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Motor planning and execution in left- and right-handed individuals during a bimanual grasping and placing task

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ABSTRACT

The issue of handedness has been the topic of great interest for researchers in a number of scientific domains. It is typically observed that the dominant hand yields numerous behavioral advantages over the non-dominant hand during unimanual tasks, which provides evidence of hemispheric specialization. In contrast to advantages for the dominant hand during motor execution, recent research has demonstrated that the right hand has advantages during motor planning (regardless of handedness), indicating that motor planning is a specialized function of the left hemisphere. In the present study we explored hemispheric advantages in motor planning and execution in left- and right-handed individuals during a bimanual grasping and placing task. Replicating previous findings, both motor planning and execution was influenced by object end-orientation congruency. In addition, although motor planning (i.e., end-state comfort) was not influenced by hand or handedness, motor execution differed between left and right hand, with shorter object transport times observed for the left hand, regardless of handedness. These results demonstrate that the hemispheric advantages often observed in unimanual tasks do not extend to discrete bimanual tasks. We propose that the differences in object transport time between the two hands arise from overt shifting visual fixation between the two hands/objects.

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1. Introduction

In the past forty years motor control research has provided illuminating insights into the constraints that underlie bimanual coordination (Franz, Zelaznik, & McCabe, 1991; Kelso, Southard, & Goodman, 1979). In general, during tasks in which the hands perform identical movements, the actions are performed with ease and accuracy. However, when the hands are required to produce different movements, each hand tends to take on some of the spatial characteristics of the other hand (Franz, 1997; Franz et al., 1991). For example, when participants draw circles with one hand and lines with the other hand, the spatial patterns of each limb assimilate such that the trajectory of the circles become more line-like, and the lines become more circle-like (Franz et al., 1991).

In recent years, several researchers have examined whether this spatial coupling can be observed on a macroscopic level; specifically in the grasp postures people adopt in order to manipulate objects (Fischman, Stodden, & Lehman, 2003; Hughes & Franz, 2008; Hughes, Haddad, Franz, Zelaznik & Ryu, 2011; Janssen, Beuting, Meulenbroek, & Steenbergen, 2009; Janssen, Craje, Weigelt, & Steenbergen, 2010; Janssen, Meulenbroek, & Steenbergen, 2011; van der Wel & Rosenbaum, 2010; Weigelt, Kunde, & Prinz, 2006). These efforts were motivated by the seminal experiments of Rosenbaum and colleagues (Rosenbaum et al., 1990; Rosenbaum & Jorgensen, 1992), who demonstrated that people grasp objects in an awkward fashion to ensure comfortable hand postures at the end of the movement. This sensitivity toward comfortable end-postures is termed the “end-state comfort effect” and implies that the motor system anticipates future body states and plans final grasp postures prior to movement execution.

Although the end-state comfort effect appears to be a predominant motor planning constraint during unimanual movements (see Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006 for a review), during bimanual movements the sensitivity toward end-state comfort is influenced by the spatial coupling tendency. Thus, the two constraints (bimanual spatial coupling and end-state comfort) often compete with one another. In general, when the objects are placed to identical end-orientations, participants adopt identical initial grips that also allow them to satisfy end-state comfort. However, when the objects are placed to non-identical end-orientations, the sensitivity toward comfortable end-postures interferes with the tendency to adopt identical initial grips, and neither end-state comfort nor bimanual coupling emerges as a dominant planning constraint (Hughes et al., 2011; Hughes & Franz, 2008).

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In addition to influences of object end-orientation on motor planning, there is a suggestion that motor planning is influenced by hand and handedness (Janssen et al., 2009; 2011). In their 2009 study, Janssen et al. (2009) asked right-handed individuals to simultaneously grasp two CD casings (one with each hand) and place them into a vertical or horizontal slot on a CD rack. They found that the tendency to avoid uncomfortable end-postures was higher and more variable for the right hand (82.0%) than for the left hand (49.8%). Closer inspection of the data revealed that these differences were strongly influenced by object end-orientation (horizontal versus vertical), such that the tendency to avoid uncomfortable end-postures was higher when the CD was to be placed in a vertical end-orientation (80.8%), than in a horizontal end-orientation (61.9%). In a later study Janssen et al. (2011) asked left-handed individuals to perform the same CD placing task. As in their previous study (Janssen et al., 2009) they found that end-state comfort was more pronounced for the right hand, compared to the left hand, especially during movements to horizontal end-orientations. Based on the results of their two studies, Janssen et al. (2011) concluded that motor planning is a specialized function of the left hemisphere, irrespective of handedness.

Manual asymmetries between the dominant and non-dominant hand have also been observed on the level of motor execution. For example, the dominant right arm of right-handed individuals can generate forces that are approximately 10% stronger than the non-dominant left hand (Brouwer, Sale, & Nordstrom, 2001; Farthing, Chilibeck, & Binsted, 2005; Provins, 1967), is faster to place pegs into target holes during tasks with high precision demands (Annett, Annett, Hudson, & Turner, 1979; Boulinguez, Nougier, & Velay, 2001; Carnahan, 1998; Todor & Kyprie, 1980; Woodworth, 1899), is less variable (Elliott, Weeks, & Jones, 1986; Peters, 1976; Todor & Kyprie, 1980), and is more adept at controlling joint torques (Sainburg, 2002; Sainburg & Kalakanis, 2000) than the non-dominant left arm.

