RESEARCH ARTICLE

An investigation into manual asymmetries in grasp behavior and kinematics during an object manipulation task

Christian Seegelke · Charmayne M. L. Hughes · Thomas Schack

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Abstract Manual asymmetries in the control of movements have been investigated in a variety of experimental paradigms. Initial studies demonstrated that the dominant right hand has advantages over the non-dominant left hand in many aspects of motor control. However, more recent studies have shown that the presence and extent of these asymmetries depends on the task context and accuracy demands. Typically, manual asymmetries on a motor planning and motor execution level are examined separately. However, given that recent research has demonstrated that specific task constraints do not influence both levels equally, the purpose of the present experiment was to investigate manual asymmetries in motor planning and execution. To this end, initial grasp behavior (motor planning) and kinematics (motor execution) were examined in thirteen right-handed participants during a unimanual grasping and placing task. We specifically manipulated grasping hand, target location, object end orientation, and object grasp time at the start location. There were three main findings. First, motor planning or movement execution was similar regardless of grasping hand. Second, prospectively planned actions were influenced by target location and the required end orientation of

C. Seegelke (⊠) · C. M. L. Hughes · T. Schack Neurocognition and Action Research Group, Faculty of Psychology and Sport Sciences, Bielefeld University, Bielefeld, Germany e-mail: Christian.Seegelke@uni-bielefeld.de

C. Seegelke · C. M. L. Hughes · T. Schack Research Institute for Cognition and Robotics (CoR-Lab), Bielefeld University, Bielefeld, Germany

C. M. L. Hughes · T. Schack Center of Excellence Cognitive Interaction Technology (CITEC), Bielefeld University, Bielefeld, Germany the object. Third, the amount of time spent in an initial posture did not influence initial grasp postures. However, it did alter the movement kinematics during the grasping (approach phase) and placing (transport phase) portion of the task. We posit that grasping and placing movements are comprised of an initial grasp and a transport component, which are differentially influenced by task constraints.

Keywords End-state comfort · Motor planning and execution · Manual asymmetries · Object manipulation

Introduction

Manual asymmetry, or handedness, is one of the most obvious manifestations of laterality. For example, when performing everyday tasks, such as writing or grasping a cup, humans typically prefer one hand over the other, with approximately 90% of the population exhibiting a preference to use the right hand to perform one-handed manual actions (Coren and Porac 1977). Coincident with the preference to use one hand over the other is the observation of manual asymmetries during the performance of unimanual actions. In one of the earliest investigations into the control of human movements, Woodworth (1899) asked participants to perform simple repetitive line-drawing movements, with manipulations on the frequency of the pacing metronome, movement distance, visual information (eyes open or eyes closed), and hand (left or right). Along with the general finding that movement accuracy decreased as speed increased, Woodworth found that movements performed by the dominant right hand were substantially more accurate than those of the non-dominant left and that this asymmetry became more pronounced at faster movement speeds.

Since Woodworth's seminal work, research from various motor tasks has revealed that the dominant hand advantage extends to a number of motor execution domains. For example, the dominant hand is often faster and more consistent than the non-dominant hand during repetitive finger tapping (Peters 1976; Peters and Durding 1979; Todor and Kyprie 1980; Todor et al. 1982), and movement times of the dominant hand are generally shorter than those of the non-dominant hand during unimanual reaching and rapid aiming movements (Annett et al. 1979; Carson et al. 1993; Roy and Elliott 1989). The longer movement times for the non-dominant hand are typically attributed to shorter time to peak velocity values, indicating that more time is required to home in on the target in order to maintain accurate movement performance (Boulinguez et al. 2001; Elliott et al. 1995; Mieschke et al. 2001; Roy et al. 1994; Todor and Cisneros 1985). Although the underlying mechanisms for the right hand advantage are still debated (see Elliott and Chua 1996 for a review), the results of the aforementioned studies support the hypothesis that the hemisphere contralateral to the dominant arm (most often the left hemisphere) has advantages in the control of both the dominant and non-dominant limbs (Haaland and Harrington 1996).

There is also evidence suggesting that hemispheric advantages extend to the motor planning level (Crajé et al. 2009; Hermsdorfer et al. 1999; Janssen et al. 2009, 2011; Mutsaarts et al. 2005, 2007; Steenbergen et al. 2004). Anticipatory motor planning implies that participants take into account future task demands or intended action goals (Johnson-Frey et al. 2004) and can be studied by examining the initial grasp postures that people use to manipulate objects. For example, Rosenbaum et al. (1990) asked participants to reach for a bar and move it from a home location to a target location. They found that participants generally took hold of the bar in a way that ensured a comfortable posture at the end of the movement even when this necessitated an uncomfortable initial posture. This phenomenon, termed the end-state comfort effect, has been observed in a number of task contexts (Cohen and Rosenbaum 2004; Herbort and Butz 2010; Rosenbaum et al. 1993; Weigelt et al. 2006) and indicates that initial grasp postures are planned prior to movement execution.

Recent studies have examined the presence of hemispheric asymmetries during motor planning in both healthy (Hughes et al. 2011b; Janssen et al. 2011) and patient populations (Crajé et al. 2009). For example, Crajé et al. (2009) examined differences in initial grasp posture planning in individuals with left- or right-sided congenital hemiparesis. In this task, participants grasped a rod placed in varying start orientations with their unimpaired hand and placed it vertically into a tight fitting box. The majority of participants (75%) with left congenital hemiparesis (i.e., right brain damage) employed a consistent switching strategy. In contrast, individuals with right congenital hemiparesis (i.e., left brain damage) either did not adjust their initial grasp postures (40%) or switched their grips in an inconsistent manner (30%). Based on the finding that the deficits in motor planning are more pronounced in individuals with right hemiparesis, compared to individuals with left hemiparesis, the authors suggest that the left hemisphere has a specialized role in motor planning processes.

