Planning and execution of
(bi)manual grasping

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Planning and execution of (bi)manual grasping

Een wetenschappelijke proeve op het gebied van de

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Proefschrift

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# Contents

**Chapter 1** General introduction 7

**Chapter 2** Combined effects of planning and execution constraints on bimanual task performance 19

**Chapter 3** Behavioral evidence for left-hemisphere specialization of motor planning 45

**Chapter 4** Motor planning in bimanual object manipulation: Two plans for two hands? 59

**Chapter 5** Typical and atypical (cerebral palsy) development of unimanual and bimanual grasp planning 77

**Chapter 6** Excitability of the motor system during observation of action preparation 93

**Chapter 7** Summary & Discussion 113

References 123

Nederlandse samenvatting 131

Dankwoord 137

Curriculum Vitae 139

List of publications 140

Series Donders Graduate School for Cognitive Neuroscience 141
Chapter 1

General introduction
Chapter 1

Introduction
Grasping is one of the most basic movement patterns that we perform continuously, seemingly without thinking. For example, imagine yourself getting a glass of cola. To do so you first need to grasp the latch of the cabinet in which you store your glasses and open the cabinet. Then you have to grasp a glass, which you probably do with your other hand. After having put your glass on the kitchen sink, you grasp the latch of the refrigerator with one hand and open its door, grasp the bottle of cola with the other hand and take it out of the fridge. While holding the bottle with one hand, you grasp the lid of the bottle with the other hand and open it. After having poured the drink into your glass you have to grasp the lid again and put it on the bottle to close it, and you have to put the cola bottle back in the fridge again. You need to grasp the latch of the fridge to close its door and then you need to grasp the glass and bring it to your mouth in order to drink from it. This ostensibly simple action sequence already consists of eight grasping movements. This is probably more than one would have thought at first hand (no pun intended). The grasping movements were of a different nature depending on the object grasped and the subsequent manipulation of the grasped object. For example, when picking up the bottle you probably used a full hand grip, or so-called power grip, using the whole hand with all fingers enclosing the bottle. However, when turning the lid of the bottle you probably used a precision grasp with only the thumb and index and middle finger, but not all fingers involved. Furthermore, knowledge of the action following a grasping movement is an important determinant of how an object will be grasped. For example, what if you intended to grasp a glass that was positioned upside down in the cabinet? You would have probably used a grip with your thumb down in order to rotate it and turn it upright, because you have knowledge that the subsequent action (pouring cola in it) demands the glass to be upright. This is a typical example of motor planning: the formulation of a plan by taking into account the physical demands of the subsequent action goal (Johnson-Frey et al. 2004). In this example the orientation of the initial grasp was adapted to the final goal such that the movement ended in a comfortable posture. When planning a movement, not only the orientation of the grasp but also other features of motor control can be adapted to the subsequent goal, such as the speed of the movement or the grasp height (Marteniuk et al. 1987; Rosenbaum et al. 2006).

This thesis describes five studies in which the planning of grasping movements is being investigated using three different, but complementary methods (see Figure 1.3): 1) behavioural experiments were used to study motor planning in bimanual object-handling, 2) children with a
typical and atypical motor development performed a motor planning task, and 3) Transcranial Magnetic Stimulation was used as a neurophysiological technique to study neural processes involved in motor planning.

**The end-state comfort effect**
In most of the experiments described in this thesis, motor planning is assessed via the end-state comfort effect, i.e., the tendency of people to adaptively structure their initial grasp in order to end a task in a comfortable posture, even when this necessitates them to use an awkward grasp at the start of the movement. The comfort of the posture can be defined as the degree to which the involved joints are in the middle of their range of motion (Rossetti et al. 1994; Rosenbaum et al. 1996). Grasping the overturned glass with a strongly pronated grip to rotate it and position it right side up while eventually pointing the thumb upwards is a typical example of the end-state comfort effect. This effect has been extensively used in experimental research of human motor planning (e.g., Rosenbaum et al. 1996; Weigelt et al. 2006; Crajé et al. 2010a).

The end-state comfort effect was first described by Rosenbaum et al. (1990) in a bar-handling paradigm. In this paradigm, the starting situation is a bar with one black end and one white end that is placed horizontally on two supports in front of a participant. The participant’s task is to pick up the bar and place it vertically with either the black or the white end pointing upwards (Figure 1.1). The results showed that participants always ended comfortably with their thumb pointing upwards, irrespective of whether this required an overhand (comfortable) or an underhand (uncomfortable) start posture when grasping the bar. The bar-handling paradigm and variations thereof has been used extensively, for example in children, in various patient groups and in bimanual settings. Several general conclusions can be drawn from these studies: Goal-posture planning develops during childhood (McCarty et al. 2001; Thibaut and Toussaint 2010), the end-state comfort effect can be extended to bimanual actions (Weigelt et al. 2006; Hughes and Franz 2008), and children with Cerebral Palsy show compromised motor planning (Steenbergen et al. 2000; Crajé et al. 2010a). Together, these studies demonstrate that the initial grip that people use to grasp an object is critically dependent on the goal posture that will be adopted when the movement terminates.

These findings are in line with the predictions from the posture-based motion planning theory that was originally developed by Rosenbaum, Meulenbroek, Vaughan and Jansen (2001). The theory’s principle claims are that 1) motion planning entails time-limited multiple-constraint
satisfaction and 2) the planning of the goal posture precedes the selection of the movement to that posture. The constraint satisfaction is based on a constraint hierarchy. For each movement situation a prioritized list of constraints is established. Examples of such constraints are the required goal orientation of objects such as the appropriate orientation of a glass when filling it, movement effort, i.e. the general aim in movement production to minimize energy, and the presence of obstacles, which limits the behavioural options to those that do not result in collisions. For the action to be planned, all movement options are considered in the light of this constraint hierarchy. The option that satisfies most prioritized constraints is the action that is performed. Comfort of the end posture is in experimental studies often a high-level constraint that is on top of the constraint hierarchy. Hence, the end-state comfort effect is abundantly shown in experimental studies. In this thesis, the boundaries of the end-state comfort effect were explored, i.e., the validity of the end-state comfort effect was tested in situations involving multiple constraints (e.g., a bimanual task) and under restricted movement capabilities (as in Cerebral Palsy).

**Figure 1.1 Typical motor planning task.** This figure is adapted from Rosenbaum et al. 1990. Participants had to grasp the horizontal bar (a) and place it vertically on the stand next to it with either the black end on top (b) or the white end on top (c).
Bimanual actions

One of the situations for which we tested the end-state comfort effect is the bimanual object manipulation task. Whereas manipulating one object at a time with one hand may be rather simple, manipulating two objects with two hands simultaneously can be quite complex, particularly when the manipulation of each object serves a different goal. In some situations, bimanual actions require that both hands act together, instead of separately. This entails that bimanual actions cannot just be regarded as the simple summation of two unimanual actions, but that other constraints come into play. For that reason, movements that are easy to perform in isolation can become difficult when performed together with two hands. For example when simultaneously drawing a circle with one hand and a square with the other hand, the circle becomes more square-like and the square becomes circle-like (Franz et al. 1991). This indicates that the movements of both limbs are spatially coupled (Carson 1995; Semjen et al. 1995; Swinnen et al. 1997).

Kelso and coworkers were one of the first to demonstrate that in bimanual tasks limbs are also temporally coupled (Kelso et al. 1979). They showed that whereas unimanual reaching movements obey Fitts’ Law (Fitts 1954), i.e., movement duration is a function of the amplitude and the precision of the target area, bimanual movements movement durations do not obey Fitts’ Law because both hands often end simultaneously, even when one hand has to move twice as far as the other hand. The temporal movement coupling of the upper limbs has also been repeatedly shown in rhythmic tapping tasks (see Summers 2002 for an overview). Bimanual tapping tasks in which both hands tap with the same frequency are easier to perform and more stable than tapping tasks in which the hands tap with different frequencies. As a result, participants tend to switch involuntarily from a less stable mode (different frequencies) to a more stable mode (same frequency), reflecting the interference between the limbs (Byblow et al. 1994).

When moving bimanually, the spatial and temporal interference between the limbs is generally smallest when both hands move in the same direction. This can be either the same direction in egocentric or in allocentric space. When the hands move in the same direction in egocentric space, it means that they move in the same direction with reference to the body, for example moving both hands towards the body. In this thesis we define this movement mode as ‘symmetric’. When the hands move in the same direction in allocentric space, this means that they move in the same direction seen from a third-person perspective, for example moving both
hands to the left or to the right. This is referred to as ‘asymmetric’ in the remainder of this thesis. Symmetric movements have been shown to be more stable than asymmetric movements, which has been attributed to the activity of homologous muscle pairs (Carson 1995; Swinnen et al. 1998). This view has been contested by the claim that the preference to move symmetrically has a perceptual origin, and not a neuromuscular or biomechanical one (Mechsner et al. 2001). In a more recent view perceptual, neuromuscular and biomechanical constraints are considered to all affect the stability of interlimb coordination. The extent to which each of these constraints prevail, is dependent on the task context (Li et al. 2004).

Thus far, bimanual task performance has mainly been studied using *cyclical* tasks with a focus on the coordination principles underlying (un)coupling or interlimb interference. *Discrete* bimanual prehension tasks have gained much less attention. Nevertheless, discrete bimanual tasks are very suitable to study the effects of task constraints on motion planning. The end-state comfort effect that we studied in the experiments reported in this thesis requires that tasks have a discrete end even though the movements may be embedded in a compound action sequence. We thus studied bimanual task performance using discrete tasks to investigate the intricate interplay between planning constraints (the end-state comfort effect) and coordination constraints (symmetry of movement).

**Hemispheric differences**

When investigating motor planning, we made a distinction between motor planning of the left hand and that of the right hand, as there are indications that planning is organized asymmetrically in the brain. This particular organization could result in differences in performance between both hands. Evidence for the left hemisphere dominance in motor planning stems, amongst others, from patient studies (Haaland et al. 2000; Frey et al. 2005). For example, patients that suffer from brain damage to the left hemisphere more often have difficulties with movement planning compared to right brain-damaged patients (Steenbergen et al. 2004; Craje et al. 2009). Furthermore, several studies have shown an increased activation in left brain areas that are involved in motor planning when participants had to imagine making a movement (Kuhtz-Buschbeck et al. 2003; Stinear et al. 2006). This activation was not, or to a lesser extent, observed in the right hemisphere. Since motor imagery (the imagination of movements without actually moving) is regarded as a specific form of motor planning, these results suggest that particularly the left hemisphere plays an important role in action planning.
(Johnson et al. 2001). Still, the differences between the left and right hand in movement performance have mainly been studied in right-handed participants. Therefore, these obtained results could also be due to experience, or hand dominance, and maybe less to a more general left-hemisphere specialization for motor planning.

In the first three experimental chapters of this thesis we describe behavioural studies in which we asked participants to perform bimanual object manipulation tasks. In one experiment, we studied whether there was a dominance of either preference for movement symmetry or end-state comfort. We performed this experiment in both right- and left-handed participants, to also examine the role of hand dominance. Furthermore, we studied the kinematics of bimanual tasks to gain knowledge about the interlimb interference in relation to movement symmetry and end-state comfort. Finally, we studied the extent to which movements are planned and executed for each hand independently.

**Motor planning in a clinical model (cerebral palsy)**

Whereas the experiments on motor planning of chapter two, three and four are performed in healthy adults, the fifth chapter concerns the study of motor planning in both typically developing children and children with a congenital movement disorder (Cerebral Palsy). The strength of the end-state comfort effect has been shown to increase with age. For example, when the bar-handling paradigm of Rosenbaum was tested in children, the end-state comfort effect was shown in less than half of the four-year-old children in the difficult condition (the condition that required an underhand grasp in order to end comfortably), and this increased with age to about 80% end-state comfort in ten-year-olds (Thibaut and Toussaint 2010). In children with Cerebral Palsy the results are more variable, although virtually all studies show impaired motor planning in these children (Steenbergen and Gordon 2006; Crajé et al. 2010a).

Cerebral Palsy (CP) is one of the most common and pervasive developmental disorders that leads to severe physical disability in childhood. It is a group of non-progressive disorders of movement and posture that originates around birth and that causes activity limitation (Bax et al. 2005). Children with CP not only experience problems with the execution of movements, but also problems with the planning of movements. Motor planning in these children is usually measured by the end-state comfort effect in tasks in which they have to pick up objects. In these tasks, end-state comfort is satisfied when the grip with which the objects are grasped is adapted
to the goal. Participants with CP do not always anticipate the grip with which they grasp the object, resulting in an uncomfortable end or even a failure to fulfill the task (Steenbergen et al. 2000; Mutsaarts et al. 2006; Craje et al. 2010a). In the fifth chapter of this thesis we studied motor planning in unimanual and bimanual actions in children with and without CP in order to gain insight in the developmental trajectory of motor planning in the typical and atypical brain.

**Neurophysiology of motor planning**

Thus far we discussed the study of motor planning by looking at the behavioural consequences (e.g., the comfort of the end posture) when performing a goal-directed action. In the last experimental chapter of this thesis we will focus on the neurophysiology of motor planning in an experimental task where participants are observing somebody else planning and executing a grasping action. In this situation, the observed action is mapped onto one’s own motor system where a motor representation is formed (Iacoboni et al. 1999; Flanagan and Johansson 2003). Stated differently, it appears that the observer makes a motor plan, but without actually executing the movement. The neural processes associated with action observation are comparable to those involved in making an action oneself (Rizzolatti et al. 2001). This makes action observation a suitable experimental paradigm to study the neural processes involved in motor planning in tasks in which participants are not allowed to move themselves.

When planning to grasp an object, the motor control processes are guided by visual information picked up from the to-be-grasped object, that is, its location, its shape, its size. This information, which enters the brain via the visual cortex, is transformed and used in the formation of goal-directed actions. These sensory-motor transformations take place mainly in the parietal areas which project to prefrontal and (pre)motor areas in the frontal lobe where the motor plan is formed. The primary motor cortex, receiving input amongst others from the premotor areas, seems to be the final ‘station’ of the planning process. From the primary motor cortex motor commands are sent to the muscles via the spinal cord. Eventually, the muscles fulfil the execution of the motor plan (Georgopoulos 2000; Rizzolatti and Luppino 2001; Rushworth et al. 2003).

The neuronal activity of the motor system at the time of motion planning can be measured by means of Transcranial Magnetic Stimulation (TMS). This is a non-invasive technique by which the brain is stimulated through a rapid changing magnetic field induced by a conducting coil placed over the participant’s head (Figure 1.2). This magnetic field penetrates
the scalp and the skull, after which it induces a current in the brain that causes activation of neurons. This neural activation can interfere with ongoing neural processes. In this way, the normal function of a particular brain region can be studied by observing changes after (repetitive) TMS is applied to a specific brain region. Applying TMS when the participant is in rest, thus without performing a certain task, does not result in any immediate observable behaviour, except when TMS is applied over the motor cortex. TMS applied over the motor cortex causes activation of corticospinal neurons, directly or via cortical interneurons. This, in turn, can cause muscles to contract, and this muscle contraction can be measured by electromyography. The location and size of the muscle contraction depends amongst others on the location and intensity of the stimulation. More important, changes in the magnitude of the muscle response can give information about the functional state of the corticospinal neurons (Barker and Jalinous 1985; Petersen et al. 2003).

![Figure 1.2 Transcranial magnetic stimulation.](image)

In chapter six we used TMS to investigate the timing of neural processes involved in motor planning during the observation of grasping movements. The use of action observation gave us the opportunity to manipulate not only the goal of the task, but also the successive execution. In
this way we could scrutinize whether the presence or lack of the end-state comfort effect affects the motor representations (motor plan) of the observer.

Compilation of the thesis
In this thesis we employed behavioural experiments, a patient study, and a neurophysiological experiment to gain fundamental insights into the planning of discrete uni- and bimanual grasping movements. The results are described in five experimental chapters.

In chapter 2 we conducted two behavioural experiments in which we contrasted constraints on planning (the end-state comfort effect) and execution (symmetry of movement) in a bimanual object manipulation task. The first experiment was focused on interlimb coupling and the way in which symmetry of movement and end-state comfort act on this. The second experiment was setup to investigate which constraint dominates bimanual movement execution when participants are free to choose their grips. The participants in these experiments were all right-handed. In chapter 3 we used the same setup as the second experiment of chapter 2, but now in left-handers. We replicated the experiment to find out if the advantage in performance of the right hand would be related to experience (right-handers are more experienced with their right hand whereas most left-handers are more experienced with their left hand) or whether these results should be attributed to a generic left-hemisphere specialization of motor planning.

In chapter 4 we studied task performance in a bimanual object manipulation task to scrutinize interlimb interference. More specifically, is the performance of the left hand influenced by an instructed action for the right hand? To test this, we had participants to pick up two objects with two hands simultaneously and place them in holders using either instructed or free-to-choose grasps. Whether motor planning of one hand could be transformed to the other hand was also one of the questions in chapter 5. However, in this chapter we tested children aged 7 to 12 years old, with and without Cerebral Palsy. We measured the level of anticipatory motor planning by inspection of the height at which the children grasped a vertical bar, when they had to transport this bar to a higher or a lower height.

In chapter 6 our focus turned to the neurophysiology of correctly and incorrectly planned movements. Therefore, we used transcranial magnetic stimulation to study the role of the motor cortex during the preparation of movements. Finally, in the last chapter, chapter 7 the most important findings are summarized and discussed, including suggestions for further research.
Figure 1.3 Triad of typical studies in cognitive neuroscience. The chapter numbers indicate the chapters that involve the particular type of study.
Chapter 2
Combined effects of planning and execution constraints
on bimanual task performance

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Chapter 2

Abstract
In this study we investigated the relative impact of planning and execution constraints on discrete bimanual task performance. In particular, in a bimanual CD-placement task, we compared people’s preference to end movements comfortably with their preference to move symmetrically. In Experiment 1 we examined the degree of interlimb coupling as participants repositioned two CDs in a CD rack by simultaneously moving their arms mirror-symmetrically or asymmetrically into comfortable or uncomfortable end postures. Interlimb coupling was stronger when the arms moved symmetrically towards uncomfortable end postures. In Experiment 2 participants were asked to realize specific end orientations of the CDs but they were free to choose an initial grip type and subsequent direction of forearm rotation. Surprisingly, the participants did not move their arms symmetrically but preferred to end in a comfortable posture with their right hand but not with their left hand. We conclude that in discrete bimanual task performance the tendency to end movements in a comfortable posture dominates over the tendency to synchronously activate homologous muscle pairs. The lateralized end-state comfort effect suggests a hemispheric specialization for motor planning.
Introduction
Every day we grasp and manipulate objects, often seemingly even without thinking or spending any effort. However, to do so optimally, we need to plan our movements before we undertake any action (Rosenbaum et al. 2001). For example, when you want to eat with knife and fork, you pick up the cutlery in such a way that they can immediately be used for eating, even if the knife lies upside down. Thus, the forthcoming action, viz., eating, is anticipated in the grip type, i.e. the orientation of the hand that is used when picking up the cutlery. Anticipation of a forthcoming action is demonstrated to have effects on reaching kinematics (Marteniuk et al. 1987; Johnson-Frey et al. 2004) and joint couplings during reaching (Steenbergen et al. 1995). In the example of eating with knife and fork, anticipatory planning is evidenced by the macroscopic variable grip type. The knife is picked up with a full grip with the thumb pointing towards the blade of the knife. However, if you pick up a knife in order to pass it to someone else, you probably adopt another grip type, with the thumb pointing towards the handle or at least such that the other person can take the knife without any danger. Rosenbaum et al. (1992) studied this phenomenon of grip type anticipation and had participants reach for a bar that had to be moved as quickly as possible from a home location to a target location. Participants generally took hold of the bar in a way that afforded a comfortable posture at the target location even when this necessitated an uncomfortable posture at the home location (Rosenbaum et al. 1992). This phenomenon was termed the end-state comfort effect. Here, comfort was defined as the degree to which the joints of the multijoint effector system are in the middle of their range of motion (Rossetti et al. 1994). The end-state comfort effect can also be deduced from the cognitive theory of posture-based motion planning by Rosenbaum et al. (2001), which presumes that planning of the goal posture precedes the execution of the movement.

Thus far, the end-state comfort effect has mainly been studied for discrete, unimanual tasks. However, more recently researchers have also focused their attention on the end-state comfort effect in bimanual tasks (Fischman et al. 2003; Weigelt et al. 2006; Hughes and Franz 2008). As an example, Fishman et al. (2003) showed that participants adjusted the height of their start grips whenever they had to place a dowel at a very low target location (prompting a high start grip) or at a very high target location (eliciting a low start grip). In line with this, Weigelt et al. (2006) showed in a bimanual object manipulation task a strong tendency for both hands to end comfortably. Their results suggest that planning for comfortable end-states dominates over processes related to movement execution of both hands. In contrast to Weigelt
et al. (2006), a large number of experimental studies, predominantly examining rhythmic cyclical tasks, did show the presence of interlimb interference at the level of movement execution. These interference effects were especially obvious when non-homologous muscle pairs were activated (Li et al. 2004). Ample studies showed an increased stability of arm movements in the symmetric mode (both hands / arms moving mirror-symmetrically with respect to the longitudinal axis of the body) compared to arm movements in the asymmetric mode (both hands / arms moving alternating with respect to the longitudinal axis of the body) (Byblow et al. 1994; Semjen et al. 1995; Swinnen et al. 1997; Swinnen et al. 1998; Li et al. 2004).

According to the parameter-specification model of Heuer (1993), intermanual interference arises whenever different parameter values have to be specified independently for the two hands. Indeed, when participants had to move a manipulandum to different amplitudes, interference effects arose, i.e. the amplitude and movement time of the one hand scaled with the amplitude and movement time of the other hand. (Spijkers and Heuer 1995; Spijkers et al. 1997; see Bingham et al. 2008 for these effects in bimanual object manipulation tasks). However, recent research findings challenged this model as interference effects at the execution level appeared to be subsidiary to the effects related to planning. Kunde and Weigelt (2005) showed a lack of the effect of moving in symmetry in an object-manipulation task. Instead, the congruency of the intended object orientations proved to have a larger effect on movement performance. Motor-symmetry effects only became substantial when the movements themselves became the action goal (Kunde and Weigelt 2005). Similarly, Diedrichsen et al. (2001) showed that bimanual interference is reduced or even disappears when direct cues were used instead of centrally-spaced symbolic cues (e.g., letters, colors) in a pointing task. They suggested that the cost to initiate asymmetric movements does not arise from spatial interference in a central motor-programming stage, but is rather a consequence of interference in the translation of symbolic information into motor commands (see also Weigelt et al. 2007).

These findings beg the question as to whether the tendency to move symmetrically is strong enough to affect goal-related action planning and the forthcoming movement execution in a discrete bimanual task. Stated differently, does either the tendency to move in symmetry or the goal-related action planning dominate task performance in a discrete bimanual object manipulation task? Although participants in the study of Weigelt et al. (2006) showed goal-related action planning (because they showed the end-state comfort effect) for both hands, the design of that study did not include ‘critical conditions’, in which a choice for one constraint is at
the expense of the other. Stated differently, the constraint with respect to movement symmetry was not very strict. In addition, they only included the macroscopic variable grip type. In the present study, we systematically investigated the impact of both types of constraints via examination of bimanual-interference effects related to end-state planning and movement execution. To scrutinize the effects of movement symmetry and end-state comfort at a more microscopic level, we included kinematic analyses of the bimanual movements that we studied.

We conducted two experiments. In Experiment 1 we focused on the effects of symmetry of moving and comfort of the end posture on interlimb coordination. The end posture of each hand was explicitly instructed. In this way, we could control the conditions and isolate the effect of end comfort on the kinematics of the bimanual movements. In Experiment 2 participants were free to choose handgrips and movement trajectories. Only the end orientation was cued. In this way, we assessed whether participants would choose to end comfortably in favor of moving symmetrically and if so, whether there would be differences with respect to the preferred and non-preferred hand in prioritizing the planning constraint.

If planning principles associated with goal states prevail, this would be a strong indication that the performance of discrete bimanual movements is related to end goals rather than to the movements required to reach these goals. Such a finding would challenge the parameter-specification model of Heuer (1993). Conversely, if a shift in prioritization towards symmetrical movements occurs, this would point to a need to reformulate existing motion-planning theories that claim that goals are always prioritized, such as is the case in the posture-based motion-planning theory (Rosenbaum et al. 2001).

**EXPERIMENT 1**

To investigate the relative impact of the planning (end comfort) and the execution (movement symmetry) constraints in a bimanual object-manipulation task, we designed a bimanual CD-placement task.

**Methods (1)**

**Participants**

Ten female university students (mean age = 20.7 years/months, SD = 1.9 years/months) participated in the experiment. All participants were right-handed as confirmed by a score of ≥
80 on the 10-item version of the Edinburgh Handedness Inventory (Oldfield 1971). Informed consent from all participants was obtained prior to the experiment. Participants were naïve with regard to the purpose of the study and received course credits for their participation. The experiments were conducted conform the standards of the declaration of Helsinki and in accordance with local ethical guidelines.