One explanation for the superiority of the right hand during goal-directed movements, is that the non-dominant and dominant hands differ in their ability to utilize visual feedback (Flowers, 1975; Honda, 1982; Todor & Cisneros, 1985). In his seminal experiment, Flowers (1975) compared arm performance in both left- and right-handed individuals during a visual aiming task and a finger tapping task. He found that performance was better for the dominant, compared to the non-dominant hand (irrespective of handedness) during the visual aiming, but not the finger tapping task. Flowers argued that the primary difference between the two tasks is the availability of proprioceptive and visual feedback, and concluded that handedness based differences arise from the length of time required for information to go through the sensorimotor feedback loop. Later research suggested that the right-hand advantage might arise from differences in visual monitoring throughout the task (Honda, 1982). For example, Honda (1982) examined eye–hand coordination patterns when participants performed bimanual aiming movements to symmetrical targets. The performance of the dominant right hand was highly influenced by visual monitoring, such that the right-hand advantage was only observed when the movements of the right hand were visually monitored. In contrast, movement times for the non-dominant left hand were not affected by visual monitoring. From these results, Honda concluded that the superior performance of the dominant hand arises because of preferential monitoring of the right hand during task execution. Although there have been other explanations for the right-hand advantage (Grouios, 2006), the differences in motor execution between the left and right hand are typically taken as evidence of hemisphere-specific functions. However, in contrast to the left-hemisphere-dominance motion-planning hypothesis of Janssen et al. (2009, 2011), the advantages in motor execution are attributed to the hemisphere contralateral to the dominant hand.

The purpose of this study was to examine if manual asymmetries during a bimanual grasping and placing task are evident during both motor planning and motor execution. Furthermore, because most of the research in the area of manual asymmetries has been conducted on right-handed individuals only, the second purpose of this study was to investigate motor planning and execution processes in both left-handed and right-handed individuals. In the present study, participants were required to grasp two objects from a table and place them onto a board to targets that required identical (congruent object end-orientations) or non-identical degrees of rotation (incongruent object end-orientations). First, based on the left-hemisphere-dominance motion-planning hypothesis (Janssen et al., 2009, 2011), we expected that the tendency to avoid initial awkward grasp postures (i.e., end-state comfort) should be more pronounced for the right hand, compared to the left hand. Furthermore, if motor planning was a specialized function of the left hemisphere then the tendency to satisfy end-state comfort should be higher for the right hand regardless of whether individuals are left- or right-handed. Second, given the wealth of literature suggesting that motor execution is a specialized function of the hemisphere contralateral to the dominant hand, it was hypothesized that right-handed individuals would demonstrate shorter object transport times, and lower endpoint errors for the dominant right hand, compared to the non-dominant left hand. Moreover, if left-hander's are the behavioral inverse of right-hander's (see Perelle & Ehrman, 2005) then we would expect the dominant left hand to yield shorter object transport times and lower endpoint errors than the non-dominant right hand.

2. Methods

2.1. Ratings of perceived comfort

2.1.1. Participants

In order to quantify the initial grasp postures (overhand vs. underhand) that would result in comfortable end-states we obtained perceived ratings of comfort ($n = 19$, mean age = 23.45, SD = 3.04, 6 men and 13 women). Participants reported normal or corrected to normal vision, and did not have any known neuromuscular disorders. The experiments were in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

2.1.2. Apparatus

Participants stood in front of a custom built placement board (2 m × 0.4 m) that was braced by two legs (Fig. 1a and b). The placing board was adjusted to shoulder height, and the center of the board was oriented so that it coincided with the midline of the participant. On each side of the board were four white target circles (10 cm in diameter), which required that the objects be rotated either 0°, 90° internally, 180°, or 90° externally.[1] The manipulated objects were two square wooden objects (17.8 cm × 17.8 cm × 3.8 cm) that had a 3.8 cm square protruding from one of the sides. The objects had a handle affixed to the center of the main body that allowed participants to either use an underhand or overhand grip. The objects were placed on a small table (50 cm × 15 cm × 5 cm), and positioned so that the protrusion always faced upwards.

2.1.3. Procedure

At the beginning of each trial the participant stood in front of the fitting board with the hands by their sides. The experimenter informed the participant what hand and grip to use and how to orient the object on the fitting board. The participant then grasped the object and moved it to the instructed end-orientation, and rated the

[1] Viewed from the participant's perspective, these were: 12 o'clock for both hands, 3 o'clock for the left hand and 9 o'clock for the right hand, 6 o'clock for both hands, and 9 o'clock for the left hand and 3 o'clock for the right hand.