Complementary evidence for left-hemisphere specialization for motor planning has come from the bimanual grasping and placing literature. In two recent studies, Janssen et al. (2009, 2011) found that participants are more likely to grasp an object with initial grasp postures that ensure comfortable end states with the right hand, compared to the left hand. Furthermore, the increased sensitivity toward comfortable end postures for the right hand was observed regardless of whether individuals were leftor right-handed. Taken together, the findings from both healthy individuals and patient populations suggest that the planning of initial grasp postures might arise from lefthemisphere specialization.

Although the presence and extent of manual asymmetries has been extensively examined in a variety of experimental paradigms (see Goble and Brown 2008 for a review), there are few studies that have examined whether these asymmetries are evident during both the motor planning and execution during the same task (see Hughes et al. 2011b for an exception). Examining motor behavior at different levels (i.e., on both a kinematic and a grasp posture level) has provided fruitful insight into the planning and control of object manipulation tasks, with the results of such studies, demonstrating that task constraints do not influence motor planning and motor execution equally. For example, Hughes et al. (2011a) recently examined how two specific task constraints (physical object coupling, end-orientation congruency) influence the planning of initial grasp postures and movement kinematics during a bimanual grasping and placing task. Participants were asked to simultaneously grasp two objects and place them to identical or different end orientations on a target board. One group of participants performed the task when the objects were not connected, whereas another set of participants performed the task when the objects were physically connected with a spring. They found that although end-orientation congruency altered both initial grasp behavior (motor planning) and interlimb coupling (motor execution), physically connecting the two objects influenced motor execution but not motor planning.

Based on the suggestion that different constraints evoke unequal effects on these two levels of motor control, the aim of the present study was to investigate asymmetries in both motor planning (i.e., end-state comfort) and execution (i.e., kinematics) during a unimanual object manipulation task. In this task, participants grasped a cylindrical object with the dominant right hand, or the non-dominant left hand, and placed it to a left or right target. In addition, the end orientation of the object was manipulated, so that the object was transported without rotation or transported and rotated 180° .

Based on the previous manual asymmetry literature suggesting that the hemisphere contralateral to the dominant hand is specialized for motor execution, it was hypothesized that dominant arm advantages would be observed during the execution of the movement. Specifically, we expected shorter approach and transport time values, and shorter deceleration times, for the dominant right arm, compared to the non-dominant arm. With regard to the planning of initial grip postures, it was hypothesized that the dominant right hand should exhibit a greater preference for comfortable end postures than the nondominant left hand. Such a finding would support the claim that the left hemisphere is specialized for motor planning. However, as Hughes et al. (2011a) have recently argued, task constraints exert differential effects on motor planning (e.g., initial grasp postures) and movement execution (e.g., interlimb coupling). Thus, we must also entertain the notion that the presence and/or extent of manual asymmetry may influence only one level of motor behavior.

A secondary purpose of the present study was to examine whether end-state comfort can be explained by the desire to minimize the total time spent in awkward postures. That is, grasping and placing tasks typically require more time at the end, rather than the start, of the movement. Thus, grasping the object with an initially awkward grasp posture would not only afford comfortable end postures but also maximize the amount of time the arm spends in a comfortable posture. A previous study (Rosenbaum et al. 1990) tested this hypothesis by varying the precision demands at the end of the movement. In that study, participants rotated a cylindrical rod 180 degrees and placed the end of the rod into either a small or a large disk. Because placing the object into the small disk is more precision demanding, Rosenbaum et al. (1990) hypothesized that participants they would be more likely to grasp the object initially with a thumb down (rather than a thumb up) grasp posture if they were trying to minimize times in awkward postures Although their findings did not confirm this hypothesis, a limitation of that study is that placing the object to the end position required more time than grasping the object (for both the small and the large disk). Thus, grips that satisfied end-state comfort also allowed participants to minimize the amount of time in an awkward posture. In the present study, we reexamined the issue and removed the possible confound between end-state comfort and time spent in a certain posture by manipulating the amount of time participants had to hold onto the object at the start location (0 or 9 s) before moving it to the end location. If participants attempt to minimize the amount of time in awkward postures, we would expect a decrease in end-state comfort satisfaction as the amount of time participants have to hold onto the object at the home location increases.

Methods

Comfort ratings

Because the experimental setup in the present study (vertical start orientation of the object) differed from that used in the previous studies (Rosenbaum et al. 1990), we obtained an independent measure of grasp comfort for adopted grip postures ("Thumb up" versus "Thumb down") to obtain estimates of perceived comfort of grasping the cylinder in every static posture that was possible in the main experiment. These ratings were later used to quantify initial grasp postures that lead to end postures that satisfied end-state comfort.

Participants

Twenty individuals from Bielefeld University (6 men, 14 women) with a mean age 26.6 years (SD = 3.73) participated in this task in exchange for course credit. All participants were right-handed (mean score = 1.00,SD = 0.00) as assessed using the Revised Edinburgh Handedness Inventory (Dragovic 2004), which ranks handedness on a scale ranging from -1.00 (strongly lefthanded) to 1.00 (strongly right-handed). Participants had normal or corrected to normal vision and did not have any known neuromuscular disorders. The experiments were conducted in accordance with local ethical guidelines and conformed to the Declaration of Helsinki.

Apparatus and procedure

The experimental apparatus was placed on a shelf, which was adjusted to participants' chest height. It consisted of a home base and two target bases. The bases were square blocks made of PVC ($18 \text{ cm} \times 18 \text{ cm} \times 3 \text{ cm}$) and contained a centrally located well of 3 mm depth and 7 cm (home base) or 9.6 cm (target base) in diameter. The home base was vertically arranged to coincide with the participants' body midline. The target bases were located 28.5 cm to either side of the home base. The cylindrical object (16 cm in height, 7 cm in diameter, and 787 g in weight) was colored red on one end and gray on the other.