Experimental setup

Figure 2.1 shows the general layout of the experimental setup. The setup consisted of two square CD boxes (15 cm x 15 cm), in which a CD casing could be placed in either a horizontal or vertical orientation. Each box was supplied with two green light-emitting diodes (LEDs) that served as visual cues. The LED on the top of the box indicated a vertical placement of the CD, whereas the LED on the side indicated a horizontal placement. Participants were comfortably seated right in front of the experimental setup, which was placed on a table with the boxes at participants’ eye height. At the start of each trial, one or two CD casings (for unimanual or bimanual tasks respectively) were present at two CD holders, which we located on the table 7 cm in front of the CD boxes. Both CD holders could be placed in two orientations: 45° or -45° with regard to the vertical, viz., upright orientation.

Figure 2.1 Photograph of the experimental setup. Seen from the viewpoint of a participant.
**Experimental design and procedure**

At the start of each trial participants held one (in unimanual conditions) or two (in bimanual conditions) CD casing(s) that rested in the holder(s), with the left hand, the right hand, or both hands. The trial started with a single tone and after a random inter-stimulus interval of 0.5 - 2.5 seconds, one (in unimanual conditions) or two (in bimanual conditions) of the LEDs were switched on providing the visual cue for CD placement. We instructed participants to react to the visual cue as fast and accurate as possible by placing the CD casing(s) in the CD box(es) in the cued orientation. Participants were instructed to keep their hand(s) in the end position for several seconds until the LED(s) switched off. Subsequently, the CD casing(s) could be replaced in its initial starting position.

All participants performed both unimanual and bimanual tasks. In all trials, the CD(s) had an oblique start orientation, either -45° or +45° with respect to the vertical. As such, the start grips had the following postures; 45° supination of the forearm, 45° pronation of the forearm, or 135° pronation of the forearm (Figure 2.2a). The end postures were either horizontal or vertical and were reached by either a pronation or supination of the forearm over a range of 45° (Figure 2.2b). Thus, we made sure that in all conditions, the same degree of forearm rotation was needed to perform the task. Manipulation of the start and end orientations resulted in 12 unique unimanual conditions (3 start orientations x 2 end orientation x 2 hands). In the bimanual conditions, orientation of the start posture could be parallel (one hand 45° forearm pronation and the other 45° forearm supination or 135° pronation, or vice versa) or non-parallel (both forearms 45° supination or 45° pronation). Parallel start orientations induced asymmetric movements, whereas the non-parallel start orientations induced symmetric movements with respect to the longitudinal axis of the body. The end orientations in the bimanual trials were always congruent, i.e. for both hands either horizontal or vertical. This yielded 12 bimanual conditions (6 start grips (4 parallel + 2 non-parallel) x 2 end grips).

Participants performed a grand total of 240 trials, subdivided in 12 blocks of 10 unimanual trials and 12 blocks of 10 bimanual trials. Each block consisted of two conditions (5 trials of each condition) with the same start grip, but different end orientations. The order of these blocks was randomized with the restriction that unimanual and bimanual blocks were alternated. Furthermore, the order of the trials was randomized within the blocks. If the participant ended the movement in the wrong orientation, or when the recording of the wrist movement failed, the trial was repeated at the end of that block.
Prior to the start of the experiment, participants performed a few practice trials to check whether the task was understood correctly, and to familiarize themselves with the task. The total duration of the experiment was about one hour.

a) **Start postures**

![Start postures](image)

- 45° supination
- 45° pronation
- 135° pronation

b) **End postures**

![End postures](image)

- horizontal overhand
- horizontal underhand
- vertical thumb up
- vertical thumb down

Figure 2.2 Start postures (a) and end postures (b) of the right hand investigated in Experiment 1.

*Data acquisition*

Hand movements were registered by two OPTOTRAK systems (Optotrak 3020, Northern Digital Inc.) with a sample rate of 100Hz. Both cameras were placed at approximately 90 degrees of each other at a height of approximately 2 metres to enhance visibility of the Infrared Emitting
Diodes (IREDs). On each wrist of the participant we attached a rigid body that consisted of a wrist band with a metal plate on the dorsal side of the wrist on which four IREDS were fixed in a rectangular fashion. We checked the position of the rigid bodies around the wrists during the practice trials to ensure that at least three of the IREDS were in view of one of the two Optotrak cameras during task performance. The coordinate frame of the Optotrak system was oriented such that x, y and z axis corresponded to the horizontal, posterior-anterior and vertical dimension with respect to the participant. Recordings started as the LED(s) turned on and ended after completion of the task. The whole experiment was videotaped using a digital camera, for future reference.

Next to movement registration we collected comfort ratings of the different postures that could be adopted at the start and the end of the trial. For this purpose, we asked participants to adopt a start or an end posture and to give a rating between 1 and 5 reflecting comfort of the posture, with 1 being very uncomfortable and 5 being very comfortable. Next, the participant was asked to change the grip type and to score this newly adopted posture. This procedure was repeated until the comfort scores of 3 different start postures (45° supinated, 45° pronated and 135° pronated) and 4 different end postures (0° (vertical with thumb up), -90° (horizontal supination), +90° (horizontal pronation) and +180° (vertical with thumb down)) were assessed for each hand (Figure 2.2). Comfort was assessed twice, once before and once after the experiment.

Data analysis
The raw Optotrak signals were partially interpolated with cubic spline interpolation (up to 10 successive samples, corresponding to 100 ms), which never occurred before movement initiation. Thereafter, they were low-pass filtered using a second order Butterworth filter (cut-off frequency of 10 Hz). The three-dimensional position data were differentiated to velocity values in three dimensions, which were integrated to obtain speed values. We defined reaction time (RT) as the point at which speed signals exceeded 5% of the maximum speed in that trial. Movement time (MT) was defined for the object transport phase, i.e. the time between RT and the first local minimum after maximum speed was reached. In addition, we calculated the relative duration in %MT of the acceleration and deceleration phases. Movement onsets, maximum speeds and movement offsets were generated semi-automatically using custom-made selection routines and checked visually. RTs and MTs that deviated more than three
standard deviations from the mean in that particular condition were discarded from further analyses. This occurred in 3.5% of the trials.

Interlimb coupling was determined by comparing rotations of both wrists along the forearm axis. We calculated Pearson’s correlation coefficient between the rotation signals of both wrists as a measure of interlimb coupling strength. The correlations were calculated in the interval from the start of the trial, i.e., LED(s) switched on, until the end of the movement time. In addition, this interval was subdivided in two parts: the acceleration time (before peak speed) and the deceleration time (after peak speed). Correlations between the wrist rotations were also calculated for these two intervals separately.

Depending on the research question and type of dependent variable under investigation, we applied repeated-measures ANOVAs and paired T-tests, which will be described separately in the relevant paragraphs of the results section.

**Results (1)**

*Comfort ratings*

Participants gave ratings to three different start postures and four different end postures per hand. As the ratings given before the experiment did not differ from those given after the experiment, we report the mean ratings of both measurements. The ratings were evaluated using two repeated measurements ANOVAs, one for the start postures and one for the end postures. The designs consisted of two within-subject factors, Hand (2 levels: left or right) and Posture (3 levels for the start postures: 45° supination, 45° pronation, and 135° pronation, and 4 levels for the end postures: horizontal overhand, horizontal underhand, vertical thumb up, and vertical thumb down).

For the start postures a main effect of Posture was observed ($F(2,18) = 70.49$, $p<0.01$). Post-hoc pair wise comparisons revealed that only comfort of the 135° pronation posture (mean comfort = 1.88) differed significantly from the other two postures (mean comfort 45° pronation = 4.78, $t(9) = 19.96$, $p<0.01$; mean comfort 45° supination = 3.93, $t(9) = 7.43$, $p<0.01$).

For the end postures we observed main effects of both Hand ($F(1,9) = 7.97$, $p<0.05$) and Posture ($F(3,27) = 35.70$, $p<0.01$). Overall ratings for the left hand (mean comfort = 3.21) were slightly lower than those for the right hand (mean comfort = 3.53). Furthermore, post-hoc analysis revealed that participants gave higher ratings (indicating more comfort) to the horizontal overhand posture than to the horizontal underhand posture ($t(9) = 2.83$, $p<0.05$).
the vertical end postures, the posture with the thumb up was rated more comfortable than the posture with the thumb down (t(9) = 16.14, p<0.01). Therefore, we defined the horizontal overhand posture and the vertical posture with the thumb up as comfortable end postures, and the horizontal underhand posture and the vertical posture with the thumb down as uncomfortable end postures.

**Symmetry effects**

In order to study the effects of movement symmetry, we performed two repeated measures ANOVAs, one for RT and one for MT. Therefore, we selected conditions in which only the factor of interest (i.e. symmetry) was manipulated while other factors (i.e. start and end posture comfort) were kept constant. Accordingly, we included four conditions, all with vertical, comfortable, end postures (i.e. with the thumb up). In order to avoid interference with start and end posture comfort, horizontal ending conditions were excluded from this analysis, as they required either the 135° pronation start posture or an underhand end posture, which are both less comfortable. Two conditions had parallel start orientations (one hand 45° supination and the other hand 45° pronation) inducing asymmetric movements, and the other two conditions had non-parallel start postures (both hands 45° pronation or both hands 45° supination) inducing symmetric movements (Figure 2.3). In addition, we used four unimanual control conditions in which the hands had the same start postures (45° pronation and 45° supination) and also ended vertically with the thumb up, thus similar to the postures of both hands in the bimanual conditions. The ANOVA designs consisted of one within-subject factor Symmetry (3 levels: symmetric, asymmetric or unimanual). For both the RT and MT, we used the mean of the two symmetric conditions, the mean of the two asymmetric conditions and the mean of the four unimanual conditions as input for the ANOVA.

The ANOVAs revealed a main effect for Symmetry on both RT (F(2,18) = 10.38, p<0.01), and MT (F(2,18) = 37.09, p<0.01). Post-hoc analysis revealed that the unimanual trials (mean RT = 283 ms, mean MT = 790 ms) started earlier and had shorter movement times than both the symmetric trials (mean RT = 321 ms, t(9) = 5.24, p<0.01, mean MT = 877 ms, t(9) = 7.15, p<0.01) and the asymmetric trials (mean RT = 337 ms, t(9) = 4.34, p<0.01, mean MT = 908 ms, t(9) = 10.67, p<0.01). Both RT and MT were not significantly different for symmetric and asymmetric movement trajectories (resp. t(9) = 1.06, n.s. and t(9) = 1.67, n.s.).
### Figure 2.3 Overview of conditions (front view of CDs) used for the symmetry analysis and the end-comfort analysis.

The top-left quadrant displays bimanual symmetric (1,2) and asymmetric (3,4) trials. The top-right quadrant displays unimanual control conditions for the symmetry analysis involving the left hand (5,6) or the right hand (7,8). The conditions for the end comfort analysis are in the bottom half of the figure. At the bottom-left are the bimanual conditions with a comfortable end (overhand grip, 9) and with an uncomfortable end (underhand grip, 10), and at the bottom-right four unimanual control conditions involving the left hand (11,12) or the right hand (13,14).

**End comfort effects**

To identify the effects of *end comfort* on the kinematics, we performed two repeated measures ANOVAs (one for RT and one for MT) for which two bimanual conditions and four unimanual conditions were selected. The bimanual conditions both started non-parallel and ended horizontal. One of these conditions ended with an overhand (comfortable) grip, the other with an underhand (uncomfortable) grip (Figure 2.3). Both conditions had symmetric movement trajectories, so that movement symmetry could not have confounded the results. In order to avoid interference with start posture comfort, vertical ending conditions were excluded from this analysis, as they required the less comfortable 135° pronation start grip for an uncomfortable end. The four unimanual conditions were similar to the bimanual conditions, but then separated per hand (Figure 2.3). The ANOVA design consisted of the following factors:
Hand (2 levels: left or right), Number of hands (2 levels: 1 or 2) and End comfort (2 levels: comfortable or uncomfortable).

The ANOVAs revealed main effects of Number of hands on both RT and MT, a main effect of End comfort on MT only, and no effects of Hand on RT or MT. As was also shown in the analyses of symmetry effects, the unimanual trials (mean RT = 285 ms, mean MT = 841 ms) started earlier (F(1,9) = 16.17, p<0.01) and had shorter movement times (F(1,9) = 57.28, p<0.01) than the bimanual trials (mean RT = 325 ms, mean MT = 937 ms). Although RTs were comparable for trials with comfortable and uncomfortable endings (mean RT = 308 vs. 303 ms respectively, F(1,9)<1, n.s.), MT was significantly shorter in trials that ended comfortably (mean MT = 833 vs. 944 ms respectively, F(1,9) = 19.67, p<0.01).

**Interlimb couplings**

In order to assess interlimb coupling strength we calculated Pearson’s correlation coefficients (r values) of the rotations of the left and right wrists for the bimanual conditions involving symmetric or asymmetric movements and those involving comfortable or uncomfortable end grips (the same conditions used as for the symmetry and end comfort analyses). Fisher’s Z transformation was applied to the r values before the analyses; average Z values were retransformed to r values for graphical display purposes.

Paired t-tests showed that interlimb coupling, as reflected by the correlation coefficient between the forearm rotations, was lower in asymmetric movements compared to symmetric movements (mean correlation = 0.78 vs 0.90 respectively, t(9) = 2.46, p<0.05, see Figure 2.4), and higher in the trials that ended uncomfortably compared to those that ended comfortably (mean correlation = 0.98 vs 0.86 respectively; t(9) = 10.92, p<0.01; see Figure 2.4). Moreover, the high correlation coefficients for symmetric and uncomfortable ending movements had, after the Fisher-z transformation, a small range whereas the smaller correlation coefficients for the asymmetric and comfortable ending movements had a larger range (Figure 2.4), which is another indication that the interlimb coupling was less strong in the latter conditions.

In addition, we scrutinized whether the correlation coefficients differed between the acceleration phase (before peak speed) and the deceleration phase (after peak speed) using a repeated measures ANOVA with a 2 (Time, acceleration vs. deceleration phase) * 2 (End comfort, comfortable vs. uncomfortable) factor design. The factor End comfort again showed a significant effect on interlimb coupling (F(1,9) = 34.20, p<0.01). However, the factor Time was
not significant \( F(1,9) = 1.58, \text{n.s.} \). The absence of both a main effect of Time and interaction between Time and End comfort \( F(1,9) = 3.84, \text{n.s.} \) indicates that the interlimb coupling was higher in trials that ended in an uncomfortable posture compared to trials that ended in a comfortable posture. This held for both the acceleration (mean correlation = 0.97 vs. 0.86 respectively) and the deceleration phase (mean correlation = 0.89 vs. 0.82 respectively).

![Figure 2.4 Interlimb correlation coefficients](image)

**Figure 2.4 Interlimb correlation coefficients** for symmetric vs. asymmetric movements (left) and for movements that end comfortable vs. movements that end uncomfortable (right). Box plots show the median, interquartile range, outliers and extreme cases.

**Discussion (1)**

In this first experiment, we studied the effect of end comfort and movement symmetry on the coordination of bimanual movement performance. As expected, and in line with previous studies (Swinnen et al. 1991; Carson 1995; Swinnen et al. 1997), interlimb coupling was lower when moving asymmetrically as compared to moving symmetrically. Interestingly, ending with both hands in an uncomfortable posture yielded a higher interlimb coupling than ending in a comfortable posture, both before and after peak velocity. These findings show that interlimb coordination is affected by the end posture during discrete bimanual tasks, even when this end posture is explicitly instructed via direct cueing.
In our second experiment we focus on the interaction between both constraints. In contrast to the first experiment, where start grip and end posture were explicitly instructed, participants in the second experiment were free to choose their start grips and the way in which they executed the movement. This set-up enabled us to study the interaction between posture planning and movement execution directly.

**EXPERIMENT 2**

The setup of the second experiment was comparable to the first experiment. However, participants could now freely choose their grip type with which they grasped the CDs before placing them in the CD boxes in a prescribed orientation. Unlike experiment 1, experiment 2 is not a reaction-time study. Instead, we analyzed the movement symmetry and end comfort of the hands for which we reported the direction of forearm rotation and the grip type that participants adopted.

**Methods (2)**

**Participants**

Ten right handed university students (2 males and 8 females, mean age = 20.6 years, SD= 1.9 years) participated in the experiment. These students did not participate in the first experiment. They were all right-handers, as confirmed by a score of ≥ 60 on the 10-item version of the Edinburgh handedness inventory (Oldfield 1971).

**Apparatus**

The experimental setup was similar to that used in the first experiment, with the exception that we now used four CD boxes (two upper boxes and two lower boxes, Figure 2.5). In both the upper and the lower CD boxes the CDs could be placed either horizontally or vertically. The two upper boxes had green LEDs on the upper and right sides, which indicated the required end orientation of the CDs. In addition, and as a further cue, the borders of the upper boxes were covered with strips of green (on the upper and right sides) and black (on the left and lower sides) paper. The CDs also had a green and a black side which enabled us to indicate either a 0 degrees orientation or a 180 degrees orientation (and either 90 degrees pronation or 90 degrees...
supination) by the instruction that the CD had to be placed with the green side facing the green LED.

Figure 2.5 Schematic drawing of the experimental setup. CDs have one black side and one green side (displayed grey) and are located in the lower boxes. The small circles on the top and right side of the upper boxes represents the LEDs. The upper boxes are covered with strips of green (displayed grey) and black paper.

Task
Participants started with their hands on the table, in front of the CD boxes and they had to pick up the two CDs simultaneously from the lower boxes and place them in the upper boxes. Using this setup, participants were left free with respect to the type of grip with which they grasped the CDs. The CDs had to be placed with their green side towards the green LEDs. Thus, when the LED on the upper side turned on, the CD had to be placed horizontally with the green side up, and when the LED on the right side turned on, the CD had to be placed vertically with the green side to the right.

Experimental design
The experiment consisted of 24 conditions in which we manipulated the start and end orientation of the CDs, the start and end orientation congruency and the required rotation. The start and end orientation of each CD could be either horizontal or vertical. Start and end orientation congruency could be either congruent (i.e., both CDs horizontal or both CDs vertical) or incongruent (i.e. one CD horizontal and the other CD vertical). The required rotation could be 0 degrees, 90 degrees supination, 90 degrees pronation or 180 degrees. In theory, participants could also make a rotation of 270 degrees in the opposite direction, but we assumed that they would choose the shortest angle of rotation.
Conditions were such that one CD always had to be rotated 180 degrees to place it horizontally or vertically. The required rotation for the other CD was 0 degrees, 90 degrees pronation or 90 degrees supination. These manipulations resulted in 2 possibilities for the 180 degrees rotating arm (2 orientations: horizontal or vertical) and 6 possibilities for the other arm (3 rotations x 2 orientations). As the rotations could be performed with either hand, this resulted in a total of 2 x 2 x 6 = 24 conditions. Conditions of interest were those that had a conflict between moving symmetrically and ending comfortably. There were 4 conditions with such a conflict, an example of which is given in Figure 2.6.

Participants performed 120 trials that were administered in five blocks of the 24 conditions in a randomized order. Trials within a block were repeated at the end of that block in case the participant ended the movement in the wrong orientation. Before the start of the experimental trials, participants performed 12 practice trials to check whether the task was understood correctly, and to familiarize themselves with the task. The total duration of the experiment was about one hour.

**Figure 2.6 An experimental condition containing a conflict between moving the hands symmetrically and ending comfortable.** The start orientation was for both hands horizontal. The end orientation for the left CD was horizontal, requiring a rotation of 180 degrees; the end orientation for the right hand was vertical, requiring a rotation of 90 degrees supination. The rotation direction of the left hand could be supination (depicted on the left), resulting in a symmetrical movement trajectory, but an uncomfortable end posture. Alternatively, the rotation direction of the left hand could be pronation (depicted on the right), resulting in an asymmetric movement trajectory, but a comfortable end posture.
Chapter 2

Comfort ratings
Similar to the first experiment, participants rated comfort of the start and end postures before and after the experimental trials. Again, the mean score of these two measurements was used for further analysis. As the start and end grips were not prescribed, all postures that were reasonably possible (biomechanically) were rated for their comfort. These included the four postures in Figure 2.6 denoted as end postures and also one additional vertical, supinated grip with the thumb down. Together, this resulted in 5 grips (2 horizontal and 3 vertical) x 2 hands x 2 orientations (start and end orientation) = 20 comfort ratings.

Data analysis
For each experimental trial we registered the rotation of the hand (pronation or supination) and the side of the thumb on the CD (on the green or on the black side) while grasping the CD. For this purpose, experimental trials were videotaped. The side of the thumb on the CD was used to categorize the adopted start and end postures into one of five possible options: a horizontal overhand posture, a horizontal underhand posture, a vertical posture with the thumb pointing up and two vertical postures with the thumb pointing down (one in pronation and one in supination). The comfort ratings were used to categorize the postures as either comfortable or uncomfortable. Based on the rotation of both hands, movements were scored as symmetrically (both hands pronation or both hands supination) or asymmetrically (one hand pronation and the other hand supination). Depending on the research question and type of dependent variable under investigation, we applied repeated-measures ANOVAs and paired T-tests, which will be described separately in the relevant paragraphs of the results section.

Results (2)
Comfort ratings
Participants gave ratings for five different start postures and five different end postures (Table 1). For this experiment however, we only analyzed the end postures. We included all conditions in the analyses and the start orientations were balanced across conditions so that start posture comfort could not confound the results. As the ratings given before the experiment did not differ from those given after the experiment, we used the mean ratings for end comfort in a repeated measures ANOVA. The design of this ANOVA consisted of two within-subject factors;
Hand (2 levels: left or right), and End posture (5 levels: horizontal overhand, horizontal underhand, vertical with thumb up, vertical pronated with thumb down and vertical supinated with thumb down). The ANOVA revealed a significant effect of End posture ($F(4, 6) = 78.8$, $p<0.001$), but not for Hand ($F(1, 9) = 3.64$, $p=0.089$). Post-hoc pair wise comparisons showed that for the horizontal postures, the overhand grip was rated more comfortable than the underhand grip ($t(9) = 5.175$, $p=0.001$). For the vertical start orientations, a grip type with the thumb pointing up was rated significantly more comfortable than both a pronated grip with the thumb pointing down ($t(9) = 8.195$, $p<0.001$) and a supinated grip with the thumb pointing down ($t(9) = 23.321$, $p<0.001$).

In sum, for the end postures a horizontal overhand grip and a vertical grip with the thumb pointing up were considered as comfortable. Conversely, a horizontal underhand grip and both vertical grips with the thumb pointing down were considered as uncomfortable.

**Table 1.1 Mean (and standard deviation) of the comfort ratings.**
Assessed by means of a 5-point scale for Start and End postures studied in Experiment 2.

<table>
<thead>
<tr>
<th>Hand</th>
<th>Orientation</th>
<th>Posture</th>
<th>Start</th>
<th>End</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left</td>
<td>Horizontal</td>
<td>Overhand</td>
<td>4.20 (0.95)</td>
<td>4.65 (0.67)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Underhand</td>
<td>4.30 (1.03)</td>
<td>3.85 (1.18)</td>
</tr>
<tr>
<td></td>
<td>Vertical</td>
<td>Thumb up</td>
<td>4.75 (0.55)</td>
<td>4.85 (0.37)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Thumb down</td>
<td>2.10 (1.21)</td>
<td>2.55 (1.28)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Thumb down</td>
<td>1.40 (0.68)</td>
<td>1.35 (0.59)</td>
</tr>
<tr>
<td>Right</td>
<td>Horizontal</td>
<td>Overhand</td>
<td>4.70 (0.66)</td>
<td>4.95 (0.22)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Underhand</td>
<td>4.05 (1.32)</td>
<td>3.25 (1.21)</td>
</tr>
<tr>
<td></td>
<td>Vertical</td>
<td>Thumb up</td>
<td>4.90 (0.31)</td>
<td>4.85 (0.49)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Thumb down</td>
<td>2.05 (1.10)</td>
<td>2.30 (1.03)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Thumb down</td>
<td>1.20 (0.41)</td>
<td>1.30 (0.57)</td>
</tr>
</tbody>
</table>
Symmetry effects

Frequencies of moving symmetrically were analyzed in conditions in which one hand rotated 180 degrees and the other hand rotated 90 degrees. Trials in which no rotation was required for one hand (8 conditions) or in which participants rotated 270 degrees instead of 90 degrees (5.3% of these trials) were discarded from the analysis.