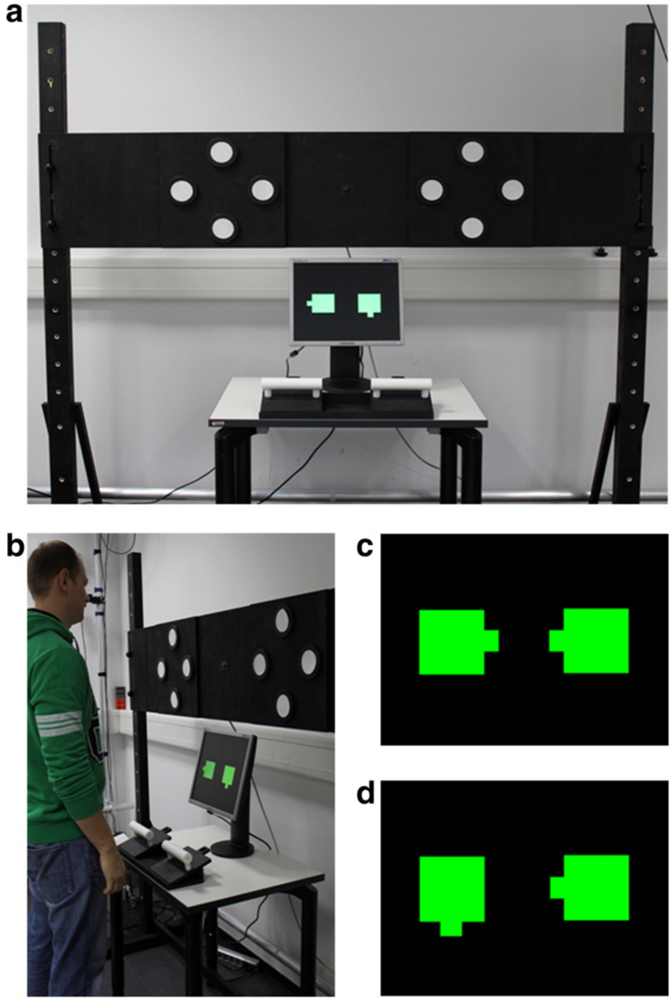

Fig. 1. a) Front view of the experimental set-up. On each side of the placement board were four white target circles (10 cm in diameter) that required the objects to be rotated either 0° (12 o'clock), 90° internally (3 o'clock for the left hand and 9 o'clock for the right hand), 180° (6 o'clock for both hands), or 90° externally (9 o'clock for the left hand and 3 o'clock for the right hand). b) Side view of the experimental set-up. At the start of each trial the objects were placed on a rack at a 45° incline. A white handle was placed on the middle of the object and participants could use either an overhand or underhand posture to grasp the object. c) Illustration of the stimuli during congruent object end-orientation trials. d) Illustration of the stimuli during incongruent object end-orientation trials.

comfort of the end-posture, with 1 being very uncomfortable and 5 being very comfortable. Following each response, the participant placed the object back to the start position and waited 30 s for the next trial to begin. The participant performed four object placements in each condition, yielding a total of 32 trials. The entire session lasted approximately 30 min and was recorded on videotape (Sony DCR-HC36) with prior consent of the participant. The ratings of perceived comfort data obtained from the video were recorded and analyzed offline.

2.1.4. Statistical analysis

Ratings of perceived comfort were analyzed using a RM ANOVA on the factors object end-orientation (0° rotation, 90° internal rotation, 180° rotation, 90° external rotation), initial grip posture (overhand, underhand), and hand (left, right). The magnitude difference in the mean comfort ratings for the overhand and underhand grip at each object end-orientation was also calculated using a RM ANOVA on the factors object end-orientation (0° rotation, 90° internal rotation, 180° rotation, 90° external rotation) and hand (left, right). For each object end-orientation, the mean comfort rating of the underhand grip was subtracted from the mean comfort rating of the overhand grip, and the absolute difference was calculated. Values closer to zero indicate that the comfort ratings for the overhand and underhand grip were more similar, whereas larger values indicate that participants preferred one grasp posture over the other.

2.2. Grasping and placing task

2.2.1. Participants

Ten left-handed (mean age = 23.30, SD = 3.62, 5 males and 5 females) and ten right-handed (mean age = 29.00, SD = 4.76, 8 men and 2 women) individuals participated in the grasping and placing task. Handedness was assessed using the Revised Edinburgh Handedness Inventory (Dragovic, 2004), which ranks handedness on a scale ranging from −1.00 (strongly left-handed) to 1.00 (strongly right-handed). Based on hand preferences from a battery of common tasks, handedness scores for the left-handed participants ranged from −0.45 to −1.00 with a mean of −0.76 (SD = 0.19). Handedness scores for the right-handed participants ranged from 0.66 to 1.00 with a mean of 0.94 (SD = 0.14). Participants did not take part in the ratings of perceived comfort experiment, had normal or corrected to normal vision, and did not have any known neuromuscular disorders. The experiments were in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

2.2.2. Apparatus and procedure

The apparatus was identical to that used in the ratings of perceived comfort experiment with the following changes. The stimuli were displayed on a computer monitor located 40 cm behind the object start location. The stimuli consisted of 2D images of the objects, which indicated the end-orientations of the objects for each hand (Fig. 1c and d).

Participants were instructed to lift the objects from the table and align them on the placement board so that the protrusion of each object was placed over the appropriate white target circle, as indicated by the stimuli. They were informed to grasp the left object with the left hand and place it to the left side of the board, and the right object with the right hand and place it to the right side of the board. However, no explicit instructions were given concerning how the hands should be coupled. Participants were told that final object end-orientation accuracy was of utmost importance, but were also instructed to perform the task as quickly as possible.

At the beginning of each trial, the participant placed both hands by their sides. One thousand milliseconds later, the word 'Achtung' was displayed on the computer monitor. After a random interval (ranging from 1500 to 2500 ms) an image demonstrating how the objects should be oriented on the placement board was displayed in green, signaling the beginning of the trial. The participant then grasped and moved the objects to the instructed end-orientations on the placement board and waited approximately 2 s for the verbal command informing them that they could place the objects back to the start position. The order of end-orientation was randomized. Participants performed five trials in each of the 16 conditions, yielding a total of 80 trials. The entire testing session lasted approximately 45 min.

Three-dimensional movement kinematics was recorded at 200 Hz using an optical motion capture system (VICON Motion System, Oxford, UK), consisting of ten Bonita cameras. Three reflective markers were placed on each object to obtain object motion, and a cluster of three markers was placed on the wrist of each hand to collect wrist motion. Four additional markers were situated on the placement board in order to calculate the final end-orientation error (measured in degrees) for each object. Each trial was recorded using a Sony DCR-HC36 digital video camera (synchronized with the VICON motion capture system) that was placed above the apparatus, providing a bird's eye view of the apparatus and the participant. The digital video camera was used to record initial grasp postures.

2.2.3. Data and statistical analysis

Trials in which the object was placed to the incorrect object end-orientation were counted as errors and not included in the analysis. The total number of rejected trials due to errors was less than 1% of the data, and was equally distributed across conditions and participants.