Prior to each trial, participants were informed of the initial grasp posture ("thumb up" or "thumb down"), which hand to use (left, right) the required object end orientation (no object rotation or object rotation) and the final target location (left or right target). Participants grasped the object from the home base and provided a rating of the initial grasp comfort on a scale ranging from 1 (very uncomfortable) to 5 (very comfortable).¹ Participants then moved the object to the target location in the required end orientation and provided a second rating of comfort with respect to the end posture. Each condition was performed six times, yielding a total of 96 trials. The order of presentation was randomized.

Grasping task

Participants

Fourteen students from Bielefeld University were recruited to take part in this experiment. These students did not participate in the comfort rating task. The dataset from one participant was removed prior to analysis because the participant did not understand the instructions. This left us with a sample of 13 participants (mean = 23.2, SD = 3.0, 3 men, 10 women) who participated in exchange for experimental course credit. All participants were righthanded (mean score = 0.93, SD = 0.26) as assessed by the Revised Edinburgh Handedness Inventory (Dragovic 2004). Participants had normal or corrected to normal vision and did not have any known neuromuscular disorders. The experiments were conducted in accordance with local ethical guidelines and conformed to the Declaration of Helsinki.

Apparatus and stimuli

The experimental apparatus was identical to that used in the comfort rating task with the following exceptions. A flat plastic disk served as the start button (7 cm in diameter), which was embedded in a square PVC block (11 cm \times 11 cm \times 3 cm). The start button was also vertically arranged with the participants' body midline and located 26 cm apart from the home base. In addition, the end location and object end orientation for each trial were presented on a 17" flat screen monitor (Sync Master 943T, Samsung), placed 50 cm in front of the participants and controlled via Presentation[®] (Neurobehavioral Systems). The stimuli consisted of a visual representation of the object (16 cm in height, 7 cm in width) and indicated the required target location (left/right) and end orientation of the object (no rotation of the object required/rotation required) (Fig. 1). A countdown timer displayed the amount of time a participant was to grasp the object at the home base.

To collect kinematic data, three retro-reflective markers (14 mm in diameter) were placed on the distal end of dorsal third metacarpal, the styloid process of ulna, and the styloid process of radius of the left and right hands. Data were recorded using an optical motion capture system (VICON Motion Systems, Oxford, UK) consisting of 10 Bonita cameras with a temporal and spatial resolution of 200 Hz and 1 mm, respectively. The experiment was videotaped using a Basler Pilot DV camera (Basler AG, Ahrensburg, Germany), which was synchronized with the motion capture system.

Procedure

After filling out the informed consent form, retro-reflective markers were placed on both hands, and participants stood in front of the shelf so that the home and the target bases were within comfortable range. At the start of each trial, the message "Put your hand on the start key!" was displayed in German, and the participant placed their hand flat against the start button. A fixation cross was then presented, and after a random interval (500-1,500 ms), the stimulus appeared. The participant grasped the object from the home base,² activating the countdown timer. After the countdown timer reached "0.0", the word "Los!" ("Go!" in German) appeared, and participants moved the object to the target location and end orientation indicated on the computer monitor. At the end of the trial, participants brought their hand back to the start position and waited for the next trial to begin. Participants were told to grasp the object with a full grip, using either a "thumb up" or a "thumb down" posture. Furthermore, the instructions emphasized that participants should move at a comfortable speed, and movement accuracy was stressed.

There were 16 different conditions consisting of the factors hand (dominant, non-dominant), target location (left, right), object end orientation (no rotation, rotation), and time spent at start position (0.0, 9.0 s). Each condition was performed four times, yielding a total of 64 trials. The factors time spent at start position and hand were blocked, and the order of blocks was randomized across participants.

¹ A Likert-type scale is commonly used to measure attitude, providing a given range of responses to a given statement. The response categories in Likert scales have a rank order, but the intervals between values cannot be presumed equal (Blaikie 2003).

 $[\]frac{1}{2}$ In order to control for perceptual effects associated with object perception, half of the subjects performed the task when the object was placed red end down at the start of the trial and the other half performed the task when the object was placed grey end down at the start of the trial.

Fig. 1 a *Front* view of the experimental setup. **b** Bird's eye view of the experimental setup. **Stimulus** indicating the time to be spent at initial grasp and the required end orientation and target. In the depicted example, participants were required to grasp and hold the object for 9 s, before placing it onto the right target with the *gray* end down



Within each block, the order of presentation was randomized.

Data collection and reduction

The 3D coordinates of the retro-reflective markers were reconstructed and labeled. The marker with the fewest missing data points³ was used for future analyses, and any missing data (less than 10 frames) were interpolated using a cubic spline and filtered using a Woltring filter (Woltring 1986) with a predicted mean square error value of 5 mm² (Vicon Nexus 1.5).⁴ Kinematic variables were calculated using custom written MatLab programs (The MathWorks, Version R2010a).

For each trial, the time series was divided into the approach phase and the transport phase. The approach phase was defined as the time period between when the hand left the start key to the time the hand contacted the object. The transport phase was defined as the time period between when the object was lifted from the home base to the time the object contacted the end target. Movement onset for each phase was determined as the time of the sample in which the resultant velocity of the hand exceeded 5% of peak velocity of the corresponding phase. Movement offset was determined as the time of the sample in which the resultant velocity dropped and stayed below 5% of peak velocity of the corresponding phase.

Approach time (AT) was defined as the time period between approach phase movement onset and approach phase movement offset, and transport time (TT) was defined as the time period between transport phase movement onset and transport time movement offset. Movement velocity for the approach and transport phases was calculated using a first-order central difference technique, and time normalized to 100 data points prior to calculation of peak velocity and time to peak velocity.

