RT cost may be caused

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23 The exception is Nagelkerke (2002) who showed that the simple RTs for bimanual asymmetric movements were significantly longer than symmetric movements. Several studies included bimanual asymmetric movements, but did not statistically compare the RTs of bimanual symmetric and asymmetric movements (Norrie 1964, 1967; Kelso et al. 1979a; Marteniuk et al. 1984; Fowler et al. 1991; Steenbergen et al. 1996).
by increased processing demands on response programming for asymmetric movements. This has been supported by a bimanual RT cost for asymmetric compared to symmetric movements with direct cues (e.g. Diedrichsen et al. 2006; Heuer and Klein 2006b; reviewed by Wenderoth and Weigelt 2009).

Bimanual asymmetric movements may take longer to program than symmetric movements because they are constrained by temporal and spatial coupling. In bimanual asymmetric reaches, the movement time of the arm with the easy target increases its duration to be similar to the arm with the hard target (Kelso et al. 1979a, b). Temporal and spatial interference could occur during information processing or transmission of the motor command (see A.3 Bimanual interference and neural pathways for more details). If there is an RT cost for asymmetric movements, then this suggests that some bimanual interference occurs during information processing. This was examined in chapter 2.

Most of the studies that have used choice RT tasks with direct cues have not included unimanual movements. Unimanual movements are required to test for an RT cost for bimanual symmetric movements compared to unimanual movements. In choice RT tasks, the RT reflects the durations of imperative stimulus recognition, target discrimination, response selection, response programming, and response initiation (Figure A.8). The RT cost for bimanual symmetric movements in simple RT suggested that response initiation takes longer for symmetric than unimanual movements. This cost for response initiation should also occur in choice RT. It is possible that target discrimination, response selection, and/or response programming may also take longer for symmetric than unimanual movements. If so, this would also contribute to an RT cost and cause a larger cost for symmetric movements in choice than simple RT tasks. The preparation of unimanual and bimanual symmetric movements in simple and choice RT were compared in chapter 2.

A few choice RT studies have included unimanual and bimanual conditions. The bimanual condition typically includes symmetric and asymmetric movements presented in 4-choice RT (the four choices being Long-Long, Short-Short, Long-Short, and Short-Long movements). As the number of choices influences RT (captured by the
Hick-Hyman law; Hick 1952; Hyman 1953; c.f. Favilla 1996; Wright et al. 2007), the unimanual condition is typically also 4-choice. The possible movements in a 4-choice, unimanual RT task are left Long, left Short, right Long, and right Short. It is important to balance the number of choice in unimanual and bimanual conditions; however, I am concerned about how unimanual 4-choice affects the stages of information processing. In unimanual 4-choice, the response could be with either your left or right arm. As either arm may be required to respond, both arms may be equally excited before the imperative stimulus. This may be indexed by comparable magnitudes of the readiness potentials in each hemisphere. The excitement of the arm that is selected to move will then increase, which may also be shown by the lateralised readiness potential or the H-reflex. Decreasing the excitement of the arm that should not respond may require inhibition (Hasbroucq et al. 2000). The 4-choice RT task may, therefore, reflect the time required to excite one arm and inhibit the other.

This potential inhibition in unimanual 4-choice does not occur in bimanual 4-choice. In bimanual 4-choice, both arms respond on every trial, so they are both excited (and neither inhibited). Potential inhibition in unimanual conditions can be avoided by employing 2-choice RT tasks. The left and right arms are tested in separate blocks where the two choices are long- or short-distance movements. This will eliminate the potential inhibition because the arm used in each block will respond on every trial. It would be unfair to test unimanual movements in 2-choice and bimanual movements in 4-choice, so bimanual movements will also be tested in 2-choice blocks: a block of symmetric movements (Long-Long, Short-Short), and a block of asymmetric movements (Long-Short, Short-Long). An advantage of testing symmetric and asymmetric movements in two blocks is that it may help to delineate the differences in information processing between them. If both types of bimanual movements are tested in the same block, then participants may plan for the worst-case scenario, which would be an asymmetric movement. Planning for the worst case has been shown when trials with and without visual feedback are combined in the same block. In this case, responses to trials with and without feedback are slightly different. The differences with and without visual feedback were much greater when the type of feedback was
held constant for the entire block (Elliott and Allard 1985; Zelaznik et al. 1983). In a similar manner, testing symmetric and asymmetric movements in separate blocks may help to differentiate their information processing.

Fifty years of research into the information processing of bimanual reaching movements has lead to many insights. This thesis extends previous studies by delving into the information processing of bimanual reaching movements. An overview of these studies is given in section 1.2.