2.2.4. Grasp behavior

Initial grasp postures that satisfied end-state comfort were based on the ratings of perceived comfort (see Results section) and coded from the video data obtained during the experimental session. Differences in end-state comfort satisfaction were analyzed using Chi-square tests of independence on the factors handedness (left-handed, right-handed), hand (non-dominant, dominant), and object end-orientation (0° rotation, 90° internal rotation, 180° rotation, 90° external rotation).

We also examined differences in initial grip behavior as a function of object end-orientation congruency, handedness, and constraint satisfaction. During congruent object end-orientation trials, the objects required the same degree of rotation, and were mirror symmetric, or identical with respect to global coordinates (independent of body position) .[2] In contrast, during incongruent object end-orientation trials, the end-orientations of the objects required different degrees of rotation. In addition, the 16 possible conditions were separated into two categories. The first category included the conditions where it was possible for the hands to 1) satisfy end-state comfort for one hand, 2) adopt identical initial grasp postures, or 3) adopt identical initial grasp postures and still satisfy end-state comfort. The second category included the conditions where it was only possible to 1) adopt identical initial grasp postures or 2) satisfy end-state comfort for both hands. Within each of the categories, the main behavioral variable of interest was the proportion of trials where participants adopted identical initial grasp postures and/or satisfied end-state comfort.

We also examined whether participants changed their initial grasp posture behavior (i.e. overhand or underhand) across the five trial repetitions. For each specific object end-orientation, we calculated the number of trials (out of five) that satisfied end-state comfort. To assess differences in trial consistency, a RM ANOVA was conducted on the factors handedness, hand, and object end-orientation congruency.

2.2.5. Kinematics

The 3D coordinates of the retro-reflective markers placed on the objects were reconstructed and missing data (those with fewer than 10 frames) were interpolated using a cubic spline. No trial included any gaps greater than this. All kinematic variables were calculated using custom written MatLab programs (Mathworks, Version 7.0). The marker coordinates were low-pass filtered at a 5 Hz cut-off, using a second order Butterworth filter. For each trial, only the time period from movement onset (time the object was grasped) to movement offset (time the object contacted the board) was further analyzed. Movement onset was determined as the time of the sample in which the resultant velocity of the object exceeded 3% of peak velocity, whereas movement offset was determined as the time of the sample in which the resultant velocity dropped and stayed below 3% of peak velocity. Thus, object transport time was defined as the time period between movement onset and movement offset. All data were time normalized to 100 data points and detrended prior to calculation of interlimb coupling variables.

To investigate interlimb coupling at the start and end of the movement, the absolute onset and offset difference was calculated. Absolute onset was determined by subtracting the movement onset of the left object from the movement onset of the right object. Absolute offset was determined by subtracting the time of left-hand contact from the time of right-hand contact on the placement board. For both absolute onset and offset, the absolute difference for each trial was calculated, and these individual trials were then averaged to provide a mean value for each condition. Interlimb coupling throughout the placing portion of the task was calculated by dividing the velocity time series into an accelerative (period between movement onset and peak velocity) and decelerative phase (period from peak velocity to movement offset). The root-mean-squared (RMS) difference was then calculated between the hands over the accelerative and decelerative portions of the movement.

Potential differences in object end-orientation error and object transport time were examined using separate 2 handedness × 2 hand × 4 object end-orientation mixed-effects ANOVAs. To examine whether object end-orientation error and object transport times were influenced by object end-orientation congruency, separate mixed effects ANOVAs were conducted on the factors handedness, hand, and object end-orientation congruency.

Interlimb coupling was examined using separate mixed-effects ANOVA's on the variables absolute onset, absolute offset, RMS difference of the accelerative portion of the velocity profile, and RMS difference of the decelerative portion of the velocity profile, using handedness as the between-subjects factor, and object end-orientation congruency (congruent, incongruent) as the within subjects factor.

3. Results

3.1. Ratings of perceived comfort

Overall, initial underhand grasp postures (3.65, SE = 0.11) were rated as more comfortable than initial overhand grasp postures (3.61, SE = 0.09), $F(1,19) = 11.64$, $p = 0.003$, $\eta^2_p = 0.39$, $1\text{-}\beta = 0.90$. A significant main effect of object end-orientation was also observed, $F(3,54) = 6.75$, $p = 0.001$, $\eta^2_p = 0.27$, $1\text{-}\beta = 0.97$. Bonferroni corrected post-hoc analyses revealed significant differences between mean comfort ratings between movements that required 0° rotation (3.99, SE = 0.15) and 90° external rotation (3.28, SE = 0.15), $p = 0.019$. No other comparisons reached significance.

A significant interaction between initial grasp posture and object end-orientation was observed, $F(3,54) = 41.89$, $p < 0.001$, $\eta^2_p = 0.70$, $1\text{-}\beta = 1.0$. Post-hoc pair wise comparisons (Bonferroni corrected) revealed that mean comfort ratings were higher for the overhand grip compared to the underhand grip when no rotation [$t(18) = 4.80$, $p < 0.001$] and 90° external rotation [$t(18) = 7.64$, $p < 0.001$] was required. In contrast, when the movement required either 90° internal rotation or 180° rotation, participants rated underhand grips more comfortable than overhand grips [$t(18) = -3.80$, $p < 0.001$ and $t(18) = -6.24$, $p < 0.001$, respectively]. Based on these results, end-state comfort was defined by the adoption of initial overhand grasp postures during movements that required either 0° rotation or 90° external rotation. In contrast, when the object required either 90° internal rotation or 180° rotation, end-state comfort was defined by the adoption of initial underhand grasp postures.