Statistical analysis

In order to assess differences in initial grasping posture ("thumb up", "thumb down"), analyses were performed on the factors hand (dominant, non-dominant), object end orientation (no rotation, rotation), target location (left, right), and time spent at the start position (0.0, 9.0 s). Differences in the kinematic and the timing structure were examined using separate repeated measures ANOVAs on the factors hand (dominant, non-dominant), object end orientation (no rotation, rotation), target location (left, right), and time spent at the start position (0.0, 9.0 s) on the factors hand (dominant, non-dominant), object end orientation (no rotation, rotation), target location (left, right), and time spent at the start position (0.0, 9.0 s) on the following variables: approach time (ms), transport time (ms), approach phase peak velocity (mm/s), transport phase peak velocity (mm/s), and transport phase time to peak velocity (% transport phase).

Results

Comfort ratings

Comfort at the start and end location was analyzed using separate repeated measures ANOVA's on the factors 2 initial grip ("thumb up", "thumb down") \times 2 end orientation (no rotation, rotation) \times 2 target location (left, right) \times hand (left, right).

Analysis of comfort at the start location (when participants grasped the object from the home base) indicated that "thumb up" grip postures (mean comfort rating = 4.75) were significantly more comfortable than a "thumb down" grip (mean comfort rating = 2.47), [F(1,19) = 97.86, P < 0.001]. No other effect or interaction reached significance.

Analysis of comfort at the end location (when the object was placed at the target) revealed higher comfort ratings

³ For all participants, this was the marker located on the styloid process of radius.

⁴ The Woltring filter is commonly in the analysis of motion capture data and is equivalent to a double Butterworth filter. The benefit to the Woltring filter is that higher-order derivatives can be calculated from the analytic derivative of the polynomial spline.

for an initial "thumb up" posture (mean comfort rating = 3.44), compared with an initial "thumb down" posture (mean comfort rating = 3.24), [F(1,19) = 17.31, P = 0.001]. In addition, higher comfort ratings were obtained when the object was to be rotated (mean comfort rating = 3.41), compared to when no rotation was required (mean comfort rating = 3.28), F(1,19) = 6.72, P = 0.018. The main effect of hand was not significant, F(1.19) =2.75, P = 0.114. Moreover, perceived end comfort was influenced by target location and hand. For the left hand, comfort ratings were higher for the left target location (mean comfort rating = 3.57) compared to the right target location (mean comfort ratings = 3.01). In contrast, for the right hand, comfort ratings were higher for the right target location (mean comfort = 3.65) compared to the left target location (mean comfort = 3.14), [F(1,19) = 37.41, P < 0.001].

Most importantly, there was a significant initial grip by end-orientation interaction, F(1,19) = 103.68, P < 0.001. When the movement did not require rotation, participants rated end position comfort as more comfortable when they grasped the object with an initial "thumb up" posture (mean comfort rating = 4.48) than with an initial "thumb down" posture (mean comfort rating = 2.07). In contrast, when the movement required rotation, participants rated end position comfort as more comfortable when they initially grasped the object with a "thumb down" posture (mean comfort rating = 4.42) than with an initial "thumb up" posture (mean comfort rating = 2.40).

Based on these results, during trials that did not require rotation, end-state comfort was defined by the adoption of initial "thumb up" postures. In contrast, when the object Exp Brain Res

required rotation, end-state comfort was defined by the adoption of initial "thumb down" postures.

Grasping task

Grasp postures

Chi-square tests revealed no differences in end-state comfort satisfaction between the dominant and non-dominant hands $[\chi^2(1) = 0.276, P = 0.599]$, the left and right targets $[\chi^2(1) = 0.125, P = 0.724]$, or as a function of time $[\gamma^2(1) = 1.12, P = 0.289]$. However, the proportion of total trials that participants ended in a comfortable posture was significantly higher when no rotation of the object was required (98%), compared to when 180° rotation was required (61%), $\chi^2(1) = 42.0$, P < 0.001. Most interestingly, for the 180° rotation trials, the sensitivity toward comfortable end postures was influenced by hand and target location. For the dominant right hand, end-state comfort satisfaction was higher for the right (73%), compared with the left target location (41%). In contrast, for the nondominant left hand, end-state comfort satisfaction was higher for the left (80%), compared to the right target location (46%) $\gamma^2(1) = 18.1$, P < 0.001. Thus, end-state comfort satisfaction was significantly lower for the contralateral target location for both the dominant and nondominant hands (Fig. 2a).

Kinematic data

Approach time values were, on average, shorter when the object was transported without rotation (1,042 ms),

Fig. 2 a End-state comfort satisfaction for rotation trials as a function of hand and target location. The bars depict the percentages of trials in which participants ended the movement in a thumb-up posture, separated for the left and *right* targets and for the right hand (black bars) and left hand (white bars). b Transport times (ms) as a function of hand and target location. White bars indicate *left* hand movements, black bars right hand movements (mean \pm SE)



compared to when the object was rotated 180° (1,133 ms), F(1,12) = 15.05, P = 0.002. For 180° rotation trials, approach time values were similar for the dominant (1,127 ms) and the non-dominant hand (1,139 ms). In contrast, when the object did not require rotation, approach times for the non-dominant hand were faster (1,020 ms) than the dominant hand (1,065 ms), F(1,12) = 6.43, P = 0.026.

In addition, peak velocity values were significantly higher for those trials that did not require rotation (712 mm/s), compared with trials that required 180° object rotation (627 mm/s), F(1,12) = 11.49, P = 0.005. The decelerative portion of the velocity profile of the approach phase was longer for 180° rotation trials (39%), compared with trials that did not require object rotation (41%), F(1,12) = 12.17, P = 0.004. A significant object end orientation by target location interaction was observed, F(1,12) = 4.84, P = 0.048. For trials that did not require rotation, the decelerative portion of the velocity profile was similar for the left and the right target (both 41%). In contrast, for trials that required 180° rotation, the decelerative portion was longer for the left (38%), compared to the right target (40%).