The hands moved symmetrically in 46.2% (SD = 6.1%). A repeated measures ANOVA with factors Hand (hand that rotated 180 degrees: left or right) and End orientation (end orientation of the CD that had to be rotated 180 degrees: horizontal or vertical) revealed no difference between trials in which the left hand rotated 180 degrees and those in which the right hand rotated 180 degrees. However, the number of symmetric movements was higher when the end orientation of the 180 degrees rotating CD was horizontal (mean symmetric movements = 49.7%, SD = 6.0%) compared to vertical (mean symmetric movements = 42.7%, SD = 6.87%; F(1,9) = 6.054, p = 0.036, Figure 2.7).

End comfort effects

For the analysis of end comfort effects, we included all conditions. The right hand ended comfortably in 82.0% (SD = 20.2%) of all trials, compared to only 49.8% (SD = 9.8%) for the left
hand. This rather large variability for the right hand suggests that the end-state comfort effect is not consistent across task conditions. Therefore, we analyzed the effects of end orientation and rotation angle on the end postures of both hands using a repeated measures ANOVA including the factors Hand (left or right), End orientation (horizontal or vertical) and Rotation angle (0°, 90° or 180°). This ANOVA revealed that participants ended more frequently in a comfortable posture when the end orientation was vertical (mean comfortable ends = 80.8%, SD = 11.3%) compared to horizontal (mean comfortable ends = 61.9%, SD = 15.7%; F(1,9) = 5.842, p = 0.039, Figure 2.8). In addition, there was an effect of rotation angle (F(2,18) = 8.204, p = 0.011): the larger the rotation angle, the smaller the number of comfortable endings.

**Figure 2.8 Percentages of trials in which the hands ended in a comfortable posture.** The trials were separated for the left and the right hand, and for a horizontal (h) and a vertical (v) end orientation. Error bars reflect Standard Errors.

As the percentage of comfortable end postures for the left hand was surprisingly low, we examined this matter in more detail. Therefore, we scrutinized the performance of the left hand in the bimanual trials. It appeared that for trials that had similar start orientations (i.e. both CDs horizontal or both CDs vertical at the start), the participants adopted predominantly the same start postures for both hands in 60.1% when the left hand ended uncomfortably. In trials in which the left hand ended comfortably the participants adopted a symmetrical start posture in only 29.7%. However, when the end orientations of the CDs were similar, the
participants adopted the same end postures for both hands in only 15.5% when the left hand ended uncomfortably. In trials in which the left hand ended comfortably the participants adopted a symmetrical end posture in 79.9%. Thus, for the left hand, participants predominantly preferred a similar start posture, but not a similar end posture to the right hand, which finally resulted in an uncomfortable end posture.

**Discussion (2)**
In the second experiment, we investigated the preference of participants either to end comfortably or move symmetrically in the bimanual CD-displacement task. As expected, and in line with previous studies on bimanual object manipulations (Fischman et al. 2003; Weigelt et al. 2006) participants chose to end comfortably, regardless of whether the comfortable end posture was reached by symmetric or asymmetric rotations of the forearms. Interestingly, the end-state comfort effect predominantly affected the right hand. These findings indicate that planning of comfortable goal states is limited in complex bimanual object manipulation tasks, but at the same time is a more powerful constraint than movement symmetry.

**General discussion**
The primary aim of the two experiments was to examine the relative importance of planning and execution constraints in discrete bimanual object manipulation. The main finding in Experiment 1 was the presence of an effect of a prescribed and cued end posture on interlimb coupling. The second experiment showed that planning constraints dominated execution constraints. This was reflected by the preference to end comfortably and an absence of a preference to move both hands in symmetry. Moreover, planning for comfortable end postures was only found to the right hand. We will elaborate on these new findings below. Apart from these new findings we replicated some well known phenomena from the literature. That is, reaction times and movement times were longer in bimanual trials compared to unimanual trials (e.g., Kelso et al. 1979; Jackson et al. 2002; Mason and Bryden 2007), and interlimb coupling was higher when moving in symmetry than in asymmetry (e.g., Swinnen et al. 1991; Carson 1995; Semjen et al. 1995).
Symmetry effects

The results of the second experiment revealed that in less than 50% of the trials participants chose to move symmetrically, i.e. almost at chance level. This finding is in strong contrast to that in cyclical tasks where symmetry of moving dominates. Particularly when high-speed requirements are imposed on the participant, there is a ubiquitous tendency for interlimb synchronization, as reflected by the occurrence of spontaneous transitions from the asymmetric to the symmetric coordination mode and the high degree of stability and accuracy in this latter mode (Byblow et al. 1994; Swinnen et al. 1997; Carson et al. 2000). The present results also argue against the parameter-specification model of Heuer (1993). In our second experiment, the participants were well able to specify different movement parameters for each hand (e.g., rotation angle, rotation direction) in order to end comfortably, without much interference effects (i.e. the tendency to move symmetrically). The present results rather suggest that the role of symmetry depends on the nature of the task. In discrete, goal-directed movements, which require that the goal of the movement is planned in advance, the symmetry constraint may play a subordinate role, or may even be absent, in contrast to cyclical movements. Moreover, Kunde and Weigelt (2005) showed that in a discrete task, symmetry effects only became apparent when the movements had no other goal than carrying out the movements itself, instead of moving towards a perceptual goal. Weigelt et al. (2006) also found a subordinate role for means-related influences at the expense of ends-related influences on action planning in discrete, goal-directed, movements. However, in their study, means-related was attributed to the symmetry of the initial handgrips instead of the symmetry of moving while manipulating the object. The present study extends the findings of Weigelt et al. (2006) by showing that the selection of handgrips is not driven by the preference to move in symmetry.

In our first experiment, the absence of RT and MT differences between the symmetric and asymmetric movements also implies that movement symmetry did not affect performance (see also Kunde and Weigelt 2005). However, our first experiment did show a strong interlimb coupling in symmetric conditions and a weak coupling in asymmetric conditions, which was shown previously in cyclical movements (Carson 1995; Swinnen et al. 1997) and in discrete movements. With respect to the latter, Kunde and Weigelt (2005) demonstrated synchronicity in bimanual object depositing in symmetric compared to asymmetric trials. The interlimb coupling in the present study was calculated over the interval from reaction time until the end of the movement, thus including object depositing. A higher coupling when moving
symmetrically, may be explained by the involvement of homologous muscle pairs that may have a centrally specified pattern of excitation, in contrast to the non-homologous muscle pairs active during asymmetric movements (Carson 1995). Nevertheless, the potential influence of simultaneous activation of homologous muscle pairs on the coordination of discrete bimanual object-manipulation is limited as only the interlimb coupling was affected and not the RT, MT, or the choice for a grip type.

**End comfort effects**

In contrast to moving symmetrically, participants did choose to end the movements in the second experiment with a comfortable posture, at least for their right hand. Surprisingly, the left hand ended in a comfortable end posture only in half of the trials. Participants preferred similar start postures instead, which often resulted in an uncomfortable end posture. These findings are in contrast with those of Weigelt et al. (2006), who demonstrated the end-state comfort effect for both hands in discrete bimanual object manipulations. However, the task and conditions that they used were less complex, i.e., the objects always had the same end orientation, i.e. congruent, whereas the objects in our experiment also had to be placed in different end orientations. We therefore suggest that the planning of a comfortable end posture for both hands depends on the complexity of the task. Increase in complexity of the task, and its concomitant larger cognitive load leads to a ‘breakdown’ of anticipatory planning of both hands, such that only the end-state comfort of the right hand is anticipated, but not of the left hand. In addition, we showed that the end-state comfort effect was reduced with larger rotation angles. This further hints to the suggestion that advance goal state planning relates to the complexity of the task, which increases with larger rotation angles.

The effects of the end comfort constraint on the kinematics of discrete bimanual object manipulations have, to our knowledge, not been demonstrated before. Although a major role is ascribed to the influence of end comfort on the selection of macroscopic handgrips for object manipulations, we showed that this constraint also affected the kinematics of movement execution. The interlimb coupling was stronger in uncomfortable ending trials than in comfortable ending trials. This difference might have a biomechanical origin. In an awkward arm-hand position, that is, in trials with an uncomfortable end posture, the hand has less freedom to move compared to a comfortable position when the hand is in the middle of the range of motion (Rossetti et al. 1994). As a consequence, coupling may be stronger. If this
hypothesis holds, then the difference in interlimb coupling between comfortable and uncomfortable ending trials should be particularly large at the end of the movement, thus after peak velocity. In contrast, we found that interlimb coupling was higher in trials ending uncomfortably both before and after peak velocity, making a biomechanical explanation of these differences unlikely. A more reasonable explanation for this difference in coupling strength is that comfortable ending trials are more experienced and that practice results in a freeing of the degrees of freedom of the action system that underlies interlimb coordination (Temprado et al. 1997).

**Hemispheric specialization**

Recent research has shown that the hemispheres have a specialized role in the control of motor actions (Gonzalez et al. 2006; Serrien et al. 2006). However, these studies focused on the execution of hand movements, whereas we showed a difference in planning of end comfort between the hands, which precedes the execution. Haaland et al. (2004a) did show left hemisphere dominance for planning of complex movement sequences, but not only for the right hand, also for the left hand. Sainburg and Schaefer (2004) examined interlimb differences regarding both planning and execution. They distinguished two features of movement control that contributed in reaching a certain peak velocity: 1. Pulse-height control, which is the adjustment of the amplitude of the initial acceleration impulse as a result of preplanning and 2. Pulse-width control, which is the adjustment of the duration of the initial acceleration impulse using sensory feedback. In right-handed individuals, they showed that the dominant hemisphere/limb system (left hemisphere, right hand) relied more on pulse-height control, whereas the non-dominant hemisphere/limb system (right hemisphere, left hand) relied more on pulse-width control. The propensity of the dominant hemisphere/limb system to use preplanning (feedforward) instead of feedback mechanisms to reach a certain peak velocity is in line with the present finding of anticipatory planning of end comfort for the right hand. However, it yet has to be established if the processes involved in preplanning of the initial acceleration impulse are connected or even similar to the processes involved in planning of such a macroscopic variable as grip type. Furthermore, on the basis of the present findings it cannot be verified whether the difference in end-state comfort effect between both hands is a result of hemispheric specialization or simply handedness, as all participants in the present study were right-handed. An experiment with left-handers could resolve that issue.
In conclusion, we showed that the coordination between the hands in bimanual object manipulations was subordinate to the planning of the movement execution. However, this planning constraint was only present for the right hand, which may be due to differences in hemispheric specializations regarding motor planning.
Chapter 3
Behavioral evidence for left-hemisphere specialization of motor planning

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Abstract
Recent studies suggest that the left hemisphere is dominant for the planning of motor actions. This left hemisphere specialization hypothesis was proposed in various lines of research, including patient studies, motor imagery studies and studies involving neurophysiological techniques. However, most of these studies are primarily based on experiments involving right-hand-dominant participants. Here, we present the results of a behavioral study with left-hand-dominant participants, which follow up on previous work in right-hand-dominant participants. In our experiment, participants grasped CD-casings and replaced them in a different, pre-cued orientation. Task performance was measured by the end-state comfort effect, i.e., the anticipated degree of physical comfort associated with the posture that is planned to be adopted at movement completion. Both left and right-handed participants showed stronger end-state comfort effects for their right hand compared to their left hand. These results lend behavioral support to the left-hemisphere-dominance motion-planning hypothesis.
Introduction

On average, 9 out of 10 individuals in the normal population is right-hand-dominant, which means that these individuals have a preference to perform unimanual actions, like reaching for a target or manipulate objects, with their right hand (a.o. Annett 2004; Goble and Brown 2008). This preference to use one hand over the other has been shown to be accompanied by an advantage in motor performance, including increases in the strength, speed and consistency of movements (see Goble and Brown 2008 for a review on upper limb asymmetries in sensorimotor performance). Although it was previously thought that the non-dominant hand was inferior for most aspects of motor control, more recent theories state that each hand is specialized for certain aspects of compound movements. For example, the dominant hand is superior for the precise control of movement trajectories whereas the non-dominant hand has a specialized role for positional control (Haaland et al. 2004b; Sainburg and Schaefer 2004; Serrien et al. 2006; Wang and Sainburg 2007). A question of interest is whether this difference between the dominant and non-dominant hand in motor execution also holds for motor planning. Motor planning can be defined as the formulation of a strategy of action taking into account the future demands associated with the goal of the action (Gentilucci et al. 1997; Johnson-Frey et al. 2004), whereas motor execution is the implementation of this strategy. Our main research question is whether motor planning of dominant hand actions is different from motor planning of non-dominant hand actions and whether this dominance is similar for both left and right hand-dominant participants.

Recently, we conducted a behavioral experiment on motor planning in right-handed individuals via the examination of the end-state comfort effect (Janssen et al. 2009). This is the phenomenon that people generally strive to end their movements or object manipulations in a comfortable posture, even when this necessitates them to grasp the object at first with an awkward posture (Rosenbaum et al. 1992; Rosenbaum et al. 1996; Weigelt et al. 2006). By analyzing how participants grasped an object, we deduced whether the movement was planned in advance. We showed that the end-state comfort effect was more often present for the participants’ right hand than for their left hand, suggesting that motor planning is a specialized function of the left hemisphere (Janssen et al. 2009).

The hypothesis that the left hemisphere plays not only a dominant role in the execution, but also in the planning of skilled movements has been repeatedly confirmed (e.g., Kim et al. 1993; Haaland et al. 2000; Leiguarda and Marsden 2000; Frey 2008). First, limb apraxia, an
impairment in the representation of limb movements or their selection or retrieval, is strongly associated with left hemisphere damage (Liepmann 1920; Rothi and Heilman 1997; Haaland et al. 2000; Leiguarda and Marsden 2000; Lunardelli et al. 2008). Second, converging evidence in participants with (congenital) left hemisphere damage shows that these participants have difficulties to anticipate their grip to the upcoming goal in an object manipulation task, which is a clear indication that they have impaired motor planning (Hermsdorfer et al. 1999; Mutsaarts et al. 2007; Crajé et al. 2009). A third line of evidence originates from motor imagery research. Motor imagery may be regarded as a prerequisite for motor planning: Individuals who are unable to imagine movements of their own body (parts) have been shown to have difficulties with anticipating the consequences of their actions (Johnson et al. 2001; Mutsaarts et al. 2007; Steenbergen et al. 2007). Left brain damaged patients showed impairments to use motor imagery in contrast to right brain damaged patients, who did not show these impairments, or to a much lesser extent (Sabate et al. 2004; Mutsaarts et al. 2007; Daprati et al. 2010). In addition, studies in healthy participants involving various neurophysiological techniques showed increased activity in left premotor, supplementary motor and parietal cortices or enhanced excitability of the left primary motor cortex during motor imagery (Bonda et al. 1995; Fadiga et al. 1999; Yahagi and Kasai 1999; Kuhtz-Buschbeck et al. 2003; Stinear et al. 2006; Stinear et al. 2007). Fourth, the preparation of overt movements was more interfered by transcranial magnetic stimulation (TMS) over the left premotor area compared to TMS over the right premotor area (Schluter et al. 1998), and brain activation patterns were more pronounced in the left sensorimotor area compared to the right one during movement preparation (Urbano et al. 1998).

The studies discussed above clearly point to left-hemisphere dominance for motor planning of skilled actions. However, an important limitation of the evidence thus far, is that the participants of the experiments were all right-hand-dominant. It may therefore well be hypothesized that the results found were due to experience, or simply hand-dominance, and less to a left hemisphere specialization. To test this hypothesis it is interesting to examine if this left hemisphere dominance for motor planning is also present in left-handed individuals when using their dominant left hand. If such a result is found, it would make a strong case for a generic left-hemisphere motion planning specialization, irrespective of hand dominance. Only a few studies have focused on this topic.
Frey et al. (2005) tested tool-use skills in two split-brain patients, of which one was right-hand-dominant and the other left-hand-dominant. Both patients performed all task conditions best with their right hand. When (visual) stimuli were presented to either their left or right visual field (corresponding to the right or left hemisphere respectively), both patients performed better with their right hand when the stimulus was presented to the left hemisphere versus their left hand when the stimulus was presented to the right hemisphere. Thus, even though the left-handed patient acted normally upon the tools with her left hand (that is controlled by the right hemisphere), her performance in this task was best with her right hand (controlled by the left hemisphere). From this study, it may be concluded that the representation of skilled actions is a left hemisphere function that is independent of handedness. Although the results are straightforward, they are based on the data of only one left-hand-dominant participant. Adding to these findings are the results of an fMRI experiment in strongly left-handed participants (Frey 2008). This study revealed that pantomiming tool use resulted in largely the same brain activations as in right-handed participants, i.e., an increase in activity within the same left-lateralized regions. The results from a TMS-experiment in which participants had to imagine tapping movements with their fingers, however, were less straightforward (Yahagi and Kasai 1999). Although right-handed participants showed MEP facilitation that was larger when they imagined moving their right hand compared to their left hand, left-handed participants showed MEP facilitations that were similar when imagining either left or right hand movements. The latter finding suggests that the processes involved in motor imagery and therefore likely also in motor planning may be less lateralized in left-handers, but not necessarily dominant in either hemisphere. This idea is supported by a recent study on grasping behavior of left-handers in a natural setting (Gonzalez et al. 2007). The researchers have observed that left-handed participants use their non-dominant hand in half of the precision grasps, whereas the right-handed participants use their non-dominant hand in less than a quarter of all precision grasps, indicating that the selection of which hand to use is less lateralized in left-handers.

To sum up, overall there are only a few studies that focused on motor planning in left-hand-dominant participants. These studies suggest that the organization of motor control in these participants is not a mirror-image of that in right-handers. Still, it is debatable whether the left hemisphere is dominant in the motor planning of left-handers, as previous studies report no asymmetry in either the facilitation of motor evoked potentials or in the actual usage of both
hands in left-handers. In the following, we will present a study in which motor planning was examined in left-handed participants to test the left-hemisphere dominance hypothesis. To that aim, we replicated a study that was performed previously in right-handed participants (Janssen et al. 2009), but now in left-handers.

EXPERIMENT
The goal of this experiment was to test the left-hemisphere dominance hypothesis for motor planning in left-hand-dominant participants. We tested this by having these participants performing a CD-placement task. The task performance was measured using the end-state comfort effect, which reflects a major component of motor planning, i.e., whether the grip posture used is adapted to the final goal (Rosenbaum et al. 1992; Rosenbaum et al. 1996; Weigelt et al. 2006). If the left hemisphere is indeed specialized for motor planning of either hand, we expect a right hand advantage for end-state comfort. Conversely, a dominant (left) hand advantage for end-state comfort would reject the left-hemisphere dominance hypothesis, and rather suggests a hand dominance effect on end-state comfort.

Methods
Participants
Ten left-hand-dominant participants (mean age = 21.1 years/months, SD = 1.10 years/months, 1 male) were included in the present study. Handedness was confirmed by a score of ≤ -55 on the ten-item version of the Edinburgh Handedness Inventory (Oldfield 1971), with a mean score of -79 (SD = 11). Participants received either course credits or 10 Euros for their participation, and they were naive with regard to the purpose of the study. The experiments were conducted conform the standards of the declaration of Helsinki and in accordance with local ethical guidelines.

Experimental setup
The experimental setup consisted of a large CD-rack consisting of four boxes (15 x 15 cm) in which the CD-casings (CDs in what follows) could be placed either horizontally or vertically (Figure 3.1). The two upper boxes had green LEDs on the upper and right sides, which indicated the required end orientation of the CDs. In addition, and as a further cue, the borders of the
upper boxes were covered with strips of green (on the upper and right sides) and black (on the lower and left sides) paper. The CDs also had a green and a black side, which enabled us to request for a CD rotation of either 0° or 180° (and 90° or -90°), by the instruction that the CD had to be placed with the green side facing the green LED.

![Figure 3.1 Schematic drawing of the experimental setup.](image)

CDs have one green side (hatched) and one black side and are located in the lower boxes. The small circles on the top and right side of the upper boxes represent the LEDs. The upper boxes are covered with strips of green (hatched) and black paper. This figure is adapted from Janssen et al. (2009).

**Task**
Participants were seated right in front of a table with the CD-rack on it. Each trial started with the participant’s hands on the table. The participant always had to pick up two CDs simultaneously from the lower boxes and place them in the upper boxes, with their green sides facing the green LEDs. Thus, when the LED on the upper side lighted, the CD had to be placed horizontally with the green side up, and when the LED on the right site lighted, the CD had to be placed vertically with the green side to the right. Participants were free to select the grips with which they grasped the CDs.

**Experimental design**
The experiment consisted of 24 conditions in which we systematically manipulated the end orientation (horizontal or vertical) and the required rotation (-90°, 0°, 90° or 180°) of the CD for each hand (left or right). This resulted also in both horizontal and vertical start orientations. Theoretically, participants could also make a rotation of 270° in the opposite direction when a rotation of 90° was required, but our previous study showed that this hardly occurred (<2% of trials). Conditions were such that one CD always had to be rotated 180 degrees to place it horizontally or vertically. The required rotation for the other CD was 0 degrees, 90 degrees
pronation or 90 degrees supination. These manipulations resulted in 2 possibilities for the 180 degrees rotating arm (2 orientations: horizontal or vertical) and 6 possibilities for the other arm (3 rotations x 2 orientations). As the rotations could be performed with either hand, this resulted in a total of 2 x 2 x 6 = 24 conditions. Participants performed 120 trials that were administered in five blocks of the 24 conditions in a randomized order. Trials within a block were repeated at the end of that block in case the participant ended the movement in the wrong orientation. Before the start of the experimental trials, participants performed 12 practice trials to check whether the task was understood correctly, and to familiarize themselves with the task.

*Comfort ratings*

To determine comfort of the postures, we asked participants to give a rating reflecting comfort to all biomechanically possible postures that could be used to end the CD placement (see Janssen et al. 2009, for a detailed description of the methods). The participant was asked to adopt each of the five end postures for each hand (i.e., horizontal overhand, horizontal underhand, vertical with thumb up, vertical pronated with thumb down and vertical supinated with thumb down, see Table 1) and to give a rating between 1 and 5 reflecting comfort of the posture, with 1 being very uncomfortable and 5 being very comfortable. Comfort was assessed twice, once before and once after the experiment.

*Data analysis*

The comfort ratings were analyzed using a repeated measures ANOVA including two withinsubject factors: Hand (2 levels: left or right) and Posture (5 levels: horizontal overhand, horizontal underhand, vertical with thumb up, vertical pronated with thumb down and vertical supinated with thumb down). Post-hoc pair wise comparisons were conducted for the different levels of Posture.

For each experimental trial we registered the rotation of the hand (pronation or supination) and the side of the thumb on the CD (on the green or on the black side) while grasping the CD. For this purpose, experimental trials were videotaped. Based on these registrations and on the results of the comfort scores, we categorized the adopted end postures to be either horizontal or vertical and comfortable or uncomfortable, and the rotation to be either 0°, 90° or 180°. We investigated which factors had influenced the proportion of comfortable end postures by performing a repeated measures ANOVA including three within-
subject factors: Hand (2 levels: left or right), Rotation (3 levels: 0°, 90° or 180°), and Orientation (2 levels: a horizontal or vertical cued end orientation of the CD).

<table>
<thead>
<tr>
<th>Posture</th>
<th>Left-handers</th>
<th>Right-handers</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Left</td>
<td>Right</td>
</tr>
<tr>
<td><img src="image1" alt="Posture Image" /></td>
<td>4.8 (0.3)</td>
<td>4.8 (0.6)</td>
</tr>
<tr>
<td><img src="image2" alt="Posture Image" /></td>
<td>3.5 (0.6)</td>
<td>3.4 (0.8)</td>
</tr>
<tr>
<td><img src="image3" alt="Posture Image" /></td>
<td>4.8 (0.4)</td>
<td>4.5 (0.5)</td>
</tr>
<tr>
<td><img src="image4" alt="Posture Image" /></td>
<td>2.6 (0.7)</td>
<td>2.7 (0.8)</td>
</tr>
<tr>
<td><img src="image5" alt="Posture Image" /></td>
<td>1.2 (0.3)</td>
<td>1.1 (0.2)</td>
</tr>
</tbody>
</table>

1 Postures are depicted for the left hand. Postures with bold borders were defined as comfortable.
Chapter 3

Results
The comfort ratings for the different end postures for each hand are shown in Table 1. The
ANOVA on the comfort scores revealed no significant effect for the factor Hand (F(1, 9) = 1.12, p
= 0.32) and a large effect for Posture (F(1, 9) = 132.94, p < 0.001). Post-hoc pair wise
comparisons showed that for the horizontal postures, the overhand grip was rated more
comfortable than the underhand grip (t(9) = 7.01, p < 0.001). For the vertical start orientations,
a grip type with the thumb pointing up was rated more comfortable than both a pronated grip
with the thumb pointing down (t(9) = 8.31, p < 0.001) and a supinated grip with the thumb
pointing down (t(9) = 17.29, p < 0.001). Therefore, similar to our previous study (Janssen et al.,
2009), we defined a horizontal overhand posture and a vertical posture with the thumb up as
comfortable, whereas a horizontal underhand posture and a vertical posture with the thumb
down were defined as uncomfortable.