We examined the magnitude difference in the mean comfort ratings for the overhand and underhand grip at each object end-orientation. A significant effect of object end-orientation was observed, $F(3,51) = 37.472$, $p < 0.001$. Larger values were observed for movements that required 90° internal rotation (mean difference = 1.55) and 90° external rotation (mean difference = 2.23), compared to movements that required 0° rotation (mean difference = 0.74) or 180° rotation (mean difference = 0.74). These results

[2] Analysis revealed no significant differences between egocentric and allocentric congruency, ($\chi^2_{(1)} = 0.024$, $p = 0.878$), thus the data were collapsed across congruency.

indicate that when the object required either 0° or 180° rotation the comfort ratings for the overhand and underhand grasp were similar. However, when the object required either 90° internal and external rotation, participants showed a clear preference for one grasp posture over the other.

3.2. Grasping and placing task

3.2.1. Grasp behavior

Chi-square tests revealed no differences in initial grasp postures between left- and right-handed individuals ($\chi^2_{(3)} = 0.07$, $p < 0.995$). When the data were specifically analyzed to examine differences in hand irrespective of handedness, initial grasp postures were similar for the non-dominant and dominant hand for both left-handed ($\chi^2_{(3)} = 1.60$, $p < 0.660$) and right-handed individuals ($\chi^2_{(3)} = 0.96$, $p < 0.992$). Because there were no differences in initial grasp postures based on hand and handedness, the data were collapsed to examine differences based on object end-orientation. During trials in which the object did not require rotation (0° rotation) participants adopted initial postures that satisfied end-state comfort in 85% of total trials. This pattern of results was similar to conditions requiring 90° internal and 90° external rotation, with participants adopting uncomfortable initial postures in 92% and 89% of total trials, respectively. In contrast, when the object was to be rotated 180°, end-state comfort satisfaction was much lower, with participants adopting initially uncomfortable postures in only 58% of the trials. One-dimensional chi square analysis confirmed that this tendency was statistically significant, $\chi^2(3) = 9.012$, $p = 0.029$.

We also examined differences in initial grip behavior as a function of object end-orientation congruency, handedness, and constraint satisfaction. During trials where both constraints could be satisfied, chi square analysis revealed significant differences in grip behavior as a function of object end-orientation congruency (congruent/incongruent), constraint satisfaction (end-state comfort for one hand only/identical initial grips/both end-state comfort), and handedness (left-handers/right-handers), $\chi^2_{(6)} = 74.7$, $p < 0.001$. We also observed significant differences when the data were analyzed with respect to object end-orientation congruency, regardless of handedness, (left-handers: $\chi^2_{(2)} = 43.5$, $p < 0.001$, right-handers: $\chi^2_{(2)} = 30.8$, $p < 0.001$). As seen in Fig. 2, participants adopted identical initial grasp postures that satisfied end-state comfort during movements to congruent object end-orientations. In contrast, when the objects were placed to incongruent object end-orientations, participants did not appear to favor a particular grip strategy. In addition, grip strategy was not influenced by handedness (congruent object end-orientations: $\chi^2_{(2)} = 1.71$, $p < 0.424$, incongruent object end-orientations: $\chi^2_{(2)} = 1.65$, $p < 0.438$).

During trials where initial grip postures could satisfy either bimanual coupling (as indicated by identical initial grips) or end-state comfort, we observed significant differences in grip behavior for both left- and right-handed participants as a function of object end-orientation congruency (respectively, $\chi^2_{(1)} = 42.3$, $p < 0.001$ and $\chi^2_{(1)} = 32.9$, $p < 0.001$). For both groups, when the objects were placed at congruent object end-orientations participants preferred to satisfy end-state comfort for both hands, rather than adopt identical initial grips, $\chi^2_{(1)} = 3.53$, $p < 0.060$. However, when the objects were placed to incongruent object end-orientations, participants did not appear to favor a particular constraint, $\chi^2_{(1)} = .504$, $p < 0.478$ (Fig. 3).

Analysis revealed that initial grasp posture consistency was similar regardless of hand [$F(1,19) = 0.50$, $p = 0.49$, $\eta^2_p = 0.50$, $1\text{-}\beta = 0.1$], and handedness [$F(1,18) = 0.24$, $p = 0.63$, $\eta^2_p = 0.01$, $1\text{-}\beta = 0.08$]. However, initial grasp posture consistency was influenced by object end-orientation congruency, $F(1,18) = 52.56$, $p < 0.001$, $\eta^2_p = 0.75$, $1\text{-}\beta = 1.0$. Specifically, initial grasp postures were more consistent for movements to congruent object end-orientations (mean congruency = 4.4/5.0), than for movements to incongruent object end-orientations (mean congruency = 3.6/5.0).

3.2.2. Kinematics

In general, object end-orientation error was very low (mean end-orientation error = 1.9°, SD = 2.09°), and not influenced by handedness [$F(1,18) = 0.78$, $p = 0.39$, $\eta^2_p = 0.04$, $1\text{-}\beta = 0.13$], hand [$F(1,18) = 0.48$, $p = 0.50$, $\eta^2_p = 0.026$, $1\text{-}\beta = 0.10$], or object end-orientation [$F(3,54) = 2.20$, $p = 0.10$, $\eta^2_p = 0.11$, $1\text{-}\beta = 0.53$].