On average, transport time values were smaller when the object did not require rotation (1,282 ms), compared to when the object required 180° rotation (1,410 ms), F(1,12) = 31.14, P < 0.001. Transport time values were also shorter when participants transported the object immediately after grasping it (1,288 ms), compared to when they had to hold onto the object for 9 s (1,403 ms), F(1,12) = 16.86, P = 0.001. A significant target location \times hand interaction was observed, F(1,12) = 23.33, P < 0.001. For the non-dominant hand, transport times were faster to the left target (1,302 ms), compared to the right target (1,354 ms). In contrast, for the dominant hand, transport times were faster to the right target (1,320 ms), compared to the left target (1,405 ms). Thus, transport times were significantly shorter for movements to the ipsilateral target for both the dominant and non-dominant hands (Fig. 2b).

In addition, a target location \times time spent at start position interaction was observed, F(1,12) = 8.30, P = 0.014. Transport time values were similar between the two target locations when participants had to hold onto the object for 9 s before transporting the object (left target: 1,398 ms, right target: 1,408 ms). In contrast, when participants did not have to hold onto the object before transporting it, transport time values were smaller for the right target (1,267 ms), compared to the left target (1,310 ms).

Peak velocity values were significantly higher for trials that required 180° rotation (582 mm/s), compared with trials that did not require rotation (535 mm/s), F(1,12) = 7.77, P = 0.016. For both hands, peak velocity values were higher for the left target location than the right target location. However, this was more pronounced for the non-dominant hand (left target: 594 mm/s, right target: 568 mm/s) compared with the dominant hand (left target: 551 mm/s, right target: 543 mm/s), F(1,12) = 8.06, P = 0.015.⁵

Discussion

In this study, we examined whether manual asymmetries are evident on both a motor planning and a motor execution level during a unimanual object manipulation task, in which target location, target orientation, and time spent in an initial posture were manipulated. The following main findings were observed. First, manual asymmetries were not observed during either motor planning or movement execution. Second, initial grasp postures and kinematics were in large part influenced by target location and the required end orientation of the object. Third, end-state comfort was not influenced by the amount of time spent in an initial posture. However, it did alter the movement kinematics of the task. The discussion will focus primarily on these new findings.

Based on previous findings from both healthy (Janssen et al. 2009, 2011) and patient populations (Crajé et al. 2009; Steenbergen et al. 2004), it was hypothesized that end-state comfort would be more pronounced for the right, compared with the left hand. However, our findings did not support this hypothesis, as end-state comfort satisfaction was similar irrespective of hand. One possible explanation for the divergent results obtained in the present experiment (see also Hughes et al. 2011b) and those of Steenbergen et al. (Crajé et al. 2009; Janssen et al. 2009, 2011; Steenbergen et al. 2004) is the degree of precision at the end of the movement. For example, in the studies of Janssen et al. (2011), participants placed a CD casing into a box, and in the Crajé et al. (2009) study, participants grasped and placed the object "vertically with the marker facing upwards in a tight fitting box" (Crajé et al. 2009, p. 60). In contrast, in the present study, the object (7 cm in diameter) was placed onto a target (9.6 cm) that had a depth of 3 mm.

⁵ We are aware that the differences in kinematics between the rotation and no rotation trials are in part due to the initial grasp posture (thumb up versus thumb down). We would have examined differences in kinematics based on the initial grasp posture; however, a number (n = 6) of the participants used the same initial grasp posture in 100% of the trials for each condition (no rotation versus rotation). Thus, when pooling the data across initial grasp posture, we encountered an empty cell problem. We do not use partial deletion techniques (listwise or pairwise) to treat the data because such techniques would have reduced the dataset to seven participants, (and thus decreased statistical power).

Thus, we believe that these "fitting" tasks require a higher level of precision at the end of the movement than the "placing" tasks that we have employed and that the presence of manual asymmetries during the planning of initial grasp postures is influenced by the precision demands of the task (Hughes et al. 2011a, b).

In addition, counter to the expectation that the dominant right arm would have a strong advantage over the nondominant hand during motor execution, we did not observe any manual asymmetries. Concurrent with the previous research, we hypothesize that the presence and degree of manual asymmetries in motor performance are influenced by the context in which the task is performed. For example, Flowers (1975) examined the performance of left- and right-handed individuals in a simple rhythmical tapping task and a complex manual-aiming task. Although large asymmetries between the two hands were observed during the manual-aiming task, there were negligible asymmetric differences in the tapping task. Furthermore, it has also been shown that precision demands (Bryden and Roy 1999), the spatial variability of the movement trajectory, and the number of spatial axis in which the movement must be controlled (Roy et al. 1995) all contribute to the degree of manual asymmetry. Thus, we believe that the presence and extent of manual asymmetry varies depending on the context in which the task is performed (Bryden 2000) and the complexity of the task (Hausmann et al. 2004).

Alternatively, it is possible that the lack of hand differences is due to the task and experimental design of the present study.⁶ We leave open the possibility that a more natural task (e.g., pouring water into a cup) might better detect differences in manual asymmetries during both motor planning and motor execution. For example, it would be worthwhile to examine manual asymmetries during goal-directed actions across a variety of task contexts. If manual asymmetries are, in part, influenced by the ecological validity, then one would expect to see increased asymmetries for more naturalistic tasks. Future researchers should investigate this issue in greater depth.

A second finding of the present study is that although end-state comfort and kinematics were not influenced by hand, both motor planning and execution were affected by object rotation requirements. Specifically, the tendency to adopt initially uncomfortable postures was lower when the object required rotation (61%), compared to when the object did not require rotation (98%). This finding is intriguing, given that previous unimanual studies typically report much higher end-state comfort proportions (Rosenbaum and Jorgensen 1992; Rosenbaum et al. 1990; Weigelt et al. 2006). Note that in those studies, participants grasped the object from a horizontal start position and rotated it 90° to place it into a vertical end position, whereas in the present study, the object was to be transported and rotated 180° from a vertical start position to a vertical end position. In both unimanual (Rosenbaum and Jorgensen 1992; Rosenbaum et al. 1990; Weigelt et al. 2006) and bimanual situations (Hughes et al. 2011b; Weigelt et al. 2006) where 90° internal or external rotation is required, end-state comfort proportions are typically higher than 90%. In contrast, when 180° rotation is required, end-state comfort is typically much lower (Hughes and Franz 2008; Hughes et al. 2011a, b). Thus, it appears that the sensitivity toward end-state comfort is strongly influenced by the degree of object rotation.