For the experimental trials, the proportion of comfortable end postures are displayed in
Figure 3.2, for the hand used, the orientation of the CD and the required rotation separately.
The ANOVA revealed significant main effects for Hand (F(1, 9) = 11.46, p < 0.01), Orientation (F(1,
9) = 73.46, p < 0.001), and Rotation (F(2, 18) = 18.21, p < 0.001), as well as an interaction effect
for Hand * Orientation (F(1, 9) = 13.89, p < 0.01). Overall, the proportion comfortable end
postures was larger for the right compared to left hand, for the vertical compared to horizontal
orientation and for small compared to large rotation angles. All other possible two- and three-
way interactions were non-significant. First, in line with the left-hemisphere dominance
hypothesis, we found that the left-handed participants ended more often comfortable with their
right (non-dominant) hand, compared to their left (dominant) hand. This indicates that advance
motor planning does not simply correlate with hand dominance or experience. Second, the end-
state comfort effect was stronger when ending vertical compared to horizontal. The horizontal
underhand posture, which we a-priori denoted as uncomfortable, may not have been that
uncomfortable compared to the vertical uncomfortable postures with the thumb down. This
was indeed confirmed by a higher comfort rating for the horizontal ‘uncomfortable’ posture
(mean rating of 3.45), compared to the vertical uncomfortable postures (mean ratings of 2.65
and 1.10). This might be explained in terms of larger differences in the precise control between
the two vertical conditions versus the two horizontal conditions. These higher precision
requirements in the vertical conditions might have caused the larger end-state comfort effect,
which is previously described as the precision hypothesis (Short & Cauraugh, 1999). Third, the
proportion comfortable endings decreased with an increase in rotation angle. This was expected as conditions involving small rotation angles did not require anticipatory motor planning (a comfortable posture at the start is also a comfortable posture at the end when the rotation angle is 0°).

The interaction effect for Hand * Orientation suggests that the difference between the left and right hand was not evenly distributed among the horizontal and vertical endings. Post-hoc analyses revealed that the proportion comfortable endings was significantly different between left and right hand only for the horizontal end postures (t(9) = 3.47, p < 0.01) and not for the vertical end postures (t(9) = 0.63, p = 0.55).

Thus, first and foremost the main effect of Hand clearly shows that the right hand performs better on anticipatory motor planning than the left hand and that this effect is primarily due to the horizontal end postures and not the vertical end postures.

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**Figure 3.2 Mean end-state comfort for both handedness groups.**

The bars and the numbers in them depict the percentages of trials in which participants ended their movements comfortably, separated for the left and right hands and for horizontal endings (filled bars) and vertical endings (hatched bars). The error bars display two standard errors. The data for right-handers (right graph) are adapted from Janssen et al. (2009).
Chapter 3

Comparison with right-handers

The results from the present study can be compared to the results from our previous study (Janssen et al. 2009), as the experimental setup and procedure were the same. In that experiment, we measured ten right-handed participants (mean age = 20.6 years/months, SD = 1.9 years/months, 2 males) all had scores of ≥ 60 on the Edinburgh Handedness Inventory, with a mean score of 80 (SD = 14). We repeated the analysis, including the data from the right-handers and adding the between-subjects factor Handedness (2 levels: left-handed or right-handed). Again, significant main effects were found for Hand (F(1, 18) = 33.78, p < 0.001), Orientation (F(1, 18) = 32.93, p < 0.001), and Rotation (F(2, 36) = 25.00, p < 0.001), as well as an interaction effect for Hand * Orientation (F(1, 18) = 12.68, p < 0.01). In addition, all other possible two-, three- and four-way interactions were non-significant. Most importantly, we did not find a significant effect for Handedness (F(1, 18) = 3.135, p = 0.09) or an interaction effect for Hand * Handedness (F(1, 18) = 1.59, p = 0.22), indicating that the results were similar for both handedness groups (Figure 3.2). To further investigate the (lack of a) relation between handedness and the end-state comfort effect we performed a correlation analyses between the degree of handedness as defined by the Edinburgh Handedness Inventory and the proportion of comfortable end postures (see also Dassonville et al. 1997). The correlation was not significant for the proportion comfortable end postures of either the left hand (r = 0.20, p = 0.41), the right hand (r = 0.38, p = 0.11), or the difference between the left and right hand (r = 0.24, p =0.32). This further emphasizes the similarity between both handedness groups, which strengthens the left hemisphere dominance hypothesis for motor planning over the hand dominance hypothesis.

One final note should be made that further supports the left-hemisphere specialization for motor planning over the alternative dominant hand experience hypothesis. It is well known that right-handers are generally less experienced with their non-dominant hand compared to left-handers with their non-dominant hand (Gonzalez et al. 2007). However, we found equal performance in the left hands of both handedness groups. This finding goes against the alternative explanation that motor planning is associated with dominant hand experience.

Discussion

In this paper, we outlined the left-hemisphere dominance hypothesis for motor planning and its support from a various lines of research mainly involving right-handed participants. A few studies also focused on left-handed individuals, and although some studies do point to clear left-
hemisphere dominance for motor planning in left-handers as well, the evidence is less conclusive than in right-handers. Therefore, we performed an experiment to add behavioral evidence by testing the performance of left-handed individuals on a motor planning task. These participants showed a stronger end-state comfort effect for their right hand (predominantly controlled by the left hemisphere) compared to their left hand, implying left hemisphere dominance for motor planning also in left-handers.

An alternative explanation for this finding is that motor planning in left-handers relies more on ipsilateral control from their right motor-dominant hemisphere to plan movements of their right hand. For right-handed participants, it has been shown that the ipsilateral (right) hemisphere can play a role in the planning of right hand reaching movements (Busan et al. 2009). However, the majority of literature report strong representations of right hand movements in the contralateral (left) hemisphere (e.g. Kim et al. 1993; Kuhtz-Buschbeck et al. 2003; Johnson-Frey et al. 2005). Furthermore, Frey (2008) has reported that left-handers show the same brain activation pattern, i.e., a distributed network of areas in the left hemisphere, as right-handers when planning and performing tool use pantomimes. This renders it unlikely that the right hemisphere in left-handers is dominant for the planning of right hand movements.

Another alternative explanation for the finding that left-handers perform better on our motor planning task with their right hand compared to their left hand, is that we live in a ‘right-handed world’ (Gonzalez et al. 2007). As most people are right-handed many tools and arrangements are adjusted to right-handers, like scissors, a computer mouse on the right side of a keyboard, etc. It could be that our left-handed participants are so well adapted to these situations, that they have become experienced with their right hand. However, from the handedness inventory we can conclude that they mostly use their left hand for a variety of (daily) tasks. In fact, all left-handed participants answered that they always, or most often, used their left hand when opening a lid from a box, which is in our view the item that most resembled picking up a CD.

A third alternative explanation for the right hand advantage in our experiment, postulates that the left hemisphere is not necessarily dominant for the planning but rather for the execution of precision grasps and that this is taken into account when planning these movements. The study on precision grasping by Gonzalez et al. (2006) might support this by showing that left-handers more often use their non-dominant hand than do right-handers in a precision grasping task. However, the left-handed participants in our study were classified as
being left-handed because they indicated that they use their left hand for the various tasks of
the handedness inventory, which consists mainly of tasks with high precision requirements. If
they prefer to use their left hand in most of these precision demanding tasks, then a left
hemisphere advantage in the execution of precision grasps seems unlikely.

The left hand dominance for motor execution in left-handers may be the cause that
some behavioral studies report equal results for both hands in left-handers and asymmetric
results for both hands in right-handers when motor tasks are considered (e.g. Gonzalez et al.
2007). In those experiments, the planning of movements as controlled by the left hemisphere
and the execution as controlled by the right hemisphere may contribute to an equal
performance for both hands. In right-handed participants, however, the left hemisphere is
dominant for both the planning and execution of movements, which leads to a better
performance for the right hand compared to the left hand. In our experiment, we measured the
performance on motor planning, not execution. Nevertheless, if the dominance on motor
execution in the right hemisphere had interfered with our measurements by improving the
performance of the left hand, the effect that we found would be even an underestimation.

In the present study, we showed asymmetries in task performance at a behavioral level.
Specifically, we showed an advantage in end-state comfort effect for the right hand also in left-
handers, which strengthens the left hemisphere dominance hypothesis for motor planning. In
addition, we showed a larger end-state comfort effect for the vertical condition than for the
horizontal condition. Although at present we do not have a conclusive explanation for this
finding it is possible that the precision requirement was larger when end-state comfort was not
met for the vertical condition than when end-state comfort was not met for the horizontal
condition.
Chapter 4

Motor planning in bimanual object manipulation: Two plans for two hands?

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Chapter 4

Abstract
We examined anticipatory motor planning and the interaction among both hands in a discrete bimanual task. To this end, participants had to grasp and manipulate two cylindrical objects simultaneously under varying conditions in which (a) the grip selection requirements, i.e. orientation of the to-be-grasped objects, differed between the two hands and (b) the type of grip for one hand was pre-instructed, while the grip for the other hand was free choice. Results showed that participants, when grasping for two bars with a free grip choice, prioritized planning for comfortable end postures over symmetry of movement execution. Furthermore, when participants were free to choose a grip for their left hand, but were instructed on how to grasp an object with their right hand, we found no interaction between the grip selections of both hands, suggesting that motor planning proceeds independently for both hands.
Introduction

Every day we perform a great number of movements using both of our hands in a coordinated fashion. Thereby, our hands can work both together, for example when unscrewing a lid, and relatively independent, for example when holding the steering wheel with one hand and the gear lever with the other hand while driving. Many studies have shown that the central nervous system (CNS) has a preference to synchronize both hands in bimanual tasks, such that movement execution is simplified (Kelso et al. 1979; Jackson et al. 1999; Riek et al. 2003). For example, when participants had to draw a line with one hand and a circle with the other hand, this resulted in a circle-like movement path for the line and a line-like movement path for the circle, suggesting spatial coupling between the hands (Franz et al. 1991).

Unlike in cyclical tasks (like the drawing task described above), in which movement execution is generally the main topic of interest, discrete tasks demand anticipatory planning of the end of the action, before objects are grasped and manipulated. As an example, consider a unimanual discrete task where one wants to pick up a hammer in order to use it. If the hammer is on a table with the hammerhead toward the person, the hand first needs to be rotated in order to pick the hammer with a grip that allows its use. Thus, one adopts an initial awkward posture that allows the proper use of the hammer once it is picked up, which implies anticipatory planning (e.g., Creem and Proffitt 2001). A well known experimental phenomenon by which this type of planning can be observed is the ‘end-state comfort effect’ (Rosenbaum et al. 1996). This effect was shown first by Rosenbaum et al. (1990), who demonstrated that participants would take hold of a horizontally supported dowel with an initial awkward grip if this ensured end-state comfort when placing one of its ends down onto a target disc. This sensitivity to avoid uncomfortable body postures at the final part of movements has been demonstrated across a number of different tasks and in different contexts (Rosenbaum et al. 1992; Short and Cauraugh 1999; Cohen and Rosenbaum 2004; Crajé et al. 2008).

Although anticipatory motor planning has been mainly studied in unimanual tasks, discrete bimanual movement performance poses an interesting control problem from a neurocognitive point of view. On the one hand, the CNS has a preference to (spatially and temporally) synchronize both hands, but on the other hand, it is engaged in anticipatory planning for both hands. This control problem is the focus of the present study. Specifically, the control problem can be studied with the bimanual-object-manipulation paradigm, which has
become a topic of recent research interest (Kunde and Weigelt 2005; Bingham et al. 2008; Hughes and Franz 2008; Kunde et al. 2009). For example, Kunde and Weigelt (2005) investigated the effect of symmetry of end goals versus symmetry of movements on the timing of a bimanual object manipulation task. They asked participants to simultaneously reach for two horizontal bars (each with a black mark on one end) and to turn the bars into either congruent (both marks up or down) or incongruent (one mark up and the other down) final orientations, using pre-instructed grasps. Depending on the bars’ initial positioning on the table, this required participants to plan and execute symmetric or asymmetric forearm rotation movements. Their results demonstrated that participants reached faster for the two objects when they had to be turned into congruent final orientations, irrespective of whether this required performing symmetric or asymmetric movements (i.e., forearm rotations). With respect to the neurocognitive control problem alluded to above, the authors concluded that for bimanual object manipulation the congruency of the objects’ intended final states are decisive for the ease with which bimanual movements can be performed, but that movement symmetry had no effect on the time needed to perform the action (Kunde and Weigelt 2005; Kunde et al. 2009).

In the bimanual-object-manipulation studies (Kunde and Weigelt 2005; Bingham et al. 2008; Kunde et al. 2009), participants were pre-instructed on how to grasp the objects. This rendered planning demands for grip selection to be low. However, when people were tested for bimanual end-state comfort and were free to choose their grasps for the manipulation manoeuvre, they reached for two objects in a way that allowed them to finish the action with both hands in a comfortable posture, even when participants had to select asymmetric initial grasps and to coordinate asymmetric movement patterns (Fischman et al. 2003; Weigelt et al. 2006). These findings suggest that participants prioritize comfortable end postures over symmetry of movement execution. A potential limitation of these previous studies (Fischman et al. 2003; Weigelt et al. 2006), however, was that the experimental task conditions may not have been capable of producing interaction effects between the two hands on the level of movement execution (i.e., symmetry of moving) and end-posture planning. Specifically, in these studies the two objects always had to be moved out of initial horizontal orientations either into two horizontal (Fischman et al. 2003), or two vertical (Weigelt et al. 2006) final positions. Therefore, the question remains whether or not individuals would also prefer comfortable end-states under conditions in which the final orientations are different rather than similar. In a recent study, we addressed this question and varied the initial and final orientations of two objects in
an object placement task (Janssen et al. 2009). In two experiments, participants were required
to transport two CDs from either the same or different initial orientation to the same or
different final orientation into a CD-rack. When participants were free to choose their grasps,
they anticipated the grasp of their right hand to allow a comfortable final position, but for their
left hand this was only the case in 50% of the trials. This finding questions the consistency of the
bimanual end-state comfort effect in complex bimanual object manipulations.

In the present study, we investigated participants’ preference for comfortable end-state
planning and symmetry of movement execution under conditions in which (a) the grasp
selection requirements, i.e., orientation and rotation of the to-be-grasped objects, differed
between the two hands and (b) the type of grasp for one hand was pre-instructed, while the
grasp of the other hand was free choice. This set-up allows us to answer two research questions:
1) Is end-posture planning prioritized over symmetry of movement execution?, and 2) Does the
pre-instructed planning for one hand affect planning of the other hand, i.e. is there an
interaction among planning of both hands?

Participants were asked to pick up two cylindrical objects, one with each hand, and
subsequently place each of the objects into a separate box. In different conditions, they were
required to either grasp two bars, one with each hand (bar-bar conditions), or to grasp a bar
with the left hand and a spoon with the right hand (bar-spoon conditions). Participants were
free to choose their grip in the bar-bar conditions, whereas the grip for the spoon (bar-spoon
conditions) was pre-instructed. Thus, the right hand had a free grip choice in the bar-bar
condition, but a pre-instructed grip in the bar-spoon condition. The grasp selection
requirements were varied between the two hands by manipulating the orientation in which the
two objects were presented. The way in which participants took hold of the objects (i.e. their
type of grip) was registered. For the bar-bar conditions, this enabled us to examine if
participants chose their initial grips in a way that allowed them to finish the task with
comfortable end-postures for both hands. Despite differences in the experimental conditions
between the present experiment and those in the experiments by Weigelt et al. (2006) and
Fischman et al. (2003), we hypothesized that participants in the present study would plan their
movements in a way that resulted in comfortable end-states for both hands. For the bar-spoon
conditions, it allowed us to investigate the extent to which posture-based planning proceeds
independently for both hands. The finding that participants in previous experiments did not
show a preference to move symmetrically may indicate a lack of interlimb interference effects.
Based on this finding, we hypothesized a lack of interaction between the ongoing planning processes of both hands, i.e. that the pre-instructed right hand does not affect the performance of the left hand.

**Methods**

**Participants**
Seventeen right handed university students (5 males and 12 females, mean age 20.7 years, SD 1.9 years) participated in the experiment. Hand dominance was confirmed using the Edinburgh Handedness Inventory (Oldfield 1971). All participants gave informed consent prior to the experiment, but were naive with regard to the purpose of the study. They were paid 8 Euros for their participation. The experiments were conducted conform the standards of the declaration of Helsinki and in accordance with local ethical guidelines.

**Experimental setup and apparatus**
The participants were seated in front of a table at which the experimental set-up was placed. The set-up consisted of a grey board of approximately one by two meters at which two axes were attached at eye height, 47 cm apart from each other. Both axes could be independently rotated manually by the experimenter who sat behind the grey board. On both axes, either a bar or a spoon could be mounted. The distance between this bar or spoon and the board was 4 cm, such that participants were not obstructed when they grasped the object(s) with a supinated or pronated grip. The bar (length: 25 cm, diameter: 2.4 cm) had one black end and one white end and the spoon (length: 24 cm) was completely black (see Figure 4.1). Participants were instructed to place the bar(s) and spoon in two round boxes that were located at the table in front of the participants. The bar at the left axis was fixated in 10 different orientations ranging from -90 to 90 in steps of 20 degrees. The bar or spoon at the right axis was fixated in 4 different orientations; -90, 0, 90 and 180 degrees. In the figure, the bar at the left axis has a start orientation of 30 degrees; the spoon at the right axis has a start orientation of 90 degrees. During the experiment, the participants wore liquid crystal occlusion goggles that occluded vision in-between trials, i.e. when the axes were manually rotated to a different orientation, thereby preventing anticipatory preparation of the action prior to the start. A video camera recorded the whole experiment with prior consent of the participants.
Two plans for two hands?

**Figure 4.1** Schematic representation of the start orientations of the left bar and the right bar / spoon.

**Task**
Participants performed two different tasks, denoted the ‘bar-bar task’ and the ‘bar-spoon task’ in what follows. In the bar-bar task, participants had to grasp the two bars bimanually (one with each hand) from the axes and place them in the boxes with the black side up. We instructed them to grasp the bars simultaneously and with a full power grip. Nevertheless, they were free to choose how to grasp the bar, i.e. the orientation of the hand could be either pronation or supination, but they were not allowed to manipulate the bar in the hand once it was grasped.

In the bar-spoon task, the bar on the right was replaced by a spoon, so that participants had to grasp a bar with their left hand and a spoon with their right hand. In this condition, participants were instructed to grasp the spoon with a full grip, in such a way that it could be used to stir in a cup or eat with it, thus with the thumb towards the bowl and ending the movement with an uncomfortable end posture (i.e., with thumb down, as described below). The spoon action of the bar-spoon task was further demonstrated to the participants by the experimenter.

**Experimental design**
The bar at the left (i.e., that was grasped with the left hand) could adopt 10 different orientations, ranging from -90 to 90 degrees in steps of 20 degrees (Figure 4.1). The black side of
the bar was always directed outward. We chose these specific orientation angles as in general switches in grip types occur in the lower half of the ‘clock face’ (Rosenbaum et al. 1992; Steenbergen et al. 2000; Gonzalez et al. 2006; Crajé et al. 2008). Moreover, the grip types adopted in the horizontal orientations (-90 and 90 degrees) have been studied extensively (Rosenbaum et al. 1990; Weigelt et al. 2006), allowing us to compare the present results with previous studies. The right bar and spoon could adopt four orientations (Figure 4.1), two horizontal orientations (-90 and 90 degrees) and two vertical orientations (0 and 180 degrees). Combining the orientations of the left and right axes resulted in 10 * 4 = 40 conditions for each task (bar-bar task and bar-spoon task). Each condition was repeated three times yielding a grand total of 40 (condition) * 2 (task) * 3 (repetition) = 240 trials. These trials were presented randomly in 6 blocks, 3 blocks with the bar-bar task and 3 blocks with the bar-spoon task. The total duration of the experiment was approximately one hour.

Data analysis
In each trial, the specific grip type used for each hand was scored. We determined grip types by using two criteria, -1- the start posture and, -2- the end posture. The start posture, i.e., the posture when taking hold of the bar, was either pronated or supinated. A supinated posture is generally assessed as less comfortable than a pronated posture (Rosenbaum et al. 1992). For the end posture, the direction of the thumb was used as criterion. In line with other studies we denoted the end posture comfortable if the thumb was pointing upward upon placing of the bar, and uncomfortable when the thumb was pointing downward (e.g., Rosenbaum et al. 1992; Weigelt et al. 2006). Combining these criteria for start and end postures resulted in four possible grip types (Table 1). Analysis of these grip types proceeded as follows.

Research question 1: end posture planning vs symmetry of movement execution
To investigate if participants preferred end posture planning or symmetry of movement execution, combinations of horizontal orientations of the left and right bar in the bar-bar task were analyzed. Hence, we investigated whether participants adapted their start posture in order to complete the task with a comfortable end posture. End comfort was established for both hands only in those critical conditions in which participants had to adopt a less comfortable
Table 4.1 Four different grip types.
The table depicts examples of the four grip types, in this case when the bar is oriented horizontally (first column). Furthermore, a short description of this grip type (column 2), the start posture (column 3) and the comfort of the end posture (column 4) are listed for each grip type.

<table>
<thead>
<tr>
<th>Grip type + example</th>
<th>Description</th>
<th>Start posture</th>
<th>End posture</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grip type -1-</td>
<td>Overhand grip with thumb towards black side</td>
<td>Pronation</td>
<td>Comfortable</td>
</tr>
<tr>
<td>Grip type -2-</td>
<td>Underhand grip with thumb towards black side</td>
<td>Supination</td>
<td>Comfortable</td>
</tr>
<tr>
<td>Grip type -3-</td>
<td>Overhand grip with thumb towards white side</td>
<td>Pronation</td>
<td>Uncomfortable</td>
</tr>
<tr>
<td>Grip type -4-</td>
<td>Underhand grip with thumb towards white side</td>
<td>Supination</td>
<td>Uncomfortable</td>
</tr>
</tbody>
</table>

supinated start posture in order to complete the task with a comfortable end posture. For the left hand this was the 90 degrees bar orientation, whereas for the right hand this was the -90 degrees bar orientation. Thus, comfort of the left hand was analyzed in the L90°/R-90° and L90°/R90° conditions and comfort of the right hand in the L-90°/R-90° and L90°/R-90° conditions. In addition, it was analyzed if participants rotated both arms mirror symmetrically,
i.e. both hands pronation or supination, in all four combinations of horizontal bar orientations (i.e., L-90°/R-90°; L-90°/R90°; L90°/R-90° and L90°/R90°). The percentage of trials in which participants ended uncomfortably and those in which they moved symmetrically were calculated, as well as the accompanying 95% confidence intervals.

**Research question 2: interaction among planning of both hands**

To investigate the interaction between the two hands, we analyzed whether motor planning of the left hand was influenced by motor planning of the right hand. First, end posture planning of the left hand in the bar-spoon task (i.e., fixed grip type for the right hand) was compared to that in the bar-bar task (i.e., free grip type for the right hand) using Z-tests. Second, start posture planning was investigated via analysis of the so-called ‘switch points’. Since we used a range of bar orientations for the left hand, we expected participants to switch between different grip types at a particular bar orientation. The bar orientation where participants switched between different grip types was denoted the ‘switch point’. We were interested if this switch point was affected by the action of the right hand, i.e., if participants would switch between grip types at a different bar orientation with their left hand depending on the motor planning of their right hand. Again, we compared conditions where participants were free to choose a grip with both hands (bar-bar condition) versus the conditions where participants had to use a pre-instructed grip type with their right hand (bar-spoon conditions). For each participant individually, the switch point of the left hand was calculated in the four conditions (bar -90°, bar 90°, spoon -90° and spoon 90°) using a logistic (S-shaped) function. For each condition a logistic function was fitted through the mean frequency of grip type 1 (see Table 1), using the function: \( y = 1 / (1 + e^{-k(x-c)}) \), where \( y \) is the location of the switch point, \( x \) is the bar orientation, \( c \) is the bar orientation of the switch point and \( k \) is a measure of the slope at that point (van Doorn et al. 2007; Crajé et al. 2008). The switch points were analyzed using a 2 (Object: bar versus spoon) * 2 (Rotation: -90° versus 90°) repeated measures ANOVA.

**Results**

**Research question 1: end posture planning vs. symmetry of movement execution**

For all participants, the percentage of comfortable end postures was 61.8% (\( SE = 9.5% \)) for the left hand and 74.5% (\( SE = 8.7% \)) for the right hand.
Table 4.2 Percentages of trials in which participants ended in a comfortable posture, and moved both hands in symmetry, separated for both strategy groups.