Object transport times were similar for the non-dominant and dominant hand [$F(1,18) = 0.23$, $p = 0.64$, $\eta^2_p = 0.01$, $1\text{-}\beta = 0.74$], and for left- and right-handed individuals [$F(1,18) = 0.60$, $p = 0.45$, $\eta^2_p = 0.32$, $1\text{-}\beta = 0.11$]. In addition, a significant main effect of object end-orientation was observed, $F(3,54) = 6.18$, $p < 0.001$, $\eta^2_p = 0.26$, $1\text{-}\beta = 0.95$. Post-hoc analysis (Bonferroni adjusted) revealed significant differences in object transport time between 0° rotation (908 ms, SE = 40) and 180° rotation (947 ms, SE = 43) conditions [$p = 0.016$], between 90° internal rotation (880 ms, SE = 41) and 180° rotation (947 ms, SD = 43) conditions ($p = 0.008$), and between 90° internal rotation (880 ms, SE = 41) and 90° external rotation (925 ms, SE = 36) conditions ($p = 0.025$). A hand × handedness interaction was also observed, $F(1,18) = 10.95$, $p < 0.01$, $\eta^2_p = 0.38$, $1\text{-}\beta = 0.88$. For left-handed individuals, object transport time values were shorter for the dominant (901 ms, SE = 64) compared to the non-dominant (989 ms, SE = 54) hand. In contrast, object transport time values were

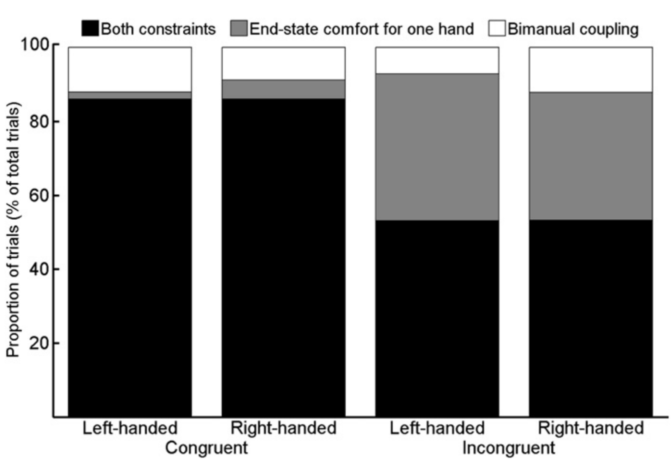

Fig. 2. Summary of conditions in which initial grips could satisfy end-state comfort for one hand, adopt identical initial postures, or adopt identical initial postures and end-state comfort for both hands.

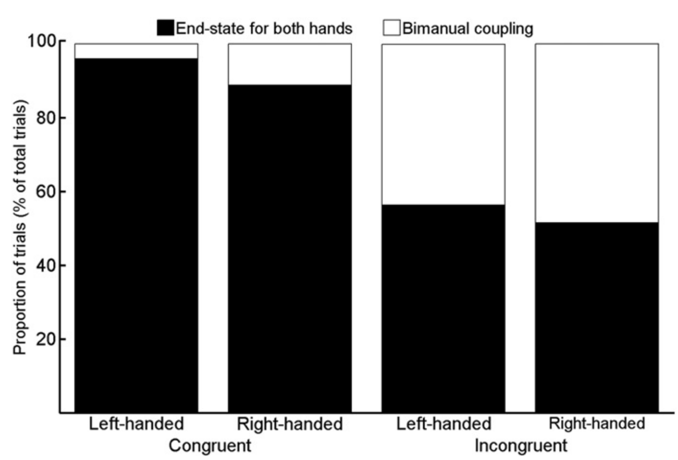

Fig. 3. Summary of conditions in which initial grips could satisfy end-state comfort for both hands or adopt identical initial postures.

shorter for the non-dominant hand (means: non-dominant hand = 825 ms, SE = 54, dominant hand = 944 ms, SE = 64) for right-handed individuals.

When the data were analyzed to examine whether object end-orientation error and object transport times were influenced by object end-orientation congruency, we did not observe differences in object end-orientation error as a function of object end-orientation congruency (congruent = 2.04°, SE = 0.19; incongruent = 1.96°, SE = 0.13) [$F(1,18) = 3.16$, $p = 0.58$, $\eta^2_p = 0.02$, 1-$\beta = 0.08$], indicating that responses were very accurate, $p > 0.05$. Mean object transport time values for movements to congruent end-orientations (867 ms, SE = 43) were, on average, shorter than movements to incongruent end-orientations (944 ms, SE = 38), $F(1,18) = 12.97$, $p < 0.01$, $\eta^2_p = 0.42$, 1-$\beta = 0.93$. However, object transport time values did not differ between the non-dominant (898 ms, SE = 39) and dominant hand (913, SE = 45) [$F(1,18) = 0.24$, $p = 0.63$, $\eta^2_p = 0.013$, 1-$\beta = 0.08$], and left-handed (933 ms, SE = 55) and right-handed (877 ms, SE = 55) individuals, $F(1,18) = 0.51$, $p = 0.48$, $\eta^2_p = 0.03$, 1-$\beta = 0.10$.

The data were also analyzed to examine differences in interlimb coupling as a function of object end-orientation congruency. Mean interlimb coupling values as a function of hand, handedness, and object end-orientation congruency are displayed in Table 1. Analysis revealed that absolute differences were similar for left- and right-handed participants at the start (left-handers = 141 ms, SE = 26; right-handers = 96 ms, SE = 26), [$F(1,18) = 1.36$, $p = 0.297$, $\eta^2_p = 0.07$, 1-$\beta = 0.20$], and end (left-handers = 330 ms, SE = 55; right-handers = 283 ms, SE = 55) of the movement [$F(1,18) = 0.081$, $p = 0.78$, $\eta^2_p = 0.004$, 1-$\beta = 0.06$]. Furthermore, absolute values were more similar during movements to congruent, compared to incongruent object end-orientations at both the start (congruent = 84 ms, SE = 11; incongruent = 141 ms, SE = 28), [$F(1,18) = 8.036$, $p < 0.05$, $\eta^2_p = 0.27$, 1-$\beta = 0.68$] and the end of the movement (congruent = 234 ms, SE = 30; incongruent = 352 ms, SE = 55), [$F(1,18) = 7.96$, $p < 0.01$, $\eta^2_p = 0.31$, 1-$\beta = 0.76$].