We observed longer approach and transport times and smaller time to peak velocity values during the approach phase, when the object was rotated 180°, compared to when the object was not rotated. These findings are congruent with the previous work, demonstrating that movement kinematics is influenced by the required angle of rotation. For example, Mason and Bryden (2007) asked participants to transport a cubic object to a target located away from the body, while also rotating the object 45° or 90°. The authors found that participants took longer to perform the task when the object required 90°, than when the object required 45° rotation. Based on these results, the authors state that hand transport and hand rotation are not independently controlled processes. Similarly, in the present study, we also observed that transporting and rotating the cylinder were performed in tandem rather than in succession, supporting this assumption.

It is possible that the decrease in end-state comfort satisfaction during trials that required 180° object rotation arises from mental rotation processes. Mental rotation involves forming an internal visual representation of an object and then transforming the internal image by rotating it until it reaches the intended end position (Shepard and Cooper 1982). In general, response times increase in a linear fashion with larger rotation angles (Shepard and Metzler 1971) and that the cognitive load imposed by the stimuli is proportional to the number of degrees that the stimuli needed to be rotated (Cooperau and Shepard 1973; Fischer and Pellegrino 1988). Thus, it is possible that the increased cognitive load associated with mentally rotating the object 180° may have impeded the ability to plan initial grasp postures that satisfy end-state comfort.

Alternatively, it is possible that the decrease in end-state comfort satisfaction is due to biomechanical factors. Compared to the 90° object rotations (horizontal-to-vertical position) in previous studies (e.g., Rosenbaum et al. 1990), satisfying end-state comfort in 180° object rotation tasks (vertical-to-vertical position) like in the present study requires tolerating more initial discomfort (see also Cohen and Rosenbaum 2011). This is because (initial) "thumb

⁶ We thank an anonymous reviewer for pointing this out.

down" postures are generally perceived as more uncomfortable compared to (initial) "underhand" postures (see Janssen et al. 2009, 2011; Rosenbaum et al. 1990). That is to say, in horizontal-to-vertical transports (90° object rotation), the overall comfort is higher when people satisfy end-state comfort, compared to when they do not satisfy end-state comfort, whereas in the vertical-to-vertical transports (180° object rotation) it is similar regardless of whether people satisfy end-state comfort or not. Thus, the weighting of the two postures might have changed causing the decrease in end-state comfort satisfaction for the rotation trials in the present experiment (see also Hughes et al. in 2011b for a similar argument.

Initial grip behavior and kinematics were also influenced by target location. In line with the previous unimanual reaching literature (Carey et al. 1996; Carey and Otto-de Haart 2001; Fisk and Goodale 1985), we observed shorter transport times when movements were made to targets located on the same side of the body (ipsilateral) as the grasping arm, compared to movements made to targets located on the opposite side of the body (contralateral) as the grasping arm for both the dominant and non-dominant hands. In addition, we also observed lower end-state comfort satisfaction (during 180° rotation trials) to movements performed to the contralateral, compared to the ipsilateral target. Based on behavioral (Brinkman and Kuypers 1972; Haaxma and Kuypers 1975; Lawrence and Kuypers 1968a, b) and neurophysiological evidence (Colebatch et al. 1991; Grafton et al. 1993; Kim et al. 1993; Nirkko et al. 2001) demonstrating stronger additional ipsilateral brain activation for movements involving axial and proximal limb muscles (e.g., shoulder) compared to distal muscles (finger) (see also Evarts 1966; Gazzaniga et al. 1967), we hypothesize that these ipsilateral target advantages arise from corticospinal projections to the distal and proximal muscles. For example, Colebatch et al. (1991) used fMRI to examine the relative contributions from primary and secondary motor areas during discrete unilateral distal finger and proximal shoulder movements. They found that the contralateral primary sensorimotor cortex (SM1) was exclusively activated during the distal finger opposition task. However, during the proximal shoulder circling task, in addition to observing contralateral activation, there was approximately 30% ipsilateral activation. In the present study, movements to the ipsilateral target require the involvement of elbow, hand, and finger muscles. In contrast, movements to the contralateral target locations require the additional involvement of the shoulder muscles, thereby activating both contralateral and ipsilateral motor areas. Consistent with neurophysiological findings, we suggest that these ipsilateral advantages during both planning and execution may have resulted from the more exclusive contralateral corticospinal activation of the distal musculature during movements to the ipsilateral target.

A corollary purpose of this study was to examine whether end-state comfort is influenced by the amount of time spent in an initial posture. Our findings, however, did not support our hypothesis since we did not observe a decrease in end-state comfort satisfaction as the amount of time participants had to hold onto the object at the home location increased. To explain this lack of results, it could be argued that the stimuli were too complex and participants could not attend to all relevant information before initiating their movements. In the current task, the stimuli contained information about the required object's end orientation and target location, as well as the time participants had to hold onto the object prior to moving it. Given the large amount of information, it is possible that participants focused primarily on the object's end orientation and target location and ignored the countdown timer. Alternatively, it is possible that participants sought to reduce the load on the elbow and shoulder joint by relaxing the arm and shoulder muscles during trials that required them to hold the object at the start position for 9 s before moving. This strategy lowered the physical demands and awkwardness associated with holding the limb in a specific posture for a certain amount of time. Current experiments in our laboratory are aimed at investigating these hypotheses.