<table>
<thead>
<tr>
<th>Participants</th>
<th>Comfortable end</th>
<th>Symmetry</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Left</td>
<td>Right</td>
</tr>
<tr>
<td>Group 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pp 4</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>5</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>6</td>
<td>83.3</td>
<td>100.0</td>
</tr>
<tr>
<td>7</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>9</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>10</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>11</td>
<td>83.3</td>
<td>83.3</td>
</tr>
<tr>
<td>13</td>
<td>83.3</td>
<td>100.0</td>
</tr>
<tr>
<td>14</td>
<td>83.3</td>
<td>100.0</td>
</tr>
<tr>
<td>17</td>
<td>66.7</td>
<td>100.0</td>
</tr>
<tr>
<td>Total</td>
<td>90.0</td>
<td>98.3</td>
</tr>
<tr>
<td>Group 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pp 1</td>
<td>16.7</td>
<td>16.7</td>
</tr>
<tr>
<td>2</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>3</td>
<td>33.3</td>
<td>100.0</td>
</tr>
<tr>
<td>8</td>
<td>0.0</td>
<td>33.3</td>
</tr>
<tr>
<td>12</td>
<td>33.3</td>
<td>33.3</td>
</tr>
<tr>
<td>15</td>
<td>0.0</td>
<td>33.3</td>
</tr>
<tr>
<td>16</td>
<td>66.7</td>
<td>66.7</td>
</tr>
<tr>
<td>Total</td>
<td>21.4</td>
<td>40.5</td>
</tr>
</tbody>
</table>

Group 1 = “Comfortable enders”
Group 2 = “Comfortable starters”
pp = participant

Strikingly, we found that not all participants showed a preference for comfortable end postures. It appeared that the participants could be divided into two groups. One group (Group 1, n = 10,
3 males) of participants predominantly planned their actions such that they ended comfortably with both hands (left hand 90.0% [SE = 3.7%]; right hand 98.3% [SE = 1.7%]) in line with the ‘end-state comfort effect’, while the other group (Group 2, n = 7, 2 males) did not end their actions in a comfortable posture with both hands (left hand 21.4% [SE = 9.4%]; right hand 40.5% [SE = 12.5%], Table 2). As participants in group 2 did not show the end-state comfort effect consistently, we examined whether they prioritized moving mirror symmetrically during the task. Surprisingly, participants in group 2 moved symmetrically in exactly 50.0% (SE = 1.8%) of all trials. This was similar to performance in group 1 where participants moved symmetrically in 52.5% (SE = 1.8%) of all trials. An alternative option that may account for the absence of the end-state comfort effect in group 2 is that participants in this group preferred a comfortable start posture, hence, at an intermediate goal, instead of the end goal (cf. Steenbergen et al. 2000; Mutsaarts et al. 2006). This preference for a comfortable start posture in group 2 was indeed confirmed by the occurrence of the pronated start posture in 78.6% (SE = 9.4%) and 59.5% (SE = 12.5%), for the left and right hand, respectively. These percentages were 10.0% (SE = 3.7%) and 1.7% (SE = 1.7%) in group 1. Thus, participants in group 2 often prioritized comfort of the start posture by using a pronated start posture. Accordingly, participants in group 2 were termed “comfortable starters”, whereas those in group 1 prioritized comfort of the end posture and were termed “comfortable enders”. The subsequent analyses were performed for both groups separately.

Research question 2: interaction among planning of both hands
As previous studies suggest a strong coupling between both hands in general, we hypothesized that explicitly pre-instructing one hand (the right hand) to plan the action in a particular way may influence planning of the other hand as well. Specifically, participants were strictly instructed to grasp the spoon with the right hand in such a way that they ended the movement with an uncomfortable end posture (i.e., thumb towards the bowl). As we found participants used two strategies, either intermediate goal planning or end goal planning, we investigated the interaction among hands both, when participants took hold of the objects, and at task completion.

For end-goal planning, we compared the proportion of comfortable end postures in the bar-bar task and the bar-spoon task. The comfortable enders (Group 1) completed the bar-spoon task in a comfortable end posture with the left hand in 83.3% (SE = 8.6%) of the trials. This performance was not significantly different from the 90% (SE = 3.7%) of comfortable end
postures for the left hand in the bar-bar task ($Z = 0.44, p = 0.64$). In a similar way, the comfortable starters (Group 2) ended with their left hand equally often in a comfortable end posture in the bar-spoon task (16.7% [$SE = 8.6%$]) and in the bar-bar task (21.4% [$SE = 9.4%$]; $Z = 0.22, p = 0.82$). Collectively, for both groups end-posture planning for the left hand was not affected by the particulars of end-posture planning of the right hand.

For intermediate-goal planning, we analyzed the location where participants switched between grip types - the switch points. Each strategy group switched between different grip types. The comfortable enders used grip type 1 when the bar was rotated clockwise from the switch point and grip type 2 when the bar was rotated counterclockwise from the switch point (see Table 1 for clarification of the grip types). The comfortable starters also used grip type 1 when the bar was rotated clockwise from the switch point, but when the bar was rotated in counterclockwise direction they used grip type 3 (see Figure 4.2). Therefore, the data in each strategy group were analyzed separately.

**Figure 4.2 Switch points for the left hand of both strategy groups.** The comfortable enders (group 1) predominantly ended comfortably by switching between grip type 1 (pronation start) and grip type 2 (supination start). The comfortable starters (group 2) preferred a comfortable (pronation) start and switched between grip type 1 (comfortable end) and grip type 3 (uncomfortable end).
Chapter 4

In Table 4.3 the average switch points are presented for the four critical conditions for both strategy groups. The mean switch point for the comfortable enders was 19.7° and the mean switch point for the comfortable starters was -8.0°. For both the comfortable enders and the comfortable starters a repeated measures ANOVA did not reveal any significant effect for object (bar or spoon) used by the right hand (for comfortable enders: $F (1, 9) = 2.36$, for comfortable starters: $F (1, 6) = 2.55$) or object orientation (-90° or 90°, for comfortable enders: $F (1, 9) = 0.40$, for comfortable starters: $F (1, 6) = 1.4$) on the location of the switch point of the left hand. Hence, as the results of the end-goal planning, the results of the intermediate-goal planning also suggest that the left hand was not affected by the particulars of posture planning of the right hand, hence there is no indication of interlimb interference at the level of anticipatory motor planning.

*Table 4.3 Location of the switch points (SP) for the left hand in degrees in four critical conditions for both strategy groups.* In the first row the 4 conditions are depicted, based on the stimulus for the right hand. The second and third rows represent the values of the switch points for the left hand with the standard error between brackets, for both strategy groups.

<table>
<thead>
<tr>
<th>Stimulus right hand</th>
<th>Bar -90°</th>
<th>Bar 90°</th>
<th>Spoon -90°</th>
<th>Spoon 90°</th>
</tr>
</thead>
<tbody>
<tr>
<td>Comfortable enders (n=10)</td>
<td>SP = 19.6 (6.5)</td>
<td>SP = 25.3 (6.0)</td>
<td>SP = 22.9 (8.3)</td>
<td>SP = 11.1 (3.2)</td>
</tr>
<tr>
<td>Comfortable starters (n=7)</td>
<td>SP = -13.4 (8.1)</td>
<td>SP = -12.4 (8.1)</td>
<td>SP = -9.4 (7.8)</td>
<td>SP = 3.2 (9.4)</td>
</tr>
</tbody>
</table>
Discussion

In the present study, participants had to perform a discrete bimanual sequential task. In half of the conditions they had to pick up a bar with both hands and place it in a box in a predefined way. In the other half of the conditions the bar of the right hand was replaced by a spoon that had to be grasped with a pre-instructed grip type that led to an uncomfortable end posture. First, we examined whether the previously shown end-state comfort effect could be generalized to this more complex sequential bimanual action or if the previously established, symmetry of movement execution during bimanual task performance was prioritized. Second, we examined if any interference effects (at the intermediate goal and at the end goal) were present among both hands with respect to planning.

Research question 1: end posture planning vs symmetry of movement execution

One rather surprising finding of the present study was that nearly half of the participants (7 out of 17, 41%) did not show a preference for end state comfort in both hands. Instead of choosing a start posture that enabled them to end the task in a comfortable end posture, these participants preferred a comfortable start posture that led to an uncomfortable end posture. A similar phenomenon was recently evidenced during unimanual task performance (Crajé et al. 2008). These participants optimized comfort of the start posture, that may be regarded as an intermediate goal in this type of sequential tasks (Mutsaarts et al. 2005). These findings suggest that the generalizability of the end-state comfort effect may be limited to simple tasks, and that it is not a general prioritization in more complex sequential tasks, such as the present task. Thus, in sequential tasks not the end posture of total task is always optimized, but some participants optimize the posture of an intermediate goal. Despite this, it became clear that symmetry of moving is subsidiary to posture planning, as movement symmetry was only observed in half of the trials for all participants. This effect, however, can be attributed to the balanced design of the study, i.e. participants would move symmetrically in half of the trials if they always adopted the same start posture, irrespective of the orientation of the bars. Most importantly, the well known preference for symmetry of movement execution was not found in the present study, because planning for end goals (comfortable end-posture) or planning for intermediate goals (comfortable start-posture) was prioritized.

These findings extend previous studies that suggested a prioritization of posture comfort over movement symmetry in discrete bimanual tasks (Fischman et al. 2003; Weigelt et
al. 2006) to more complex tasks, requiring the anticipation of similar and/or dissimilar final postures. In the study of Weigelt et al. (2006), the start orientation of the objects was always horizontal, placing lower demands on the start posture and posing no conflict for the concurrent planning of different end postures between the two hands. The present study, however, posed a conflict between the tendency to move in symmetry and the tendency to end both hands in a comfortable posture. This contrasts a study by Hughes & Franz (2008), in which participants were able to comply with both symmetry (or bimanual as Hughes and Franz denote it) and end-state comfort constraints simultaneously. Although, apart from the trials where both constraints were met, participants in their study did not show end-state comfort more often than symmetry, and the authors suggested no obvious hierarchy of constraints. In the present study, we would also not have observed a prioritization of the planning constraint if we had not subdivided participants into two groups: the comfortable starters and the comfortable enders. It is presently unclear, why some of the participants optimized comfort of the intermediate goal, while others optimized comfort of the end of the task. It may be speculated that the former participants are less proficient planners than the latter group. A similar observation was made in participants with left congenital brain damage (Mutsaarts et al. 2006) who are known to have a compromised motor planning ability (see also Crajé et al. 2009). Also, it may be speculated that these participants may have focused on speed while performing the task, even though, no instruction relative to speed of task performance were given and no time measurements were taken in the present study. Focussing on speed can lead to a less optimal end posture selection (Rosenbaum et al. 2001).

Summing up, the present findings show that the end-state comfort effect in bimanual tasks is not as consistent as the effect in unimanual tasks, particularly when different grip selections are required for both hands (Hughes and Franz 2008; Janssen et al. 2009). Rather, participants used two main strategies to cope with the bimanual object manipulation task in our experiment: prioritization of comfort of the end goal or prioritization of comfort of the intermediate goal.

Research question 2: interaction among planning of both hands

Previous studies on interference effects during bimanual execution have shown assimilation effects, such that a strong influence or interference among both hands exists. One such example is the temporal assimilation of both hands under bimanual responding despite differences in movement duration in unimanual responding (e.g., Kelso et al. 1979; Steenbergen et al. 1996).
These effects have been attributed to processes related to interhemispheric transfer (Jeeves et al. 1988), bilateral innervation (e.g., Wiesendanger et al. 1994), or neural crosstalk at different levels of the central nervous system (e.g., Carson 1995). In the present study we sought to find out whether such interference could also be revealed with respect to motor planning. That is, is the posture of each hand planned in isolation (mediated by distinct and isolated neural processes), or is there any interference between planning of both hands’ postures? We compared conditions, in which both hands were left free with respect to grip choice (bar-bar conditions), with those where the right hand was explicitly instructed to grasp the spoon in a particular way, such that this hand would end in an uncomfortable end posture (bar-spoon conditions). It was shown that planning of the left hand was not affected by the end posture of the right hand. That is, there were no differences found for the end or start posture adopted by the left hand among the bar-bar and the bar-spoon conditions. Furthermore, an analysis of the switch points, i.e., the rotation angle of the left bar at which participants changed their type of grip, showed that the location of the switch point was similar among the ‘bar-bar’ and ‘bar-spoon’ conditions. These findings suggest that for the present bimanual task posture planning is performed for each hand separately. Thus, in contrast to findings showing interference effects at the level of execution (e.g., Kelso et al. 1979), no such interference was observed for motor planning\(^1\) in the present task.

This finding begs the question as to the origin of this absence of planning interaction effects, despite well known execution interaction effects. It has previously been proposed that control of limb trajectories and of postures may be implemented by distinct mechanisms (e.g., Gottlieb 1996). Further evidence suggests differences between the dominant and non-dominant arm with respect to movement planning (Annett et al. 1979). For example, Carson (1995) showed that manipulation of goal information prior to movement onset leads to longer reaction times for the dominant arm, as compared to the non-dominant arm. These findings combined with the present finding of a lack of interaction between both limbs suggest that motor planning may be mediated by distinct neural mechanisms that do not interact.

\(^1\) With motor planning we mean the specification of content parameters of the movement as a whole, which we operationalized in our experiment as the selection of a grip type. This is in contrast with the term motor programming, which is the specification of spatiotemporal parameters of movement segments.
Chapter 5

Typical and atypical (cerebral palsy) development of unimanual and bimanual grasp planning

Published as:
Chapter 5

Abstract

In the present study we tested 13 children with cerebral palsy (CP) and 24 typically developing children (7-12 years old) in a unimanual and bimanual motor planning task. We focused on two research questions: (1) How does motor planning develop in children with and without CP? and (2) Is motor planning facilitated when the task is performed with both hands? Participants had to grasp one or two vertical oriented cylinder(s) and transport it/them to a platform that had different heights. As a measure of motor planning, we registered the height at which participants grasped the cylinder. Here, anticipation of grasp height upon the height of the upcoming target(s) is reflective of proper forward motor planning as it leads to a comfortable posture at the end of the task.

In the unimanual task the typically developing children showed a significant grasp height effect, which increased with age. In contrast, no grasp height effect, or age related changes therein were found for the children with CP, suggesting a compromised development of motor planning in these children. Interestingly, when children had to transport one cylinder to a high shelf and one cylinder to a low shelf, the more affected hand of the CP children clearly anticipated the grasp height to the upcoming target height. The less affected hand did not show such anticipation. Taken collectively, these findings suggest a delayed or compromised development of motor planning in children with CP compared to typically developing children. At the same time, the facilitated motor planning of the more affected arm in the bimanual task offers a valuable entry point for intervention to improve motor planning in CP.
Introduction

Motor planning can be defined as the formulation of a strategy of grasping by taking into account the future demands associated with the goal of the action (Gentilucci et al. 1997; Johnson-Frey et al. 2004). It can be studied with different experimental paradigms, for example by measuring movement kinematics, via examination of effector selection for object use, or by observing the initial grip with which an object is grasped. With respect to movement kinematics and effector selection, children as old as one year show some form of motor planning (McCarty et al. 1999; Claxton et al. 2003; Claxton et al. 2009). Claxton et al. (2003) had 10-month old infants reach for a ball in order to fit it in a clear tube or to throw it in a large plastic tube. When the children had to fit the ball, peak speed and overall speed during the reaching phase were lower than when they had to throw the ball. Thus, they adjusted their movement speed depending on the subsequent goal of the task, similar to what was found in adults (Marteniuk et al. 1987; Steenbergen et al. 1995). With respect to effector selection, toddlers at the age of 19 months were shown to be able to select the appropriate hand for reaching for a spoon overloaded with food, even when this demanded that they used their non-preferred hand (McCarty et al. 1999).

Concerning the developmental trajectory of grip selection, the results are less clear cut. A vast amount of studies have been performed to study motor planning via grip selection, predominantly in adults. Here it was repeatedly shown that individuals grasp an object with an initial grip that allows them to end the object manipulation task with a comfortable posture, even when this necessitates them to use an awkward initial grip. This has been termed the end-state comfort effect (Rosenbaum et al. 1990; Rosenbaum et al. 1996). Ending the task with a comfortable posture allows for more precise manipulation. This was empirically confirmed in a study with adult participants. Here it was shown that an increase in the precision requirements at the end of the task resulted in an increased occurrence of the end-state comfort effect (Short and Cauraugh 1999). In a simple bar-handling task, adults all adapted their initial grasp to end comfortably (Rosenbaum et al. 1990), even when they had to do this bimanually where two hands had to grasp two bars simultaneously (Weigelt et al. 2006). However, the end-state comfort effect decreased in adults when the bimanual task had higher cognitive demands and when symmetry of movement execution was compromised (Hughes and Franz 2008; Janssen et al. 2009; van der Wel and Rosenbaum 2010).
Children aged 2-3 years old did not select an appropriate grip when asked to turn over a plastic drinking cup for pouring water in it, and this was only found to a small extent in children of 5-6 years old (Adalbjörnsson et al. 2008). In addition, Manoel and Moreira showed that children aged 2.5-6 years old did not show the end-state comfort effect, even when precision demands of the task were increased (Manoel and Moreira 2005). In contrast, recent studies that included children in a broader age group do show a developmental trend in motor planning, as exemplified by an increase in the end-state comfort effect with age (Crajé et al. 2010a; Thibaut and Toussaint 2010; Weigelt and Schack 2010). Thibaut and Toussaint (2010) tested 120 children aged 4, 6, 8 and 10 years old using a simple bar-handling paradigm. Children had to pick up a horizontally orientated bar and place it vertically, using either an overhand or an underhand grip. The authors found that the end-state comfort effect increased with age, with only 10 year-olds performing at ‘adult-level’. Likewise, Crajé et al. (2010a) showed that the occurrence of the end-state comfort effect was less than 10% in 3 year-olds, but increased to 75% in 6 year-olds. In this study, age-matched children with unilateral cerebral palsy (CP) were also tested. Although the children with unilateral CP scored comparable to control children at age 3 and 4, children with unilateral CP of 5 and 6 years old performed worse than controls. More specifically, these children did not show a developmental trend in motor planning. Importantly, however, this study also showed that motor planning in children with unilateral CP improved after eight weeks of intervention.

CP is one of the most common and pervasive developmental disorders that leads to severe physical disability in childhood (Blair and Watson 2006). CP is a group of non-progressive developmental disorders of movement and posture, causing activity limitations (Bax et al. 2005). Recently it was suggested not only that deficits in movement execution lead to activity limitation in CP, but that movement planning problems contribute to them as well (Steenbergen and Gordon 2006). The results of Crajé et al. (2010a) suggest that the development of motor planning in CP might be delayed or compromised, but amendable to improvement after intervention. Bimanual training is a likely candidate for this improvement (Steenbergen et al. 2008). These findings combined with findings in adults with CP that showed motor planning deficits as well (Steenbergen et al. 2000) may lead to the conclusion that motor planning does not properly develop in individuals with CP. Importantly, however, these studies tested motor planning using a dichotomous outcome measure (grip selection). This may potentially cloud developmental trends in motor planning for two reasons. First, his outcome measure may not
be sensitive enough to monitor the development of motor planning. Second, children with CP were previously shown to have different preferences regarding comfort of postures compared to controls (Steenbergen et al. 2000). Therefore, in the present study, we will obviate these shortcomings by scrutinizing the developmental trajectory of motor planning through a more sensitive continuous outcome measure, namely the height at which an object is initially grasped prior to placement at another location.

The first aim of this study was to examine the developmental trajectory of motor planning in children with CP aged 7-12 years old. An age-matched control group of typically developing children was also included. Children had to pick up and transport a vertical cylinder to either a lower or a higher shelf. In adults, the grasp height at which the participants took hold of the cylinder was shown to be inversely related to the height of the target location, which is in accordance with the end-state comfort effect (Cohen and Rosenbaum 2004). Hence, the continuous outcome measure ‘grasp height’ is indicative for motor planning. We chose to include children aged 7-12 years old, as we expected critical changes in the planning in that particular age range, as it is also associated with large developments that take place in the fronto-parietal networks that support motor planning (Casey et al. 2005). We hypothesized that typically developing children adapt their grasp height to the height of the subsequent target location, and that this effect increases with age. In children with CP we expect a lack of these effects.

The second aim of this study was to investigate motor planning in a bimanual task for both groups of children. Specifically, for the children with CP it was examined if bimanual performance would facilitate motor planning as was recently shown after an eight-week intervention period (Crajé et al. 2010a). Using a bimanual grasping task we recently showed that the planned grasp orientation for one hand did not interfere with grasp orientation of the other hand in healthy adults (Janssen et al. 2010). Still, when using a more continuous measure of planning van der Wel and Rosenbaum (2010) did show such bimanual interference effects. In their task participants had to transport plungers and the results indicated that the adaptation of the grasp height decreased when symmetry of movement was in conflict with end-state comfort, i.e., when the plungers had to be transported to different heights (van der Wel and Rosenbaum 2010).

Research on bimanual movement coordination in adolescents with CP showed some form of coupling between both limbs (Sugden and Utley 1995; Steenbergen et al. 1996; Utley
and Sugden 1998; see Gordon and Steenbergen 2008 for an overview). Although children with unilateral CP showed large differences in movement time between both arms when moving unimanually, their arms were synchronized when performing a bimanual movement task (Volman et al. 2002; Hung et al. 2010). In general, the less affected arm adapted to (the level of) the more affected arm. Some authors, however, suggested that the more affected arm might benefit from the less affected arm, based on the finding that the performance of the affected arm is improved in bimanual compared to unimanual tasks (Volman et al. 2002; Gordon and Steenbergen 2008). In the present study, we examined if such facilitation is present at the level of movement planning. This second aim of the study is closely aligned to recent discussions on compromised motor planning in CP and possible scientific-based interventions by which this can be facilitated (Steenbergen and Gordon 2006; Steenbergen et al. 2009; Crajé et al. 2010a; Craje et al. 2010b; Williams et al. 2010).

Methods
Participants
Forty children participated in the experiment, of which 16 were diagnosed with CP. Parents of all 40 children completed an informed consent form and all children agreed to participate. Participants with CP were recruited from two special education schools, whereas control participants were recruited from a regular primary school. Data from three children with CP were excluded, because they had not fulfilled the task correctly. The remaining 13 children with CP (six boys and seven girls) had a mean age of 9.2 y/m (range 7.0–12.5 y/m). Six of these children reported that their left hand was their preferred hand (and their right hand affected) and seven reported that their right hand was their preferred hand (and their left hand affected). The typically developing children (7 boys and 17 girls) had a mean age of 9.4 y/m (range 7.1–12.3 y/m), and none of them had known neurological deficits. Only one of the control participants reported to be left-handed. Hand function was tested using the Box and Blocks test for gross dexterity (Mathiowetz et al. 1985) and the Purdue Pegboard test for fine dexterity (Tiffin 1968) (Table 1). The scores on these tests were used to confirm the hand preferences that were reported by the participants. The experiments were conducted conform the Declaration of Helsinki and in accordance with local ethical guidelines.

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2 For one right-handed participant (nr. 7, see table 1) the left hand score for the Box and Blocks test was larger than the right hand score, indicating a left hand preference. Conversely, the left hand score for the
Perdue Pegboard test was smaller than the right hand score, confirming a right hand preference. Combined with his own indication of a right hand preference, we therefore regarded his right hand as the preferred / less affected hand. Nevertheless, exclusion of this participant’s data would not have affected any of the results in this study qualitatively.

Table 5.1 Participant information of the CP group.