RMS difference values were similar for both left- and right-handed individuals during the accelerative [$F(1,18) = 0.04$, $p = 0.95$, $\eta^2_p < 0.001$, 1-$\beta = 0.05$], and decelerative portion of the movement [$F(1,18) = 2.77$, $p = 0.11$, $\eta^2_p = 0.13$, 1-$\beta = 0.35$]. Lastly, congruency effects were observed during the accelerative [$F(1,18) = 5.33$, $p = 0.33$, $\eta^2_p = 0.23$, 1-$\beta = 0.59$], and decelerative portion [$F(1,19) = 4.126$, $p = 0.05$, $\eta^2_p = 0.19$, 1-$\beta = 0.49$] of the movement, with greater interlimb coupling during movements to congruent, compared to incongruent object end-orientations. No other effects reached significance.

4. Discussion

In this study we examined motor planning and execution processes during a bimanual grasping and placing task, and sought to ascertain whether these processes are mediated by hand (non-dominant, dominant) and handedness (left-handed, right-handed). Based on the left-hemisphere-dominance motion-planning hypothesis, we expected that end-state comfort should be more pronounced for the right hand, compared to the left hand, regardless of whether individuals were left- or right-handed. Our results, however, do not confirm this hypothesis. In fact, in contrast to previous work by Janssen et al. (2009, 2011), we found that initial grasp postures were similar for both the non-dominant and dominant hand, regardless of whether the individuals were left- or right-handed. However, our findings replicate those of a recent study (Hughes et al., 2011) where we also failed to observe differences in initial grip behavior between the left and right hand in right-handed individuals using the same grasping and placing paradigm.

How can we reconcile the findings from these two laboratories? We have previously suggested (Hughes et al., 2011) that methodological differences may explain the divergent results obtained in the studies conducted by Janssen et al. (2009, 2011) and our group (Hughes et al., 2011, present study). That is, in the grasping and placing paradigm we employed, participants were required to place the objects on a fitting board, whereas in the studies of Janssen et al. (2009, 2011) participants placed a CD casing into a box. Thus, it could be argued that the CD placing task required a higher level of precision at the end of the movement than placing an object on a fitting board, and that the planning of initial grasp postures is influenced by the precision demands of the task. However, there is evidence from both the present study and previous research that suggests this might not be the case. First, in the present task, object end-orientation error was very low (mean object end-orientation error = 1.94°), and was similar across all conditions (e.g., object end-orientation congruency, hand) and handedness, indicating that participants were very accurate when placing the object on the fitting board. Second, hand-based differences in motor planning have not been reported in other studies that also employed high precision tasks (Weigelt et al., 2006). For example, Weigelt et al. (2006) had participants simultaneously reach for two bars (2 cm in diameter) and place the ends of the bars into a round target hole (2.5 cm). They found that participants almost always adopted initial grips that allowed them to end the movement in a comfortable grasp posture, regardless of hand. In fact, hand-based differences in grasp posture behavior have only been observed in the CD placing paradigm (Janssen et al., 2009; Janssen et al., 2011), and not for tasks that involved bar transport (Fischman et al., 2003; Weigelt et al., 2006), plunger transport (van der Wel & Rosenbaum, 2010), cylinder transport (Hughes & Franz, 2008), bar-and-spoon rotation (Janssen et al., 2010), or abstract objects (Hughes et al., 2011), regardless of the required level of precision. Even though this hypothesis requires further confirmation, it is plausible that the reduction in end-state comfort for the left hand observed by Janssen et al. (2009; 2011) is specific to their experimental task and paradigm.

In this study we also investigated whether hand and handedness-based differences would be present at the motor execution level. We found that interlimb coupling at the start, the end, and throughout the movement was similar, regardless of whether participants were left- or right-handed. However, we did observe shorter object transport times for the left, compared to the right hand, for both left-handed and right-handed participants. This finding is intriguing given that previous research has demonstrated that motor execution is a specialized function of the hemisphere contralateral to the dominant hand. However, if hemispheric specialization advantages had been apparent then we would have expected shorter object transport times for the dominant hand, regardless of handedness. Interestingly, although the bimanual coordination literature has revealed that the dominant hand leads the non-dominant hand (Amazeen, Amazeen, & Treffner, 1997; Franz, Rowse, & Ballantine, 2002; Semjen, Summers, & Cattaert, 1995) and performs the subtask that requires continuous

Table 1
Mean interlimb coupling and standard deviation (in parentheses) values for congruent and incongruent object end-orientation conditions in left- and right-handed individuals.

	Absolute onset	Absolute offset	RMS velocity difference (accelerative portion)	RMS velocity difference (decelerative portion)
Congruent				
Left-handers	111 (15)	245 (54)	74 (25)	80 (18)
Right-handers	115 (16)	222 (77)	80 (21)	75 (16)
Incongruent				
Left-handers	159 (76)	382 (160)	80 (37)	97 (19)
Right-handers	122 (21)	320 (179)	85 (21)	83 (11)

and precise adjustments of speed and force (Peters, 1990), these hand based differences are limited to continuous bimanual tasks. Studies involving discrete bimanual tasks (such as rapid aiming, reaching and grasping, and grasping and placing) have typically failed to reveal any hand based differences in movement execution (Bingham, Hughes, & Mon-Williams, 2008; Hughes et al., 2011; Jackson, German, & Peacock, 2002; Jackson, Jackson, & Kritikos, 1999; Mason & Bruyn, 2009; Neely, Binsted, & Heath, 2005; Riek, Tresilian, Mon-Williams, Coppard, & Carson, 2003). That previous studies have failed to observe manual asymmetries between the hands suggests that the hemispheric advantages in motor performance for the dominant hand often observed during unimanual and continuous bimanual tasks do not extend to discrete bimanual tasks (see Neely et al., 2005 for a similar argument).