Interestingly, although the amount of time spent in an initial posture did not influence end-state comfort, it did alter the movement kinematics of the task. We observed shorter transport times when participants could transport the object immediately after grasping it, compared to when they had to hold onto the object for 9 s. In the 0 s condition, participants were able to grasp the object while still moving and thus did not need to fully stop their hand while grasping the object. Because participants did not need to overcome inertia in order to transport the object, this grasping strategy allowed for faster movement times during the transport portion of the task. In contrast, in the 9 s condition, the constraint to hold onto the object at the start position required that participants arrest their hand movements. In order to initiate the transport phase of the task, participants had to produce more inertial force to move the hand and object from a static position; resulting in increased transport times.

In summary, initial grasp behavior and kinematics were similar regardless of hand. However, target location and object end orientation altered both initial grasp behavior and kinematics. In contrast, time spent in an initial posture did not influence end-state comfort (initial grasp behavior), but it did influence how the movement was executed. The divergent influence of specific constraints on initial grasp behavior and kinematics has also been observed in bimanual grasping and placing movements (Hughes et al. 2011a). Hughes et al. (Hughes and Franz 2008; Hughes et al. 2011a) postulate that successful task performance is contingent on the action goals of the task, which guide the selection of lower-level action features (e.g., initial grasp postures), as well as the manner in which the task is performed (e.g., kinematics). In particular, grasping and placing movements can be separated into an initial grasp and a transport component, within which there are a number of constraints that the system seeks to satisfy. For example, the study of Hughes et al. (2011a) examined how physically connecting two objects might influence bimanual grasping and placing movements to identical or different object end-orientation targets. They found that although object end-orientation congruency influences both the grasping and transport components of the task, physically connecting the two objects altered only the degree of interlimb coupling between the hands (e.g., on a kinematic level). Taken together, these results indicate that constraints may not elicit equal effects on both the grasping and transport components, and a more holistic approach to human object manipulation may provide insights that might not be apparent otherwise. The challenge now is to examine how specific constraints mediate motor behavior and to investigate how these constraints interact with one another during object manipulation tasks.

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References

- Annett J, Annett M, Hudson PT, Turner A (1979) The control of movement in the preferred and non-preferred hands. Q J Exp Psychol 31:641–652
- Blaikie N (2003) Analysing quantitative data. Sage Publications, London
- Boulinguez P, Velay JL, Nougier V (2001) Manual asymmetries in reaching movement control. II: study of left-handers. Cortex 37:123–138
- Brinkman J, Kuypers HG (1972) Splitbrain monkeys: cerebral control of ipsilateral and contralateral arm, hand, and finger movements. Science 176:536–539
- Bryden PJ (2000) Lateral preferences, skilled behavior and task complexity: hand and foot. In: Mandal MK, Bulman-Fleming MB, Tiwari G (eds) Side bias: a neuropsychological perspective. Kluwer, Dordrecht, pp 225–248
- Bryden PJ, Roy EA (1999) Spatial task demands affect the extent of manual asymmetries. Laterality 4:27–37
- Carey DP, Otto-de Haart EG (2001) Hemispatial differences in visually guided aiming are neither hemispatial nor visual. Neuropsychologia 39:885–894
- Carey DP, Hargreaves EL, Goodale MA (1996) Reaching to ipsilateral or contralateral targets: within-hemisphere visuomotor processing cannot explain hemispatial differences in motor control. Exp Brain Res 112:496–504

- Carson RG, Elliott D, Goodman D, Thyer L, Chua R, Roy EA (1993) The role of impulse variability in manual-aiming asymmetries. Psychol Res 55:291–298
- Cohen R, Rosenbaum D (2004) Where grasps are made reveals how grasps are planned: generation and recall of motor plans. Exp Brain Res 157:486–495
- Cohen RG, Rosenbaum DA (2011) Prospective and retrospective effects in human motor control: planning grasps for object rotation and translation. Psychol Res 75:341–349
- Colebatch JG, Deiber MP, Passingham RE, Friston KJ, Frackowiak RS (1991) Regional cerebral blood flow during voluntary arm and hand movements in human subjects. J Neurophysiol 65:1392–1401
- Cooperau LA, Shepard RN (1973) The time required to prepare for a rotated stimulus. Mem Cogn 1:246–250
- Coren S, Porac C (1977) Fifty centuries of right-handedness: the historical record. Science 198:631–632
- Crajé C, van der Kamp J, Steenbergen B (2009) Visual information for action planning in left and right congenital hemiparesis. Brain Res 1261:54–64
- Dragovic M (2004) Categorization and validation of handedness using latent class analysis. Acta Neuropsychiatrica 16:212–218
- Elliott D, Chua R (1996) Manual asymmetries in goal-directed movements. In: Elliott D, Roy EA (eds) Manual asymmetries in motor performance. CRC, Boca Raton, pp 143–158
- Elliott D, Lyons J, Chua R, Goodman D, Carson RG (1995) The influence of target perturbation on manual aiming asymmetries in right-handers. Cortex 31:685–697
- Evarts EV (1966) Pyramidal tract activity associated with a conditioned hand movement in the monkey. J Neurophysiol 29:1011–1027
- Fischer SC, Pellegrino JW (1988) Hemisphere differences for components of mental rotation. Brain Cogn 7:1–15
- Fisk JD, Goodale MA (1985) The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. Exp Brain Res 60:159–178
- Flowers K (1975) Handedness and controlled movement. Br J Psychol 66:39–52
- Gazzaniga MS, Bogen JE, Sperry RW (1967) Dyspraxia following division of the cerebral commissures. Arch Neurol 16:606–612
- Goble DJ, Brown SH (2008) The biological and behavioral basis of upper limb asymmetries in sensorimotor performance. Neurosci Biobehav Rev 32:598–610
- Grafton ST, Woods RP, Mazziotta JC (1993) Within-arm somatotopy in human motor areas determined by positron emission tomography imaging of cerebral blood flow. Exp Brain Res 95:172–176
- Haaland KY, Harrington DL (1996) Hemispheric asymmetry of movement. Curr Opin Neurobiol 6:796–800
- Haaxma R, Kuypers HG (1975) Intrahemispheric cortical connexions and visual guidance of hand and finger movements in the rhesus monkey. Brain 98:239–260
- Hausmann M, Kirk IJ, Corballis MC (2004) Influence of task complexity on manual asymmetries. Cortex 40:103–110
- Herbort O, Butz MV (2010) Planning and control of hand orientation in grasping movements. Exp Brain Res 202:867–878
- Hermsdorfer J, Laimgruber K, Kerkhoff G, Mai N, Goldenberg G (1999) Effects of unilateral brain damage on grip selection, coordination, and kinematics of ipsilesional prehension. Exp Brain Res 128:41–51
- Hughes CML, Franz EA (2008) Goal-related planning constraints in bimanual grasping and placing of objects. Exp Brain Res 188:541–550
- Hughes CML, Haddad JM, Franz EA, Zelaznik HN, Ryu JH (2011a) Physically coupling two objects in a bimanual task alters