<table>
<thead>
<tr>
<th>Participant</th>
<th>Sex</th>
<th>Age</th>
<th>Pref</th>
<th>Box &amp; Blocks</th>
<th>Perdue Pegboard</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pref N-pref</td>
<td>Pref N-pref</td>
</tr>
<tr>
<td>1</td>
<td>F</td>
<td>8.7</td>
<td>R</td>
<td>28 12</td>
<td>9   0</td>
</tr>
<tr>
<td>2</td>
<td>F</td>
<td>7.2</td>
<td>L</td>
<td>28 19</td>
<td>5   2</td>
</tr>
<tr>
<td>3</td>
<td>F</td>
<td>7.2</td>
<td>L</td>
<td>20 19</td>
<td>9   3</td>
</tr>
<tr>
<td>4</td>
<td>F</td>
<td>8.6</td>
<td>L</td>
<td>24 14</td>
<td>7   2</td>
</tr>
<tr>
<td>5</td>
<td>M</td>
<td>7.0</td>
<td>R</td>
<td>26 25</td>
<td>8   7</td>
</tr>
<tr>
<td>6</td>
<td>F</td>
<td>8.9</td>
<td>R</td>
<td>15 14</td>
<td>0   0</td>
</tr>
<tr>
<td>7</td>
<td>M</td>
<td>12.5</td>
<td>R</td>
<td>51 57</td>
<td>18  14</td>
</tr>
<tr>
<td>8</td>
<td>M</td>
<td>9.4</td>
<td>L</td>
<td>27 12</td>
<td>9   0</td>
</tr>
<tr>
<td>9</td>
<td>M</td>
<td>9.6</td>
<td>L</td>
<td>32 22</td>
<td>6   2</td>
</tr>
<tr>
<td>10</td>
<td>M</td>
<td>7.9</td>
<td>L</td>
<td>31 28</td>
<td>7   1</td>
</tr>
<tr>
<td>11</td>
<td>F</td>
<td>11.9</td>
<td>R</td>
<td>28 24</td>
<td>6   4</td>
</tr>
<tr>
<td>12</td>
<td>M</td>
<td>11.9</td>
<td>L</td>
<td>34 22</td>
<td>11  5</td>
</tr>
<tr>
<td>13</td>
<td>F</td>
<td>9.0</td>
<td>R</td>
<td>34 33</td>
<td>10  7</td>
</tr>
<tr>
<td>Mean</td>
<td>6M / 7F</td>
<td>9.2</td>
<td>7L / 6R</td>
<td>29.1 23.2</td>
<td>8.1  3.6</td>
</tr>
<tr>
<td>SD</td>
<td>1.8</td>
<td>8.5</td>
<td>12.0</td>
<td>4.1  3.9</td>
<td></td>
</tr>
</tbody>
</table>

Controls

| Mean        | 7M / 17F | 9.4 | 1L / 23R | 40.1 39.8 | 28.9 21.5 |
| SD          | 1.6 | 7.8 | 7.7 | 8.1 12.0 |

Pref = preferred / less affected hand; N-pref = non-preferred / more affected hand
**Experimental setup**

The experimental setup consisted of a metal frame with five height-adjustable shelves and two identical plastic cylinders (Figure 5.1). Each cylinder had a diameter of 3 cm, the circular foot had a diameter of 10 cm, the length was 40 cm, and the mass was 162 g. The cylinders had vertical stripes every 2 cm, to enable off-line scoring of the grasp height. The cylinders were positioned on the middle shelf of the frame, the so-called home shelf, which measured 30 x 23 cm. This home shelf was adjusted to the height of each participant’s belly button. The other four shelves were target shelves, measured 15 x 20 cm, and had different colors for instructional purposes. The top target shelves were adjusted to a height 40 cm below the maximal reach height of the participant while standing (for each hand separately), which enabled participants to place the 40-cm-long-cylinder on a top shelf while holding the cylinder at the top. The bottom shelves were adjusted to the height of the participant’s hands while standing upright, and letting their arms hang by their sides. This allowed the participants to place the cylinder on the bottom shelf while holding the cylinder at the bottom. One top shelf and one bottom shelf were attached to the left leg of the frame, centered 25 cm to the left of the center of the middle shelf. The other top shelf and bottom shelf were attached to the right leg of the frame, centered 25 cm to the right of the center of the middle shelf.

**Figure 5.1 The experimental setup.**

The shelves had different colors and their height was adjusted for each participant.
Task and procedure
Participants were instructed to stand facing the experimental setup, after which the shelves’ heights were adjusted to each individual, as described above. They started with the unimanual task in which one cylinder was placed on the home shelf. Participants were instructed to grasp the cylinder and to transport it to one of the target shelves. They had to use the left hand for transport to the left target shelf and the right hand for transport to the right target shelf. The experimenter gave a verbal instruction in which participants were told which hand to use and to which target shelf the cylinder had to be transported. The latter was indicated by naming its color. After placing the cylinder on the target shelf, the participant was asked to release the cylinder and lower the hand before grasping it again to transport the cylinder back to the home shelf. After the participant had lowered the hand again, the experimenter instructed to transport the cylinder to another target shelf. This was repeated until all four target shelves were completed. This complete session was repeated three times.

The bimanual task was similar to the unimanual task, but now participants had to grasp two cylinders, one with each hand, and transport one cylinder to the left target shelf and one cylinder to the right target shelf. This was again verbally instructed by the experimenter, who named the colors for the target shelves for both hands. The bimanual task consisted of two congruent conditions in which both hands moved to the same height (both cylinders to the top shelves or both cylinders to the bottom shelves) and two incongruent conditions in which both hands moved to different heights (left cylinder to the top and right cylinder to the bottom or vice versa). These four trials were administered in a randomized order, and the complete session was repeated three times.

During the experiment grasping of the cylinder was videotaped, enabling off-line analysis of the grasp heights afterwards.

Data analyses
The grasp height(s) for each trial was/were determined by counting the number of stripes from the foot of the cylinder to the top of the index finger at the time participants took hold of the cylinder. From this, the grasp height in centimeters above the cylinder’s foot was calculated. The grasp heights were averaged per hand across the trials in each condition. Subsequently, the grasp height difference was calculated by the difference between the average grasp height when placing the cylinder on the bottom shelf (which is expected to be a relatively large value in
controls) and the average grasp height when placing the cylinder on the upper shelf (which is expected to be a relatively small value in controls). This is a crucial variable to assess motor planning. The calculation was made for each hand of each participant, and for the unimanual, bimanual congruent and bimanual incongruent conditions separately. We interpreted a positive grasp height difference as a measure of motor planning as it indicates an adaptation of the grasp height to the upcoming target height.

First, we analyzed motor planning in the unimanual conditions followed by the bimanual conditions. For each of the conditions (unimanual, bimanual congruent, and bimanual incongruent) we used t-tests to analyze whether the grasp height differences of each hand in each group were significantly larger than zero, which is an indication of motor planning. Second, to examine the developmental trajectory of motor planning in the unimanual conditions, we calculated Pearson’s correlation coefficients between the mean grasp height difference and age for both groups.

Results

Unimanual task

First, Figure 5.2a shows the mean grasp height differences for the preferred / less affected and non-preferred / more affected hands of children with CP and typically developing children in the unimanual task. The t-tests revealed that the grasp height difference in control children was significant for both hands (preferred hand: $M = 1.72$ cm, $t(23) = 2.53, p = 0.019$; non-preferred hand: $M = 3.69$ cm, $t(23) = 3.52, p = 0.002$), but not in children with unilateral CP (less affected hand: $M = 1.38, t(12) = 1.51, p = 0.16$; more affected hand: $M = 0.33, t(12) = 0.25, p = 0.81$). These results suggest that control children do adapt their grasp height to the upcoming target, in contrast to CP children.

Second, to examine the developmental trend in planning, we calculated Pearson’s correlations between the grasp height difference and age for each group separately. In the typically developing children, a significant positive correlation between grasp height difference and age was found ($r = 0.42, p = 0.04$, see Figure 5.3b). For the children with CP we did not find such a developmental trend ($r = -0.33, p = 0.27$, see Figure 5.3a).
Figure 5.2 Grasp height differences in unimanual (a), bimanual congruent (b), and bimanual incongruent (c) conditions. The black bars display the grasp height differences for the preferred or less affected hand and the hatched bars display the grasp height differences for the non-preferred or more affected hand.
Chapter 5

Bimanual congruent task

The results for the bimanual congruent task are shown in Figure 5.2b. Similar to the results in the unimanual task, the grasp height difference for each hand was significant in typically developing children (preferred hand: $M = 4.19$, $t(23) = 5.67$, $p < 0.001$; non-preferred hand: $M = 2.89$, $t(23) = 4.91$, $p < 0.001$), but not in children with unilateral CP (less affected hand: $M = 0.72$, $t(12) = 0.48$, $p = 0.64$; more affected hand: $M = 1.72$, $t(12) = 1.46$, $p = 0.17$).

![Graph](image)

Figure 5.3 Correlation between grasp height difference and age in CP (a) and controls (b).
Bimanual incongruent task

We examined the bimanual incongruent task conditions, in order to scrutinize the potential facilitation effect of one hand on the other hand with respect to motor planning. The pattern of results for the bimanual incongruent task differs substantially from that for the bimanual congruent task (Figure 5.2c). In the incongruent task there was a significant positive grasp height difference for the non-preferred / more affected hand, not only in the control group but also in the children with CP (control: $M = 1.94$, $t(23) = 2.64$, $p = 0.015$; CP: $M = 4.56$, $t(12) = 3.22$, $p = 0.007$; see hatched bars in Figure 5.2c). This indicates motor planning for this hand. Strikingly, for the preferred / less affected hand there was a significant negative grasp height difference in both groups (control: $M = -1.36$, $t(23) = -2.44$, $p = 0.023$; CP: $M = -2.97$, $t(12) = -2.24$, $p = 0.045$). Thus, the bar was grasped higher with their preferred / less affected hand when it was placed on the upper shelf compared to the lower shelf, suggesting a lack of motor planning.

Discussion

In this study we examined the development of motor planning in a group of typically developing children and in a group of children with a congenital developmental disorder, i.e., cerebral palsy. The research led to three important results. First, when using one hand in the cylinder placement task we showed motor planning in typically developing children, but a lack thereof in children with CP. Second, we found a developmental trend of motor planning in the typically developing children (age 7-12 years), but not in the children with CP. Third, in the bimanual conditions where both hands had to transport the two cylinders to different heights, we found that motor planning of the affected hand in children with CP was facilitated. Below we will elaborate on these main findings, and their implications for therapy.

To our knowledge, this is the first study that examines the typical and atypical development of motor planning via a continuous planning measure. The height at which the cylinder was grasped prior to placement on a high or a low shelf served as a representative measure of motor planning. In previous research this paradigm has been validated in adults (Cohen and Rosenbaum 2004; Rosenbaum et al. 2006; van der Wel and Rosenbaum 2010). Using a similar set-up in adults, Cohen and Rosenbaum (2004) showed that the difference in grasp height between transporting a dowel to the lowest and the highest shelves (comparable in height to our shelves) was between 7 and 12 cm. In the present study, the mean grasp height
difference in control children was between 1.7 and 3.7 cm (for preferred and non-preferred hand respectively), whereas this was not significant for children with CP. An obvious explanation for these different values between healthy control children and adults is that motor planning is not completely developed in the age range of the children in the present experiment. This is corroborated by our finding of a significant positive correlation between the increase of grasp height and age. In contrast, however, a recent study showed that children aged 10 years old displayed planning levels similar to adults (Thibaut and Toussaint 2010). Still, in that study, the dependent measure to represent motor planning was grip orientation. We argue that grip orientation is a rather dichotomous variable (either overhand or underhand grip) that may not be sensitive enough to uncover true developmental trends in motor planning. As we showed, grasp height is a more sensitive measure that develops with age in the age range between 7 and 12 years.

This developmental trend in motor planning provides behavioral evidence for the neurological findings that showed structural and functional changes to occur in the brain over the lifespan and in particular during childhood between 5 and 10 years of age (Casey et al. 2005). Notably, childhood has been suggested to be a decisive period for the development of motor planning and internal forward models (Maruff et al. 1999; Wilson et al. 2002). Motor planning is grounded within theories of internal forward models, which control movement by predicting the future state of the moving limb based on the motor command (Miall and Wolpert 1996; Wolpert 1997).

It has been argued that motor problems in children with Developmental Coordination Disorder are due to a deficit in the build-up of internal forward models (Wilson et al. 2004). Our results showed a lack of motor planning in the unimanual task, as well as a lack of development therein for the children with CP aged 7-12 years old. These results are in line with recent studies showing compromised motor planning in young adolescents with CP (Steenbergen et al. 2000; Mutsaarts et al. 2006; Craje et al. 2010b). It may be hypothesized that a deficit in the use of internal models to predict movements lies at the basis of motor planning problems in CP. Indeed, recent studies indicated that deficits in motor imagery, the ability to imagine movements without actually executing them, may cause compromised motor planning (Craje et al. 2010b; Williams et al. 2010). Furthermore, it has been shown that adolescents with CP do have problems using motor imagery (Mutsaarts et al. 2007; Steenbergen et al. 2007). Finally, in a recent study Craje et al. (2010b) had adolescents with CP perform both a motor planning task as
well as a motor imagery task and found impairments in the performance of both tasks, suggesting a relationship between the two. From these converging lines of evidence, it could be speculated that motor imagery training might be beneficial to improve motor planning. Previous studies have shown promising results of motor imagery training in stroke patients and in children with Developmental Coordination Disorder (Wilson et al. 2002; Braun et al. 2006; Sharma et al. 2006). Thus far no studies on the use of motor imagery training for upper limb recovery have been done in patients with CP, despite its feasibility (Steenbergen et al. 2009). However, incorporating motor imagery training in intervention programs for children with CP might be a challenge, as intervention programs for these children usually start at young age, and it might be difficult to engage these children in motor imagery tasks.

Another, important question that first needs to be answered is: Can motor planning be ameliorated in children with CP? Our findings in the bimanual incongruent conditions showed that motor planning in the more affected hand was facilitated when it performed the action together with the less affected hand. That is, the more affected hand was shown to plan in advance, whereas the less affected hand adapted to it, i.e., grasped the bar at about the same height as the more affected hand, resulting in an awkward end-posture. These findings are in close concordance with those of Volman et al. (2002). They had children with CP perform an asymmetrical bimanual circle drawing task. In these conditions the spatiotemporal performance of the more affected arm improved at the expense of the less affected arm. Performance of this arm aggravated. According to Volman et al. (2002), the children choose a cognitive strategy in which they focused attention in this difficult task on the more affected arm. A similar explanation may also hold for our results, i.e., in the conditions in which the cylinders had to be transported to different heights for each hand, children focus attention on the more affected hand. As a consequence, performance of this hand improves (see also Steenbergen et al., 1996). This hypothesis could be confirmed in future research by combining a motor planning task with EEG measurements. If facilitation of the more affected hand is indeed related to focused attention, it may be expected that components related to focused attention (P3b) and anticipation (CNV) are most prominent in the hemisphere contralateral to the more affected hand in the bimanual incongruent conditions.
Chapter 5

Conclusion
Taken collectively, in the unimanual conditions our results showed no motor planning in children with CP or a developmental trend therein. However, in the bimanual incongruent conditions motor planning of the more affected hand was shown to be facilitated. These findings are promising for intervention. Recently, (Craje et al. 2010a) showed an improvement in motor planning following eight weeks of intervention. Thus, although there does not appear to be a natural development of motor planning, it is a feature of motor performance that is amendable for training. The results of the present study suggest that intervention should at least include bimanual tasks that have asymmetrical elements. These protocols could be implemented in current intervention protocols based on forced use combined with bimanual training (Gordon et al. 2007; Aarts et al. 2011).
Chapter 6

Excitability of the motor system during observation of action preparation

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Chapter 6

Abstract

Action observation activates brain areas associated with action execution, including the primary motor cortex (M1). Using transcranial magnetic stimulation (TMS), it has been shown that the excitability of corticospinal projections from M1 changes in a functionally specific fashion while a grasping action is observed, and that this modulation of excitability is in accordance with the timing of the kinematic profile of the observed hand movement.

In the present experiment, we had participants watch videos in which an actor grasped an object either at its small end using a precision grasp or its large end using a whole-hand grasp and subsequently inserted the other object-end in one of two holes in a wooden block. Before the actor grasped the object, a cue indicated in which hole the object should be inserted so that the observer could infer which object-end would be grasped and which grasp the actor would use. In most trials the cue was indicative for the upcoming action, however, in some trials we introduced an erroneous cue. We investigated the effect of the cue on the observer’s corticospinal excitability when the cue was presented (action preparation) and during the subsequent grasping action (action execution).

Corticospinal excitability was increased during the observation of action preparation, but this increase was not functionally specific, i.e. it did not depend on the type of the upcoming grasp (precision or whole-hand grasp) that was indicated by the cue. In contrast, during observation of action execution the modulation of corticospinal projections to individual hand muscles was dependent on the type of the grasp being performed by the actor. Furthermore, after the presentation of an erroneous cue, the corticospinal excitability first ensued the pattern for the cued action but changed to coincide with the observed action.

In sum, these findings show that the observation of cues that dictate the processing that must occur during preparation for action gives rise to an increased but non-specific excitability in an observer’s corticomotor system. However, observation of directional cues does give rise to muscle-specific effects during the actions that are subsequently observed.
Introduction
How we grasp an object is dependent on the purpose of the action. For example, if we grasp a cup that is upside down, we would use a different grip when we want to pour milk in it compared to placing it in the dishwasher. This is repeatedly shown by the end-state comfort effect: the preference for a comfortable joint-angle configuration at the end of a movement, even when this necessitates an awkward posture when first grasping the object (Rosenbaum et al. 1992). Thus, when planning how to grasp an object, we take into account the forthcoming demands associated with the goal of the action sequence (Johnson-Frey et al. 2004). This anticipatory planning implies that people’s behaviour is sequentially organised; first the goal of a movement is planned and second, the grip is selected with which an object is grasped as well as the corresponding movement trajectory towards the object.

It has been shown that people’s behaviour can be anticipatory not only when they make an action themselves, but also when they observe other’s actions. For example, when participants observed an actor performing a block-stacking task, their eye-movements were proactive, i.e., they directed their gaze towards the grasp sites of the blocks to be picked up and the landing sites where the blocks were subsequently placed, similarly to when performing the task themselves (Flanagan and Johansson 2003). This implies that people can predict the intention of an actor before the actor has actually completed the action. This corresponds to the direct matching hypothesis, which states that observed actions are mapped onto one’s own motor system where a motor representation is formed (Iacoboni et al. 1999; Rizzolatti et al. 2001; Flanagan and Johansson 2003). The resonant motor representation is hypothesized to be used for understanding and / or imitation of the action made by another (Rizzolatti and Craighero 2004). Neurons that have been shown to fire both during execution of an action as well as during the observation of the same action made by another, are termed mirror neurons. These neurons have been found mainly in the premotor area. This area projects to the primary motor area and this activation can be quantified by measuring corticospinal excitability using transcranial magnetic stimulation (TMS) (Hari et al. 1998; Fadiga and Craighero 2004; Rizzolatti and Craighero 2004). An increase in corticospinal excitability results in an increased motor evoked potential (MEP) as can be shown with electromyography recordings after administration of a single magnetic stimulus to the scalp over the motor cortex.

In line with the direct-matching hypothesis, it has been shown that corticospinal excitability increases not only during and just prior to action execution, but also during motor
imagery (Fadiga et al. 1999; Stinear and Byblow 2003) and during action observation of natural movements (Fadiga et al. 1995; Clark et al. 2004; Gangitano et al. 2004). Moreover, this modulation of the cortical excitability is highly specific for the action that is imagined or observed. First, the modulation seems to be specific for the target muscles that are active when the imagined or observed movement would actually be executed (Fadiga et al. 1995; Fadiga et al. 1999; Stinear and Byblow 2003; Alaerts et al. 2009). Second, the force requirements of the actor also map to the excitability of the observer (Alaerts et al. 2010). And third, the modulation of cortical excitability is lateralized to the contralateral hemisphere when right- vs left-hand actions are observed (Aziz-Zadeh et al. 2002). Although there is an abundance of studies reporting on motor activation during observation of action execution, the literature on motor activation during the observation of action preparation is scarce. A notable exception is the study by Gangitano et al. (2004) in which both observation of action preparation and execution was studied. They showed that passive observation of a natural reaching-grasping movement evoked a profile of cortical excitability that was in concordance with the timing of the kinematic profile of the shown finger movements. The MEP of the first dorsal interosseus (FDI, causes an attracting movement between thumb and index finger) of the observer modulated well with the grasp aperture between thumb and index finger of the actor’s grasping movement, i.e., the MEP amplitudes were largest when the grasp aperture was largest. Moreover, the MEPs were increased with respect to baseline level during the observation of movement preparation, i.e., when the actor’s hand was at rest on the table before grasping a ball. However, it is unclear whether this increase in excitability was specific for the muscle used in the upcoming grasp action, as the MEP in the non-involved abductor digit minimi (ADM) muscle also inconsistently increased at this time point.

Another important finding of Gangitano’s study (2004), was the lack of an increased corticospinal excitability when the observed grasping movement proceeded differently than would be expected from natural movements (i.e. a delayed aperture of the fingers or an early closing of the hand). After an initial increase, the corticospinal excitability decreased to baseline level once the observer noticed that the observed movement did not proceed naturally. The authors reasoned that the resonant motor plan, as initially formed by the observer upon seeing the start of the movement, was not modulated or substituted when the observed action did not proceed according to the plan. Whether this is due to the abnormality of this action or to the fact that the observed movement was different than expected cannot be distinguished on the
basis of these results. When a semantic cue (e.g. ‘light’ or ‘heavy’) conflicts with the physical characteristics of the object of an observed action, the modulation of corticospinal output is also reduced, but not reversed (Senot et al. 2011).

In the present study we will investigate whether the excitability of the motor cortex is modulated in accordance to the observation of an action being prepared and subsequently executed. Therefore, we had participants watch videos of actors performing object manipulations, while TMS was administered at specific temporal landmarks. The experiment follows up on the experiment of Gangitano et al. (2004) with important additions. First, the actor in our videos used two different grasping movements: a precision grasp and a whole-hand grasp (termed ‘full grasp’ in the remainder of this chapter), enabling us to determine whether the change in excitability during observation of the action (preparation) was specific for the observed grasping movement. Second, we introduced a goal cue that indicated the final goal of the object manipulation. By doing so, participants could infer, that is plan, the grasp that was going to be used by the actor. Thus, they could anticipate the action before the actor had started the movement. Third, and more speculative, we added a condition in which the observed action was not in accordance with the goal cue. This condition informs us on adaptation of the observer’s motor representation that was created based on the initial goal cue if the observed action mismatches this goal cue.

Based on Gangitano’s findings during action observation (Gangitano et al. 2004), we hypothesized that the MEPs modulate dependent on the observed grasp. That is, during observation of a precision grasp the MEP will be largest in the FDI muscle, which is involved in this grasp, whilst during the observation of a full grasp the MEP will be largest in the ADM muscle, which is involved in a full grasp. For the preparation phase of the action observation we hypothesized that the MEPs also modulate differentially based on the upcoming grasp, as was also found during the preparation of own movements (Davare et al. 2009). Finally, we hypothesized that an erroneous cue would initially result in increased MEPs in those muscles that are specific for the cued grasp. However, when the observed movement unfolds differently than expected, we hypothesized that the corticospinal output generally reduces, and that the pattern of corticospinal excitability changes such that only the MEPs are elevated for muscles that are involved in the observed (not the cued) action.
Materials & Methods

Participants
Thirteen healthy, right-handed adults (six males, seven females, aged 18-38 years) participated in the experiment. All participants gave written informed consent to the experimental procedures, which were approved by the local ethical committee and conducted in accordance with the Declaration of Helsinki.

Materials
The stimuli consisted of a set of twelve videos displaying an actor’s right arm performing an object manipulation task. The actor’s goal was to reach for and grasp an object, and insert it in either of two holes in a wooden block (Figure 6.1). The object consisted of two parts: a vertical black bar (diameter 14 mm, length 70 mm) attached at one end to the centre of a round white disk (diameter 108 mm, thickness 12 mm). The object was placed on a red holder, such that it could be grasped easily with either a full grasp - on the white disc, or a precision grasp - on the black bar (Figure 6.2A and 6.2B respectively). The wooden block (length 370 mm, height 140 mm and depth 68 mm) had two round holes: a small hole in which the black bar fitted precisely, and a large hole in which the white disc fitted precisely. Comfortable insertion of the object into the small hole required a full grasp of the white disc, whereas comfortable insertion of the object into the large hole required a precision grasp of the black bar. An arrow was fixed to the block between the two holes. This provided a cue specifying the goal of the forthcoming action. The arrow could point either to the small hole (indicating that a full grasp was required), or to the large hole (indicating a precision grasp), or perpendicular to the two holes (providing no indication of the required action).

All videos started with the object shown in the holder, the wooden block positioned to the left, and the actor’s prone (right) hand to the right (Figure 6.1). The block was oriented with either the small hole on the left and the large hole on the right, or vice versa. After 1000 ms a yellow ring (diameter 100 mm) appeared around the arrow to highlight the goal cue for 2000 ms. The hand started moving 1000 ms after the disappearance of the ring, and subsequently reached and grasped the object either by holding the black bar using a precision grasp, or by holding the white disc using a full grasp.

In the majority of trials (67%) the grasp used was in accordance with the goal cue (i.e. arrow pointing to the small hole followed by a full grasp; arrow pointing to the large hole
followed by a precision grasp), and the object was inserted in the target hole. These were termed “congruent trials”. In some trials however (22%), the grasp used was not in accordance with the goal cue (i.e. arrow pointing to the small hole followed by a precision grasp; arrow pointing to the large hole followed full grasp) and the object could not be inserted in the hole. These were termed “incongruent trials”. As a reference condition, we included “no-cue trials” (11%) in which the arrow provided no indication of the required action. In these trials the actor used either a precision or a full grasp, and always inserted the object in the corresponding hole.

The twelve different videos thus comprised the combinations of 3 different trial types (congruent, incongruent and no-cue), 2 different grasps (precision grasp and full grasp) and two block orientations (small hole left and large hole right, or vice versa). All videos were of 10,480 ms duration, sampled in 262 frames. They were followed by the presentation of a black screen for 2000 ms.

**EMG recording and TMS**

The electromyographic (EMG) activity of the first dorsal interosseus (FDI) and abductor digiti minimi (ADM) of the right hand was recorded using bipolar surface electrodes. For the FDI, the electrodes were located in a tendon-belly arrangement over the metacarpal-phalangeal joint of the index finger and over the bulk of the FDI muscle respectively. For the ADM, we placed both electrodes over the muscle belly. A common ground electrode was placed on the lateral epicondyle of the right elbow. EMG signals were amplified and bandpass (30 Hz - 1 kHz) filtered. The signals were digitized at a 16 bit analogue-to-digital interface with a sampling rate of 5000 Hz.

Single-pulse TMS was delivered to the left primary motor cortex (M1) by a Magstim 200 stimulator (Magstim, Whitland, Dyfed), using a (85 mm outer diameter) figure of eight coil, located at the optimal position (“hot spot”) to evoke a short-latency response (motor evoked potential (MEP)) in the right abductor digitii minimi (ADM). The coil was placed such that the axis of intersection between the two loops was oriented at approximately 45 degrees to the sagittal plane, to induce posterior to anterior current flow across the motor strip in the primary motor cortex. Once the hot spot was established, the lowest stimulation intensity at which MEPs could be recorded from this muscle with peak-to-peak amplitude of at least 50 μV evoked in three out of five trials was taken as resting motor threshold (RMT). Stimulation at this intensity also evoked a motor potential in the right first dorsal interosseous (FDI). The level of stimulation that
Figure 6.1 The sequence of events during a single trial. The video started at t = 0 ms, a yellow ring to highlight the goal cue appeared at t = 1000 ms and disappeared at t = 3000 ms and the hand started moving at t = 5000 ms. The video lasted 10480 ms and was followed by a black screen. The pictures are snapshots obtained from the video at time intervals at which a single TMS pulse could be delivered, i.e., at disappearance of the yellow ring (3000 ms), 100 ms before movement onset (4900 ms), just after movement onset but with the grasp as yet unrevealed (5280 ms), at maximal grasp aperture for the precision grasp (5680 ms), at maximal grasp aperture for the full grasp (6080 ms, note that the figure displays a precision grasp), and during lifting of the object prior to transport (7280 ms).
was used during the experiment was 120% of RMT. Prior to and following the experimental trials, three blocks of ten control MEPs were recorded with inter-stimulus-intervals of 4-6 seconds and inter-block-intervals of 1 min.

Procedure
In a short practice period, the participants were first familiarized with the object manipulation task that was shown to them subsequently on video. Sitting at a table, they were instructed to grasp the object and insert it in the hole in the wooden block - as cued by the arrow (using the precision or full grasp as appropriate). The participant was then asked to close their eyes. The experimenter changed the orientation of the block and/or the direction of the arrow. Following a verbal go-signal from the experimenter, the participant opened their eyes and performed the task again. This was repeated until the participant completed 20 successive trials using the correct grasp (i.e., a full grasp when the small hole was cued and a precision grasp when the large hole was cued).

Throughout the experiment, the participants were seated in a comfortable chair that provided support for the head, neck, and torso. Their forearms were supported and stabilized in a neutral (semi-prone) position with the elbows semi-flexed. They were instructed to attentively observe the videos that were displayed on a computer screen located 1 m in front of them. In a randomly defined selection of the trials (18 out of 288 trials), the participant was asked after the display of the video to imitate the movement they had just observed. In most respects this aspect of the procedure was similar to that employed during initial practice. There was however one key exception. The interleaved test movements were executed using the left hand rather than the right hand. For this purpose, the wooden block and black-white object were positioned within reach on a stand to the left of the participant. The purpose of these imitation trials was to ensure that the participants remained engaged in the observation of the videos.

During each observation trial, a single TMS pulse was delivered at one of six delay intervals (phases) relative to the start of the video. These corresponded to the disappearance of the yellow ring highlighting the goal cue (3000 ms), 100 ms before movement onset (4900 ms), just after movement onset but with the grasp as yet unrevealed (5280 ms), at maximal grasp aperture for the precision grasp (5680 ms), at maximal grasp aperture for the full grasp (6080 ms), and during lifting of the object prior to transport (7280 ms). In order to limit the total duration of the experiment, and to maintain a high proportion of congruent trials relative to
Chapter 6

incongruent trials, we administered TMS at all six time intervals during the congruent trials, at four time intervals during the incongruent trials, and at two time intervals during the no-cue trials. As the videos for the congruent and incongruent trials were exactly the same during the movement preparation phase (see Figure 6.1), we elected not to obtain responses to TMS during these time intervals for the incongruent trials. In contrast, as the no-cue trials acted as a control condition principally with respect to the preparation phase, we administered TMS only at delay intervals of 3000 and 4900 ms during the no-cue videos. Each of the 24 congruent trials (4 videos x 6 TMS intervals) was repeated eight times (192 in total). Each of the 16 incongruent trials (4 videos x 4 TMS intervals) was repeated four times (64 in total), and each of the 8 no-cue trials (4 videos x 2 TMS intervals) was repeated four times (32 in total). These variants were delivered in a random order. Short breaks were scheduled after each imitation task.

Data Reduction and Analyses
The peak-to-peak amplitude of the MEPs recorded in the right FDI and ADM, and the root mean squared (RMS) amplitude of the EMG signal recorded 100 ms prior to the delivery of each stimulus, were calculated. If the RMS EMG in either muscle exceeded 10 μV, the corresponding MEPs for both muscles were excluded from further consideration. The amplitudes of MEPs recorded during the observation trials were normalized separately for each participant with respect to the magnitude of the responses obtained at the beginning and at the end of each testing session.

The inferential analyses comprised both tests of difference (planned comparisons of means using repeated measures analysis of variance (ANOVA) models) and of equivalence (paired t-test for equivalence (Wellek, 2010)). To aid in the interpretation of the statistical tests, effect sizes were calculated for the planned comparisons (Cohen, 1988). The effect size (f) describes the degree of departure from no effect, in other words, the degree to which the phenomenon is manifested.

Results
The results are described separately for the time intervals before the observed movement onset (action preparation) and time intervals after the observed movement onset (action execution).
**Action preparation**

We measured the participant’s corticospinal excitability in trials in which there was no cue or a directional cue, before the observed movement onset. MEPs were evoked at the termination of the circle appearance highlighting the cue (or no cue), and 100 ms prior to the onset of movement (precision or full grasps were shown subsequently).

*No Cue.* We examined situations in which no advance information was provided concerning the action that might follow, in order to provide a context in which to interpret variations in corticospinal excitability. In these trials, it was verified that for FDI and ADM respectively, the amplitudes of the MEPs elicited in these conditions did not vary systematically from one another (F ≤ 1, p > 0.30 for all pairwise comparisons). On this basis, means and corresponding 95% confidence intervals (Loftus and Masson 1994) were obtained for each muscle (Figure 6.2 C – F). These provided references with respect to which the values, obtained in the cue condition during the observation of action preparation and action execution, could be assessed. It was also thereby established that corticospinal excitability was elevated in this no-cue condition. All values deviated from unity (the magnitude of the control responses) by more than the confidence interval.

*Directional cue.* To examine the effect of a directional cue on the corticospinal excitability, participants were shown a directional cue before onset of the movement, indicating the use of either a precision grasp or a full grasp. Like in the no-cue conditions, the amplitudes of the MEPs for FDI and ADM did not vary systematically from one another (F < 1, p > 0.40 for all pairwise comparisons). Importantly, this finding indicates that the corticospinal excitability did not vary between conditions in which a cue for a full grasp or a cue for a precision grasp was observed. The MEPs in these conditions did also not differ from those in the no-cue condition (F < 1, p > 0.30 for all pairwise comparisons), and did not exceed the confidence intervals established on the basis of the no-cue condition. Together, these results indicate that corticospinal excitability during the observation of action preparation was elevated compared to baseline level.

**Action execution**

Following the observed movement onset, we measured the participant’s corticospinal responses in trials in which the observed action was in concordance with the cue (congruent cue), and in trials in which the observed action was not in concordance with the cue (incongruent cue).
Figure 6.2 Main results.
A, Given an instructional cue in which the arrow pointed to the small hole, the actor is shown using a full grasp to insert the object into the target (small) hole.
B, Given the cue in which the arrow pointed to the large hole, the actor is shown using a precision grasp to insert the object into the target (large) hole. The four video frames (from the 262 of the full display sequence) correspond to phases at which TMS was delivered following the onset of movement. Amplitudes of compound muscle action potentials evoked in the quiescent C, right FDI and D, right ADM by left M1 stimulation are shown for the condition in which a full grasp was cued (the arrow pointed to the small hole) and a precision grasp observed. The responses obtained when a precision grasp was cued (the arrow pointed to the large hole) and a full grasp observed, are shown for the right FDI in E, and for the right ADM in F. The values (mean of 13 participants) are normalised with respect to the controls obtained prior to and following the observation trials.
Figure 6.2 (continued)
Confidence intervals (95%) enclosing the means of responses obtained prior to the onset of the action (no cue trials) are represented as grey shaded areas. Values that differed from these means by more than the intervals are represented as filled symbols. Responses obtained in the (congruent) cue: full; grasp: full condition are shown as triangles, and in the (congruent) cue: precision; grasp: precision condition as diamonds; in the (incongruent) cue: full; grasp: precision as circles, and in the (incongruent) cue: precision; grasp: full as squares. The character * indicates instances in which the values obtained in the cue: full; grasp: full and cue: full; grasp: precision conditions were statistically equivalent (p < 0.05). The character † indicates instances in which the cue: precision; grasp: precision and cue: precision; grasp: full conditions were statistically equivalent (p < 0.05).
Congruent Cue. In circumstances in which the observer saw a full grasp both cued and executed, the MEPs elicited in FDI diminished in amplitude following the onset of the actor’s movement and reached their nadir prior to the maximum aperture of the grasp. In contrast, when a precision grasp was specified, the excitability of projections to this muscle was elevated during the phase in which the object was lifted (Figure 6.2 C & E). The difference between the conditions was most pronounced by the time of the maximum aperture of the precision grasp ($F(1, 108) = 5.91, p < 0.05, f = 0.48$).

The pattern of variation observed for ADM was both distinct from that expressed for FDI, yet also consistent with the functional role of the muscle in the context of the actions that were observed. When a full grasp was cued and demonstrated, MEPs elicited in ADM were elevated further during the phase of the actor’s movement in the maximum aperture. Whereas, when a precision grasp was cued and then seen performed, MEPs elicited in ADM diminished in amplitude during this phase (Figure 6.2 D & F). Thus, the greatest difference between the conditions coincided with the time of the maximum aperture of the full grasp ($F(1, 108) = 11.08, p < 0.01, f = 0.65$).

Incongruent Cue. After having established the clear, functionally specific, variations in corticospinal excitability that were present when the advance information and the following action were congruent, we sought to delineate the effects when they were incongruent. When a full grasp was cued and a precision grasp demonstrated subsequently, the amplitude of MEPs elicited in FDI matched initially those obtained for the full grasp (i.e. correctly cued) condition (Figure 6.2 C). Inferential tests of equivalence (Wellek 2010) confirmed that the MEP amplitudes equated to those of the congruent condition immediately following the onset of the observed movement, through to the phase during which the maximum aperture of a full grasp would have been anticipated ($p < 0.05$). The sustained impact of the advance information (i.e. a full grasp cued) was such that: at the time the maximum aperture of the precision grasp was observed, the MEP amplitudes remained markedly lower than those obtained when a precision grasp was both cued and observed ($F(1, 108) = 4.34, p < 0.05, f = 0.41$). During the final phase of the movement in which the actor was seen to lift the object using a precision grasp however, the MEPs were elevated in amplitude, such that they were equivalent ($p < 0.05$) to those recorded in the precision grasp (i.e. correctly cued) condition (Figure 6.2 C).

A corresponding transition was evident for the condition in which the advance information indicated (erroneously) that a precision grasp would follow (Figure 6.2 D). In these
circumstances FDI MEPs were of equivalent amplitude (p < 0.05) to those exhibited for the condition in which a precision grasp was both cued and executed, during the phase in which the maximum aperture of a precision grasp would have been anticipated, and also during the phase in which the maximum aperture of the full grasp was observed. The impact of the advance information was such that during the former phase, the MEP amplitudes were reliably greater than when a full grasp was both cued and observed (F(1, 108) = 4.79, p < 0.05, f = 0.43). During the final lift phase of the depicted (i.e. full grasp) action, the MEP amplitudes decreased to a level such that they could not be discriminated (p < 0.05) from those obtained when the (full) cue and grasp were congruent (Figure 6.2 D).

The influence of an incongruent cue was expressed in a complementary fashion via the projections to ADM. After the presentation of an incorrect cue, the variations in corticospinal excitability expressed during the observation of a specific action were attenuated relative to circumstances in which the same action had been cued faithfully (Figure 6.2 D & F). Thus, when a full grasp was cued and a precision grasp demonstrated subsequently, the variations of MEP amplitude through the initial phases of the observed action were similar to, but less marked than, those elicited when a precision grasp was cued and then observed (Figure 6.2 D). During the phase in which the maximum aperture of the full grasp was observed, this pattern found expression in a difference (F(1, 108) = 4.80, p < 0.05, f = 0.43) - relative to the condition in which a full grasp was both cued and observed, that was of smaller magnitude than obtained when a precision grasp was cued and then seen performed (f = 0.65). Similarly during this phase, when a precision grasp was cued and a full grasp demonstrated (Figure 6.2 F), the difference relative to the condition in which a precision grasp was both cued and observed (F(1, 108) = 6.86, p = 0.01, f = 0.51), was smaller than that which differentiated the two congruent conditions. There was also a delay in the zenith of the changes in corticospinal excitability that accompanied performance of the observation task. Following the presentation of an incongruent cue indicating a precision grasp, MEPs elicited in ADM were largest during the phase in which the actor was seen to lift the object. When the full grasp had been cued reliably, the phase in which the largest MEPs were obtained coincided with the (preceding) phase during which the maximum grasp aperture occurred (Figure 6.2 F).
Discussion
In the present experiment we used TMS to study the corticospinal excitability during observation of the preparation and execution of grasping actions. Therefore, we had participants observe videos of an actor making different grasping actions in response to a cue. We had three main interests, the results of which we will shortly summarize first, after which the findings will be discussed in more detail together with their theoretical implications.

First, we investigated whether the MEPs modulated in concordance with the kinematic profile of the observed action and whether this modulation was specific for the muscles that were involved in the observed action. The results showed that the observation of a *full grasp* modulated excitability of corticospinal projections to the ADM. Specifically, the ADM-MEP was elevated at the time at which most ADM-activity was required in the observed grasp, namely at the maximum grip aperture. In contrast, the FDI-MEP decreased after movement onset to reach a minimum prior to the observation of the maximum grip aperture. Observation of a *precision grasp* resulted in a reversed pattern of corticospinal excitability. The FDI-MEP increased when the object was seen lifted, which is the moment at which the FDI is most active when executing the movement. The ADM-MEP, however, decreased after movement onset and reached a minimum just before the object was seen grasped. These findings confirm the hypothesis that observation of a grasping movement results in a muscle-specific pattern of MEP-modulation, in concordance with the timing of the observed grasp.

Second, introduction of a goal cue enabled us to study the corticospinal excitability during the preparation of an upcoming grasp, but in which there was no movement observed yet. In this situation the MEPs were increased with respect to baseline level. However, this increase was not specific for the type of cue. Stated differently, the FDI-MEPs were not larger when a cue for a precision grasp was presented compared to a cue for a full grasp or no cue at all, and the ADM-MEPs were also similar for the three different cue types (full cue, precision cue, no cue). This suggests that it might not have been the cue per se that induced an initial, non-specific rise in corticospinal excitability, but that it also might have been the observation of the experimental setup including the hand that triggered an increase in excitability.

Third, we studied the effect of goal cueing on the observation of the subsequent action by showing participants grasping movements that were either congruent or incongruent with the goal cue. In case the goal cue was incongruent with the subsequent action, the FDI-MEP initially matched the pattern of excitability of the expected grasp based on the cue (precision or
full). At the time of object lifting, however, the FDI-MEP matched the pattern of excitability of the observed grasping movement. For the ADM, the presentation of an erroneous did not markedly change the pattern of corticospinal excitability. Still, MEP modulation seemed less pronounced and delayed compared to the congruent condition. Thus, although the cue did not exert a muscle-specific effect in the observer before the movement onset, a specific effect of an erroneous cue was present during the observation of subsequently shown action.

**Observation of action execution**

Our experiment was in part based on the study by Gangitano et al. (2004). The present finding that the corticospinal excitability modulates according to the timing of the displayed grasping movement is in line with their findings. Nevertheless, there are some subtle differences between their and our findings. In their first experiment, the FDI-MEP amplitude correlated well with the grasping aperture when observing an ordinary grasping action, i.e., the FDI-MEPs were largest at the time of observed maximal grasping aperture. In our experiment, however, the pattern of MEPs coincided with the muscle activity involved in the observed grasp, rather than the grasping aperture, i.e., the FDI-MEPs were largest during observation of the lifting of the object. These findings support the notion that the observed action is represented in the same way as to when making the action oneself, with the temporal modulation of the FDI-MEP corresponding to the temporal modulation of FDI activity in the observed action.

The modulation of corticospinal excitability corresponded also spatially with the observed action. The increase in MEPs depended on the muscles involved in the observed action. Previously, Davare et al. (2009) showed that the outputs of the primary motor cortex could be modulated by projections from premotor areas depending on the type of grasp being prepared. Preparing to grasp a pen (precision grasp) predominantly increased the FDI-MEP, whereas preparing to grasp a disc with the whole hand (full grasp) predominantly increased the ADM-MEP. Similarly, in the present experiment, the modulation of MEPs in these specific muscles depended on the muscle activity involved in the observed grasp.

The spatial and temporal similarity of the represented action with the observed action raises support for the direct-matching hypothesis, which states that observed actions are accurately represented in motor areas in one's own brain. This motor representation is supposed to help understand the observed action (Rizzolatti and Craighero 2004).
Chapter 6

Observation of action preparation
In line with the study of Gangitano et al. (2004), we found that MEPs were increased with respect to baseline before the movement on the video had started. However, this increase was not specific to the observed cue, and was observed for both the FDI and ADM. The patterns of MEPs for FDI and ADM started to deviate only when it could be derived from the hand path of the observed grasp being used. Similar results were reported by Lago & Fernandez-del-Olmo (2011). They delivered TMS to participants while they watched a still hand or foot at the start of a grasping action, or an effector-object interaction at the final phase of that action. When participants watched the still effector, the FDI-MEP was increased, independent of whether a hand or a foot was shown. In contrast, during the observation of the effector-object interaction, the FDI MEP was elevated only during observation of the hand grasping action (in which the FDI plays a major role), and not the foot grasping action. Thus, there was an initial increase in corticospinal output that was not specific for the effector that was used in the upcoming grasp. Later during interaction with the object, however, the MEPs were specific for the muscles of the observed effector. These findings fit with the hypothesis that motor resonance in the initial phase relies on a first rapid mapping of the observed or expected action. At second, the action is resonated by a more slowly and refined mechanism, taking into consideration specific muscle activity, goal inference and action understanding (Lepage et al. 2010).

Effect of a(n) (erroneous) cue
Although the observed cue did not have a direct specific effect on the corticospinal excitability, the direction of the cue did exert differential effects during observation of the subsequent movement. For the ADM, the pattern of corticospinal excitability was delayed and attenuated, similar to what Senot et al. (2011) found in the condition that the cue was not in accordance with the subsequent action kinematics. For the FDI, however, the pattern of corticospinal excitability first matched that of the expected movement based on the cue. Later, the pattern matched that of the observed movement. This suggests that the observation of a directional cue is sufficient to trigger a motor representation of the movement indicated by the cue.

Using fMRI it was noted that participant’s mirror neuron brain areas are activated not only upon seeing a finger lifting movement after having performed that movement theirselves, but also when seeing a static hand with a cross on the finger to be lifted (Jacoboni et al. 1999). These results are in line with our finding that observation of a symbolic cue can have an effect
Excitability of the motor system during observation

on brain areas that code motor representations. The cues in our experiment were even indirect, i.e., only the final goal of the movement was cued. In conclusion, the present study shows that even indirect cues are capable of triggering a motor representation.
Chapter 7

Summary and discussion
Chapter 7

Introduction
Grasping an object demands the specification of parameters in advance of the execution of the grasping movement. One of these parameters is the grip with which an object is grasped, which is the main topic of the studies reported in this thesis. Specifically, we studied the phenomenon that people generally adapt their grip such that the object manipulation terminates in a comfortable body position, even when this requires them to use an awkward grip at the start of the movement. This is termed the end-state comfort effect, which we exploit as a means to study anticipatory motor planning. In five experimental chapters we reported studies on anticipatory motor planning in unimanual and bimanual object manipulation tasks, using three different approaches: i) we performed three behavioural studies in which we observed the participant’s grasping behaviour and measured movement kinematics (chapters 2, 3, and 4), ii) we observed grasping behaviour in a patient population (chapter 5), and iii) we measured neurophysiological parameters in participants that observed an action being planned (chapter 6). In the current chapter we summarize our main findings and discuss their implications.

Summary
Chapter 2 reports two experiments in which we investigated the relative impact of cognitive and coordination constraints on movement kinematics and on grip selection in a bimanual object-manipulation task. In both experiments participants had to grasp CD casings that had to be rotated and (re)inserted in a CD box in a predefined position. In the first experiment the grasp that participants used was pre-instructed. We studied 3D kinematics of the limbs while the hands were moving either mirror symmetric or asymmetric when rotating the CDs. Furthermore, the hands ended the movement either in a comfortable end position or an uncomfortable end position. The results showed that interlimb coupling (as measured by means of the correlation between forearm rotations of both arms) was larger for symmetric compared to asymmetric grasping movements, which could be attributed to the preference to use homologous muscle pairs in the symmetric condition (Carson 1995; Swinnen et al. 1997). Furthermore, interlimb coupling was larger when the movement ended uncomfortably compared to when the movement ended comfortably. We reasoned that comfortably ending movements are probably experienced more frequently and that the extended practice of these movements has resulted in an increased independent control of both arms.
In contrast to the first experiment, participants in the second experiment were free to choose the grips of both hands for grasping the CDs, while only the end orientations were cued. We included conditions in which there was a conflict between symmetry of movement and end-state comfort. Hence, participants had to choose which constraint to comply with. In general, participants did not have a preference to move their hands mirror-symmetrically, since they moved symmetrically in only half of the trials. In contrast, participants chose to use grips that resulted in a comfortable end-state. Surprisingly, this end-state comfort effect was only found for the right hand, not for the left hand. This might have been due to experience, since all participants in the experiment were right-handed. Alternatively, this difference in end-state comfort effect between the hands might have been due to a left-hemisphere-dominance for motor planning.

The experiment in chapter 3 was set up to test the left-hemisphere-dominance hypothesis raised in chapter 2. To this end, we tested left-handed participants on the bimanual CD-placement task that was used in chapter 2 (experiment 2). Thus, left-handed participants had to grasp two CDs with two hands simultaneously and insert them in a CD-box in pre-cued orientations. Similar to the right-handed participants, the left-handers showed the end-state comfort effect more often for their right hand compared to their left hand. This suggests that it is not experience that caused the right hand advantage in right-handed participants. Rather, it confirms the hypothesis that the left-hemisphere is dominant for motor planning both in left- and right-handers.

In chapter 4 we reported a study in which we tested whether the end-state comfort effect would be preserved in bimanual object manipulations under various circumstances. Again, we had participants pick up and rotate two objects. This time, however, the orientation of the to-be-grasped objects was not only horizontal or vertical, but we tested an entire range of orientations. Furthermore, we tested whether a pre-instructed planning for one hand affected movement planning for the other hand.

In a first task participants had to grasp two bars that were perpendicularly fixated on two rotating axes that could adopt ten (left axis) or four (right axis) different orientations. The bars, half painted in black and half in white, had to be grasped with two hands simultaneously and rotated such that the black side of the bar ended on top. Similar to previous experiments,
participants did not prioritize to move both hands mirror-symmetrically, but they rather optimized the end posture. Surprisingly, not all participants showed the end-state comfort effect. Apart from ten participants who did end their movements in a comfortable posture, seven participants optimized comfort of the intermediate goal posture, i.e., they chose a grip that was comfortable at the time they grasped the object. This shows that the end-state comfort effect in complex bimanual tasks is not as consistent as the effect in unimanual tasks (see also Hughes and Franz 2008).