kinematics but not end-state comfort. Exp Brain Res 211: 219-229

- Hughes CML, Reißig P, Seegelke C (2011b) Motor planning and execution in left- and right-handed individuals during a bimanual grasping and placing task. Acta Psychol. doi:10.1016/j.actpsy. 2011.05.013
- Janssen L, Beuting M, Meulenbroek R, Steenbergen B (2009) Combined effects of planning and execution constraints on bimanual task performance. Exp Brain Res 192:61–73
- Janssen L, Meulenbroek RGJ, Steenbergen B (2011) Behavioral evidence for left-hemisphere specialization of motor planning. Exp Brain Res 209:65–72
- Johnson-Frey S, McCarty M, Keen R (2004) Reaching beyond spatial perception: effects of intended future actions on visually guided prehension. Vis Cogn 11:371–399
- Kim SG, Ashe J, Hendrich K, Ellermann JM, Merkle H, Uğurbil K, Georgopoulos AP (1993) Functional magnetic resonance imaging of motor cortex: hemispheric asymmetry and handedness. Science 261:615–617
- Lawrence DG, Kuypers HG (1968a) The functional organization of the motor system in the monkey. I. The effects of bilateral pyramidal lesions. Brain 91:1–14
- Lawrence DG, Kuypers HG (1968b) The functional organization of the motor system in the monkey. II. The effects of lesions of the descending brain-stem pathways. Brain 91:15–36
- Mason AH, Bryden PJ (2007) Coordination and concurrency in bimanual rotation tasks when moving away from and toward the body. Exp Brain Res 183:541–556
- Mieschke PE, Elliott D, Helsen WF, Carson RG, Coull JA (2001) Manual asymmetries in the preparation and control of goaldirected movements. Brain Cogn 45:129–140
- Mutsaarts M, Steenbergen B, Bekkering H (2005) Anticipatory planning of movement sequences in hemiparetic cerebral palsy. Mot Control 9:439–458
- Mutsaarts M, Steenbergen B, Bekkering H (2007) Impaired motor imagery in right hemiparetic cerebral palsy. Neuropsychologia 45:853–859
- Nirkko AC, Ozdoba C, Redmond SM, Bürki M, Schroth G, Hess CW, Wiesendanger M (2001) Different ipsilateral representations for distal and proximal movements in the sensorimotor cortex: activation and deactivation patterns. NeuroImage 13:825–835
- Peters M (1976) Prolonged practice of a simple motor task by preferred and nonpreffered hands. Percept Mot Skills 42:447–450

- Peters M, Durding B (1979) Left-handers and right-handers compared on a motor task. J Mot Behav 11:103–111
- Rosenbaum DA, Jorgensen MJ (1992) Planning macroscopic aspects of manual control. Hum Mov Sci 11:61–69
- Rosenbaum DA, Marchack F, Barnes HJ, Vaughan J, Slotta JD, Jorgensen MJ (1990) Constraints for action selection: overhand versus underhand grips. In: Jeannerod M (ed) Attention and performance XIII. Erlbaum, Hillsdale, pp 321–342
- Rosenbaum DA, Vaughan J, Jorgensen MJ, Barnes HJ, Stewart E (1993) Plans for object manipulation. In: Meyer DE, Kornblum S (eds) Attention and performance XIV (silver jubilee volume): synergies in experimental psychology artificial intelligence and cognitive neuroscience. MIT Press, Cambridge, pp 803–820
- Roy EA, Elliott D (1989) Manual asymmetries in aimed movements. Quart J Exp Psychol Sect A Hum Exp Psychol 41:501–516
- Roy EA, Kalbfleisch L, Elliott D (1994) Kinematic analyses of manual asymmetries in visual aiming movements. Brain Cogn 24:289–295
- Roy EA, Winchester T, Elliott D, Canahan H (1995) Manual asymmetries in visual aiming movements: the effect of spatial variability. J Inter Neuropsychol Soc 1:133
- Shepard RN, Cooper LA (1982) Mental images and their transformations. MIT Press, Cambridge
- Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects. Science 171:701–703
- Steenbergen B, Meulenbroek RGJ, Rosenbaum DA (2004) Constraints on grip selection in hemiparetic cerebral palsy: effects of lesional side, end-point accuracy, and context. Cogn Brain Res 19:145–159
- Todor JI, Cisneros J (1985) Accommodation to increased accuracy demands by the right and left hands. J Mot Behav 17:355–372
- Todor JI, Kyprie PM (1980) Hand differences in the rate and variability of rapid tapping. J Mot Behav 12:57–62
- Todor JI, Kyprie PM, Price HL (1982) Lateral asymmetries in arm, wrist and finger movements. Cortex 18:515–523
- Weigelt M, Kunde W, Prinz W (2006) End-state comfort in bimanual object manipulation. Exp Psychol 53:143–148
- Woltring HJ (1986) A Fortran package for generalized, crossvalidatory spline smoothing and differentiation. Adv Eng Softw Workst 8:104–113
- Woodworth RS (1899) The accuracy of voluntary movement. Psychol Rev 3:1–119