For the second task we changed the bar on the right side for a spoon. This facilitated an instructed grip for the right hand. We asked the participants to grasp the spoon in such a way that it could be used to stir in a cup or eat with it, that is, with the thumb toward the bowl and ending the movement in an uncomfortable posture. Simultaneously, the bar at the left side had to be grasped with the left hand. The grip that was used to grasp this bar with the left hand was not affected by the instructed grasp for the right hand. Also, the orientation of the spoon did not affect grip planning for the left hand. From this, we conclude that grip planning proceeds independently for both limbs, despite the well-known interaction effects at the level of action execution (e.g., Kelso et al. 1979).

Whereas the previous chapters all involved healthy adults, in chapter 5 we tested children with and without cerebral palsy to study typical and atypical development of grip planning. Children with cerebral palsy are particularly known for having deficits in the execution of movements. More recently, experimental studies showed that these children also have problems with the planning of movements (e.g. Crajé et al. 2010a). We tested motor planning in a unimanual and a bimanual task, in the children with cerebral palsy and in healthy control children, all aged 7-12 years old. They had to grasp a vertically oriented bar and transport this bar to a lower or a higher shelf. We observed whether the height at which the children grasped the bar was influenced by the height of the shelf to which the bar had to be transported, which would be an indication for anticipatory motor planning (cf. Cohen and Rosenbaum 2004). In the unimanual task, children with cerebral palsy did not adapt their grasp height to the height of the goal shelf and this did not change with age. In contrast, healthy controls did adapt their grasp height and the effect did increase with age. Similar results were found for the bimanual task in which the children had to transport both bars to shelves of the same height. However, when one bar had to be transported upwards and the other bar transported downwards, the control children
planned the grasp height only for their non-dominant hand. The bar for the dominant hand was grasped at approximately the same height in each trial, and thus not adapted to the height of the goal shelf. Surprisingly, children with cerebral palsy showed the same pattern, i.e., they planned the grasp height for the most affected hand, whereas the least affected hand grasped the bar at a comparable height in all trials. The performance of the most affected arm thus improved at the expense of the least affected arm. We hypothesize that the children in this difficult task chose a cognitive strategy in which they focussed their attention to the most affected arm. This would suggest that attention may ameliorate motor planning in these children (Volman et al. 2002). Thus, although children with cerebral palsy show a delayed or compromised development of motor planning compared to typically developing children, motor planning in cognitive demanding tasks may be facilitated by an increase in attention.

In the study reported in chapter 6 we studied motor planning from a neurophysiological perspective. To control for effects due to movement execution, we had participants observe actions being planned and executed instead of having them perform the tasks themselves. This enabled us to study neural processes related to the observation of actions and action planning. The observation of an action causes a motor representation to be formed in the observer. Using Transcranial Magnetic Stimulation (TMS) we studied the timing of ongoing neural processes during observation of an object being grasped and subsequently inserted in one of two holes in a wooden block. The action was preceded by a goal cue that indicated in which of the two holes the object needed to be inserted. From this, participants could deduce which type of grasp (precision grasp or whole hand grasp) was being used to pick up the object. Observation of the cue without having seen any movement execution yet resulted in a facilitation of motor evoked potentials (MEPs) measured in the hand muscles. However, this facilitation was not specific for the upcoming grasp and the muscles involved in that grasp. Observation of the subsequent action did result in a specific facilitation of MEPs in the hand muscles that were involved in the grasping action. The modulation of MEPs was different when the action was preceded by an erroneous instead of a correct directional cue. These findings show that the observation of a movement cue may cause a general, non-specific increase in activation in the projections to the hand muscles. However, the observation of a directional cue specifically alters the motor representation that is formed of the subsequent movement.
Chapter 7

Discussion
What do these findings implicate and what questions remain? In the next part answers to those questions will be formulated from two perspectives. First, I will contrast constraints regarding motor planning versus constraints regarding motor execution. Second, the differences in motor performance between the hands are discussed in relation to hemispheric differences.

Planning versus execution
The end-state comfort effect suggests that biomechanical constraints associated with the execution of isolated, unimanual and discrete movements have a powerful impact on motion planning. People are generally willing to adopt uncomfortable postures as long as they can end their movement comfortably. This implies that people first plan the desired goal of a movement, and subsequently plan the movement trajectory towards that goal, after which the movement is executed. For this reason we have termed the end-state comfort effect a ‘motion planning constraint’. When we turn to bimanual movements, dynamical constraints come into play that induce a general preference for symmetrical movements, i.e. the simultaneous contraction of homologous muscle groups of two limbs. In this thesis we sought to find out whether planning constraints (here, the end-state comfort effect), always prevail, particularly in the case that execution (dynamic) constraints become increasingly effective, as in bimanual movements. The experiments reported in chapters 2, 3 and 4 all show that the end-state comfort effect prevails over symmetry of movement during bimanual object manipulation tasks, in complex tasks with different goals for both limbs (chapter 2), for both left- and right-handers (chapter 3) and when the grasp to be used was instructed for one limb (chapter 4). Nevertheless, the dominance of the end-state comfort effect was smaller compared to unimanual tasks and some participants even preferred to optimize comfort of the intermediate goal instead of the end goal (chapter 4). Other studies that have investigated the relation between planning and execution constraints in bimanual tasks also emphasized the dominance of the end-state comfort effect, particularly in the situation that both hands have congruent goals (Fischman et al. 2003; Weigelt et al. 2006; Hughes and Franz 2008; van der Wel and Rosenbaum 2010). From this we may conclude that by default, people strive towards comfortable end postures when executing movements. However, there are exceptions.

One of those exceptions is the bimanual condition in which the goals for both hands are incongruent. While participants in the experiments in chapter 2 and 3 still predominantly strived
for comfortable end postures when both arms had different goals, the children in the experiment in chapter 5 did not optimize comfort for both limbs when asked to move two bars to two different goal locations. Both the children with and without cerebral palsy optimized end-state comfort only for their non-dominant (or most affected) arm. The grasp height for the dominant (or least affected) hand was comparable to that of the other hand, which could be seen as a form of symmetry (though the symmetry referred to before was related to the rotation of the hands whereas in this case it refers to the height at which objects are grasped). Similar results were found in adults that performed the same task (van der Wel and Rosenbaum 2010), or a different task in which they had to rotate two cylinders (Hughes and Franz 2008). We suggest that these complex tasks have relatively high cognitive demands and that participants focused their attention on only one limb. As a consequence, the goal for the other limb was not anticipated, rather, this limb simply ‘followed’ the movement pattern of the focused limb (Volman et al. 2002). Moreover, participants might have preferred to move fast and to optimize speed of performance even though that was not instructed. Speed has been shown to reduce the end-state comfort effect (Short and Cauraugh 1999).

Deviations from end-state comfort have mainly been found in complex bimanual situations as described above, whereas in unimanual tasks (healthy) participants always ended object manipulations in a comfortable posture (Rosenbaum et al. 1992; Weigelt et al. 2006). In unimanual tasks, comfortable end postures are anticipated not only when executing an action oneself, but even when observing others manipulating objects. When observing an actor grasping an object, the same grasping action is represented in the observer’s brain (e.g., Rizzolatti et al. 2001). The study reported in chapter 6 showed that when an actor grasped an object with a grip that resulted in a comfortable end-posture, the profile of corticospinal excitability in the observer was accurately in concordance with the profile of muscle activation involved in the observed grasping movement. However, when the actor grasped the object with a grip that would result in an uncomfortable end-posture, the profile of corticospinal excitability was (initially) deviant from the muscle activation profile of the observed movement. These findings suggest that the participants even anticipated a comfortable end-state when observing others grasping an object, which emphasizes the strength of the end-state comfort effect.
Hand differences

An interesting result that we found in the study reported in chapter 2 and also in chapter 3 was the advantage for the right hand over the left hand regarding motor planning. We attributed this advantage to a left hemisphere specialization for motor planning. Ample evidence indicates that the left hemisphere plays a dominant role in the planning of grasping movements and this is largely derived from patient studies and brain imaging studies (e.g., Leiguarda and Marsden 2000; Johnson-Frey et al. 2005). In chapters 2 and 3 we reported a behavioural experiment and found differences in the motor planning performance between the left and right hand in both left-handed and right-handed participants. These differences lend support for the left-hemisphere dominance hypothesis (see chapter 3). It is remarkable that we did not find differences in motor planning between the hands in chapter 4, and also that these differences are not consistently found in the literature (Weigelt et al. 2006; Hughes and Franz 2008). A possible explanation might be sought in differences in task complexity. In the CD placement task of chapters 2 and 3, both the start and the end orientations were variable for both CDs (either horizontal or vertical). In contrast, in other motor planning tasks that did not show differences in performance between the hands, the orientation of the objects at the start and / or the end was fixed, for example always vertical (chapter 4, Weigelt et al. 2006; Hughes and Franz 2008). This suggests that hand differences only appear in highly complex tasks that are cognitively more challenging. A complicating aspect here is that different cognitive strategies may come into play to keep the complexity of the required task under control. We found that increased attention to one of the two limbs is such a strategy. For children with hemiparetic cerebral palsy this meant a special focus on their least-affected limb. Another strategy may pertain to flexibly adapting the chunking of the required motion sequence. In chapter 5 we found that five of the twelve participants favored comfortable postures at an intermediate stage of task execution over a comfortable posture at the end. Indeed, the end-state comfort effect depends on how subjects define a motion task, either as a single, multicomponent action that requires a series of chained submovements, or as a series of multiple actions, each having its own end state. In our view, chunking strategies have generally been undervalued in studies of anticipatory motion planning, whether they involved uni- or bimanual movements.

In chapter 5, hand differences in motor planning performance were indeed only found in the most complex condition, i.e., the bimanual incongruent task. We suggest that the children in this experiment consciously focused their attention to the least skilful hand to ensure a
comfortable end for this hand. Could attention differences also account for the difference between the hands in the CD placement task? In other words, could it be that the participants in the CD placement task have just focused their attention to the right hand that, as a result, more often ended in a comfortable position with this hand? This seems unlikely since both left-handed and right-handed participants then would have focused their attention to the right hand, which is the most skilful hand for right-handers. Given these arguments, we do not yet have a conclusive answer as to why hemispheric differences do not always account for differences in motor planning performance between the hands. Future research should therefore be directed at the role of attention in complex bimanual tasks.

We hypothesized that a left-hemispheric specialization could also have resulted in differences in motor planning performance between children with a left hemiparesis (right brain damage) and those with a right hemiparesis (left brain damage). However, in chapter 5, we did not compare these two groups of children for two reasons: the groups were too small and the exact brain lesions were unknown. Previous studies did show differences in motor planning between children with a left hemiparesis and those with a right hemiparesis (Steenbergen et al. 2004; Craje et al. 2009). Children with a right hemiparesis (thus with left brain damage) less often planned a movement in advance, which corroborates the left-hemisphere specialization for motor planning. Repeating the experiment of chapter 5 in a larger group of children with well-defined left and right unilateral cerebral palsy could confirm this hypothesis.

Conclusions

The grip that people select when manipulating an object is dependent on the goal of their action. Usually, people have a tendency to end their movement sequences with a comfortable end posture. In complex bimanual tasks that induce a preference for the simultaneous contraction of homologous muscles at both sides of the body, the end-state comfort effect continues to have its impact on motion planning but with diminished strength, particularly for the left hand. Atypical development may modulate the impact of the end-state comfort effect. For example, children with cerebral palsy hardly adapt their grip to the prevailing action goals even though they show signs of anticipatory motion planning. In healthy adults movements are also planned also when they observe others making a movement. Collectively, the findings reported in the present thesis offer various opportunities for interventions aimed at improving motion planning. For example, in children with hemiparetic cerebral palsy such interventions
may exploit the bimanual object-manipulation tasks as reported, in combination with instructions that elicit focused attention on one, the other, or both limbs and time constraints that modulate the chunking of the required action sequences. Finally, action observation seems also a promising intervention in this context.
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Nederlandse samenvatting

Inleiding
Wanneer we een voorwerp grijpen moeten vooraf een aantal parameters worden gespecificeerd. Een van deze parameters is de greep waarmee we een voorwerp grijpen, dit is tevens het belangrijkste onderwerp van de studies in dit proefschrift. In het bijzonder hebben we gekeken naar het ‘end-state comfort effect’; het fenomeen dat mensen hun greep aanpassen zodanig dat ze eindigen in een comfortabele houding, zelfs als dit een oncomfortabele houding vereist aan het begin van de beweging. Dit effect hebben we gebruikt om motorische planning te bestuderen. In vijf hoofdstukken staan experimentele studies beschreven op het gebied van motorische planning van één- en tweehandige grijptaken. Hierbij zijn drie verschillende aanpakken gekozen: i) in drie studies hebben we proefpersonen een voorwerp laten grijpen en hebben we hun gedrag geobserveerd en de kinematica van hun bewegingen bestudeerd (hoofdstuk 2, 3 en 4), ii) we hebben grijpwijzigingen geobserveerd in een patiëntengroep (hoofdstuk 5) en iii) we hebben de neurofysiologie bestudeerd van proefpersonen tijdens actie-observatie (hoofdstuk 6). Hieronder staan de belangrijkste bevindingen kort samengevat.

Samenvatting
Hoofdstuk 2 beschrijft twee experimenten waarin we de relativa bijdrage van cognitie en coördinatie aan de bewegingsplanning en -uitvoering hebben onderzocht in een tweehandige grijptaak. In beide experimenten moesten proefpersonen cd-hoesjes oppakken en in een cd-rek plaatsen in een vooraf bepaalde oriëntatie. In het eerste experiment werden de proefpersonen geïnstueerd over de greep waarmee ze het cd-hoesje moesten pakken en hebben we met behulp van driedimensionale bewegingsregistratie de armbewegingen bestudeerd. De armen van de proefpersoon maakten een spiegelsymmetrische of asymmetrische beweging wanneer de proefpersonen de cd’s roteerden om ze in de juiste oriëntatie in het rek te plaatsen. Bovendien eindigden de proefpersonen in een comfortabele of oncomfortabele houding. De resultaten laten zien dat de koppeling tussen de armen (gemeten met behulp van de correlatie tussen de rotaties van beide onderarmen) groter is voor symmetrische dan voor asymmetrische bewegingen. Dit kan verklaard worden door het gebruik van homologe spiergroepen bij
symmetrische bewegingen. Daarnaast is de koppeling tussen de armen groter wanneer de proefpersonen eindigen in een oncomfortabele houding in vergelijking met een comfortabele houding. Dit is waarschijnlijk te verklaren doordat mensen meer ervaren zijn in bewegingen waarin comfortabel wordt geëindigd, wat heeft geleid tot een meer onafhankelijke controle van beide armen.

In tegenstelling tot het eerste experiment, waren proefpersonen in het tweede experiment vrij om te kiezen welke greep ze wilden gebruiken om de cd’s op te pakken. Alleen de eindoriëntatie van de cd’s werd vooraf geïnstrueerd. In sommige gevallen was er een conflict tussen symmetrisch bewegen en een comfortabel eind waardoor proefpersonen gedwongen werden een keuze te maken tussen beide. Meestal kozen de proefpersonen voor een comfortabele eindhouding. Tot onze verrassing was dit veel vaker het geval voor de rechterhand dan voor de linkerhand. Mogelijk kan dit verklaard worden doordat alle proefpersonen rechtshandig zijn en daardoor meer ervaren zijn met hun rechterhand. Een andere mogelijkheid is dat dit verschil voortkomt uit een linkerhemisferische dominantie voor motorische planning.

In hoofdstuk 3 hebben we een experiment uitgevoerd om de hypothese uit het voorgaande hoofdstuk, over de linkshemisferische dominantie voor motorische planning, te testen. Hiervoor hebben we hetzelfde experiment gebruikt als in hoofdstuk 2 (tweede experiment), maar nu uitgevoerd door linkshandige proefpersonen. Dus, linkshandige proefpersonen werden nu geïnstrueerd twee cd’s gelijktijdig met twee handen op te pakken en in een cd-rek plaatsen in een vooraf aangegeven oriëntatie. Net als de rechtshandige proefpersonen kozen de linkshandige proefpersonen vaak voor een greep die resulteerde in een comfortabele eindhouding, eveneens vaker met hun rechterhand dan met hun linkerhand. De hypothese dat het verschil tussen beide handen wordt veroorzaakt door meer ervaring met de dominante hand lijkt hierdoor onwaarschijnlijk geworden. Daarentegen ondersteunen deze resultaten in zowel links- als rechtshandige proefpersonen de hypothese dat de linkerhemisfeer dominant is voor motorische planning.

Hoofdstuk 4 bevat een studie waarin de consistentie van het ‘end-state comfort effect’ is getest onder verschillende omstandigheden. Weerom hebben we proefpersonen gelijktijdig twee voorwerpen laten oppakken en roteren. Deze keer was de oriëntatie van het voorwerp echter niet alleen horizontaal of verticaal, maar hebben we een hele range van oriëntaties getest.
Daarnaast hebben we onderzocht of het instrueren van de greep voor één van beide handen een invloed had op de motorische planning van de andere hand. In een eerste taak moesten proefpersonen twee staven grijpen die verschillende oriëntaties konden aannemen. De twee staven (half wit, half zwart) moesten met twee handen tegelijkertijd worden vastgepakt en daarna geroteerd naar een verticale oriëntatie, zodanig dat ze met de zwarte helft naar boven eindigden. Net als in voorgaande experimenten kozen de meeste proefpersonen er in de conflicterende situatie niet voor om met beide handen spiegelsymmetrisch te bewegen, maar in plaats daarvan prefereerden ze een comfortabele eindhouding. Echter, niet alle proefpersonen deden dat: zeven van de zeventien proefpersonen kozen voor een greep die comfortabel was op het moment dat de staaf werd vastgepakt, in plaats van aan het eind van de beweging. Dit laat zien dat het ‘end-state comfort effect’ in tweehandige taken minder consistent is dan in eenhandige taken.

Voor de tweede taak hebben we de rechterstaaf vervangen door een lepel, zodat de greep voor de rechterhand gemakkelijker te instrueren was. We hebben proefpersonen gevraagd om de lepel zodanig te grijpen dat ze ermee konden roeren of eten, zodat de duim naar de bolle kant van de lepel wijst en de beweging oncomfortabel eindigt. Wederom moest tegelijkertijd de linkerstaaf met de linkhand opgepakt worden. De zelfgekozen greep voor deze linkerhand bleek niet te worden beïnvloed door de geinstrueerde greep voor de rechterhand. Ook de oriëntatie van de lepel had geen invloed op de greepplanning voor de rechterhand. Hieruit kunnen we concluderen dat de planning van de greep voor beide handen onafhankelijk plaatsvindt, ondanks welbekende interactie-effecten tijdens de bewegingsuitvoering.

Waar het in de voorgaande hoofdstukken allemaal gezonde volwassen proefpersonen betrof, hebben we in hoofdstuk 5 kinderen met en zonder cerebrale paresie getest om de typische en atypische ontwikkeling van greepplanning te bestuderen. Kinderen met cerebrale paresie staan met name bekend om hun problemen met het uitvoeren van bewegingen. Recente studies hebben aangetoond dat deze kinderen ook problemen hebben met het plannen van bewegingen. Wij hebben de motorische planning getest met een eenhandige en een tweehandige taak in kinderen met cerebrale paresie en in gezonde kinderen, allemaal in de leeftijd van 7 tot 12 jaar oud. Ze werden gevraagd een verticaal georiënteerde staaf te grijpen en verplaatsen naar een hogere of een lagere stelling. Hierbij observeerden we of de hoogte van de greep waarmee ze de staaf vastpakten werd beïnvloed door de hoogte van de stelling waarnaar
de staaf verplaatst werd. De mate waarin deze grijphoogte wordt beïnvloed is een maat voor motorische planning. In de eenhandige taak was er geen invloed van de hoogte van de stelling op de grijphoogte voor de kinderen met cerebrale paresis en dit veranderde ook niet met de leeftijd. De gezonde controles daarentegen pasten hun grijphoogte aan de hoogte van de stelling aan en dit effect was sterker naarmate de kinderen ouder waren. Vergelijkbare resultaten werden gevonden voor de tweehandige taak waarin kinderen de staven naar dezelfde hoogte moesten verplaatsen. Echter, wanneer de ene staaf naar boven moest worden verplaatst en de andere staaf naar beneden, pasten de gezonde controlekinderen alleen de grijphoogte van hun niet-dominante hand aan. De staaf voor de dominante hand werd steeds op ongeveer dezelfde hoogte vastgepakt en de grijphoogte van de dominante hand werd dus niet aangepast aan de doelhoogte. Verrassend genoeg lieten kinderen met cerebrale paresis in deze situatie hetzelfde patroon zien: ze planden de grijphoogte voor de meest aangedane hand, terwijl de minst aangedane hand de staaf steeds op ongeveer dezelfde hoogte vastpakte. Kortom, de prestatie van de meest aangedane hand verbeterde ten koste van de minst aangedane hand. We veronderstelden dat kinderen in deze moeilijke taak kozen voor een cognitieve strategie waarbij ze hun aandacht focussen op de meest aangedane arm. Uit deze studie kunnen we concluderen dat de ontwikkeling van motorische planning in kinderen met cerebrale paresis gestoord is in vergelijking met typisch ontwikkelende kinderen, maar dat motorische planning in cognitief uitdagende taken mogelijk geholpen kan worden door gerichte aandacht.

In de studie in hoofdstuk 6 hebben we motorische planning vanuit een neurofysiologisch perspectief bestudeerd. Om te controleren voor effecten van bewegingsuitvoering hebben we proefpersonen laten kijken naar de planning en uitvoering van acties in plaats van ze de bewegingen zelf te laten uitvoeren. Dit maakt het mogelijk om neurale processen te bestuderen die gerelateerd zijn aan actie-observatie en actieplanning. Wanneer men een actie observeert, wordt er in de hersenen een representatie van die actie gevormd. Met behulp van transcraniële magneetstimulatie (TMS) hebben we de timing bestudeerd van neurale processen die zich afspelen op het moment dat de proefpersoon een voorwerp geeft. Hiervoor hebben we in de handspieren van de proefpersoon zogenaamde ‘motor evoked potentials’ (MEPs) gemeten. Dit zijn signalen die optreden als gevolg van magnetische stimulatie van motorische hersengebieden en die kunnen veranderen van amplitude wanneer bewegingen
worden uitgevoerd of waargenomen. Proefpersonen zagen herhaaldelijk een voorwerp gegrepen worden dat vervolgens geplaatst werd in het grote of kleine gat van een houten blok. Voorafgaand aan deze actie verscheen een pijl in de richting van het gat waarin het voorwerp geplaatst zou gaan worden. Op basis daarvan konden proefpersonen afleiden of het voorwerp met een precisiegreep of een krachtgreep opgepakt moest worden. Wanneer de proefpersoon slechts de pijl zag, zonder enige handbeweging, werd de amplitude van de MEPs groter. Echter, deze toenam van de MEP-amplitude was niet specifiek voor de daaropvolgende grijpbeweging en daarmee samenhangend de spieren betrokken bij die grijpbeweging. Wanneer de grijpbeweging vervolgens werd geobserveerd volgde wel een specifieke toenam van de MEP-amplitude in de handspieren betrokken bij die grijpbeweging. De modulatie van MEPs als gevolg van het observeren van de grijpbeweging was anders wanneer de actie werd voorafgegaan door een incorrecte pijl (wijzend naar het verkeerde gat). Deze resultaten geven aan dat de observatie van een bewegingscue (in dit geval een pijl) kan zorgen voor een algemene, niet-specifieke activatie van projecties naar de handspieren. Echter, de motorische representatie die wordt gevormd van de daaropvolgende beweging lijkt afhankelijk te zijn van de gegeven cue.

Conclusie
De greep waarmee voorwerpen worden vastgepakt is afhankelijk van het doel van de actie. Over het algemeen hebben mensen een voorkeur om een beweging te eindigen in een comfortabele eindhouding. In complexe tweehandige bewegingen waar tevens een voorkeur is voor gelijktijdige aanspanning van homologe spieren aan beide lichaamsdelen, speelt het ‘end-state comfort effect’ nog steeds een belangrijke rol bij bewegingsplanning. Dit effect is in dat geval wel minder sterk, met name voor de linkerhand. Een atypische ontwikkeling kan gevolgen hebben voor het ‘end-state comfort effect’. Bijvoorbeeld kinderen met cerebrale parese passen hun greep nauwelijks aan hun actiedoel aan, hoewel er aanwijzingen zijn dat ook deze populatie onder bepaalde omstandigheden in staat is bewegingen van te voren te plannen. Planningsprocessen voor bewegingen zijn bij gezonde volwassenen ook aanwezig wanneer ze anderen een beweging zien maken. Tezamen laten de bevindingen uit dit proefschrift zien dat er verschillende mogelijkheden zijn voor interventie om bewegingsplanning te verbeteren. In kinderen met cerebrale parese bijvoorbeeld, zouden hiervoor de tweehandige taken zoals beschreven in dit proefschrift gebruikt kunnen worden, in combinatie met de instructie om te
focussen op de gewenste hand. Tot slot lijkt actie-observatie in deze context ook een effectieve interventie.
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