We postulate that the differences in object transport times between the left and right hand arose because of the limitations of the human visual system — it is simply not possible to visually attend to more than one hand or object at a time, especially when the targets for the two hands are spatially separated (Bingham et al., 2008; Hesse, Nakagawa, & Deubel, 2010; Mason & Bruyn, 2009; Riek et al., 2003). In the present experiment, the objects were located within a single foveal span (spatial separation = 25 cm) at the start of the movement. However, the distance between the two targets at the end of the movement was much greater (80 cm). Thus, participants may have divided their attention between the left and right objects and hands to ensure successful and accurate placement of the two objects. Although we did not collect eye-tracking data in the present experiment, there is strong evidence that participants utilize a sequential gaze strategy during bimanual movements (Riek et al., 2003; Srinivasan & Martin, 2010). In general those studies reveal that participants first fixate on one target and correct any spatial end-point errors for the hand moving toward that target. Participants then shift fixation to the other target, and correct for any spatial error in the hand moving toward that target.

The hypothesis that participants divide visual attention between the left and right objects and hands is further supported by the interlimb coupling data, which revealed that the hands were more coupled at the start of the movement (absolute onset) compared to the end of the movement (absolute offset). Recent studies have demonstrated that the degree of interlimb coupling often decreases toward the end of the movement, especially when the spatial separation between the two targets is beyond a single foveal span (Bingham et al., 2008; Mason & Bruyn, 2009). For example, in the Bingham et al. (2008) study, participants reached to grasp two objects that were separated by a distance of 20, 30, or 40 cm. Bingham et al. (2008) found that the degree of bimanual coupling decreased as the spatial separation between the two targets increased. Mason and Bruyn (2009) observed similar results during a bimanual task in which participants reached for, grasped, and lifted two cylinders. Taken together, it appears that the shorter object transport times for the left hand, and the decrease in interlimb coupling at the end of the movement, result from costs associated with shifting visual fixation between the two hands/objects, and that these costs are present during all phases of the movement (e.g., both the reaching-to-acquire phase, and the grasp and place phase).

Although motor planning and execution were not influenced by handedness, both processes were mediated by end-orientation congruency. During movements to congruent object end-orientations, participants typically adopted identical initial grips that also satisfied end-state comfort. In comparison, when the objects were placed to incongruent object end-orientations, participants did not appear to favor a particular grip strategy. A similar pattern was observed during trials where initial grip postures could satisfy either bimanual coupling or end-state comfort. When the objects were placed at congruent object end-orientations, participants preferred to satisfy end-state comfort for both hands, rather than adopt identical initial grips. However, when the objects were placed to incongruent object end-orientations, participants did not appear to favor bimanual coupling or end-state comfort. Congruency effects were also observed during motor execution, such that the hands were more coupled during movements to congruent object end-orientations than to incongruent object end-orientations.

The influence of object end-orientation (or target) congruency on movement execution is well documented (Hughes & Franz, 2008; Kelso et al., 1979). These congruency effects are commonly attributed to neuronal cross-talk in efferent pathways (Franz, Eliassen, Ivry, & Gazzaniga, 1996), the selection of movement goals (Hazeltine, Diedrichsen, Kennerley, & Ivry, 2003), or during the specification of parameters specific to planning and execution of bimanual movements (Heuer, 1993). Although the present experiment does not allow us to determine the level at which this neuronal cross-talk occurs, the results of the present experiment clearly show that object end-orientation congruency influences both motor planning (initial grasp behavior) and motor execution (interlimb coupling) and that these congruency effects are present in both left- and right-handed individuals.

An interesting finding to emerge from the present study was that end-state comfort satisfaction was lower for movements that required 180° rotation (than for movements that required 0°, 90° internal, or 90° external rotation) indicating that the tendency toward end-state comfort is influenced by the required end-orientation of the object, and the required degree of rotation. We hypothesize that this decrease in end-state comfort might result from cognitive processes associated with mental rotation, and/or biomechanical constraints. Firstly, the ability to plan initial grasp postures might be influenced by cognitive processes required to mentally rotate the object prior to movement execution. This viewpoint is supported by previous studies that have examined cognitive demands involved with mental rotation. In one of the earliest experiments to investigate this phenomenon, Shepard and colleagues (Shepard & Cooper, 1982; Shepard & Metzler, 1971) asked participants whether two images were identical or mirror reflections of a rotated object. The authors found that response time increased in a linear fashion as the angular difference between two objects increased. This general finding has been replicated and extended using a number of experimental paradigms, including mental rotation of alphanumeric characters (Cooper & Shepard, 1973), and novel shapes, cubes and polygons (Cooper, 1975, 1976), and is interpreted as evidence that individuals mentally rotate an object through space along the same continuous trajectory, as if they were actually physically rotating it. Thus, the additional cognitive demands associated with larger rotation angles, might have lead to a reduction in the ability to prospectively plan initial grip postures, and thus end-state comfort satisfaction.

Alternatively, it is possible that our results have a biomechanical explanation. During movements that require 90° internal, or 90° external rotation, grips that do not satisfy end-state comfort place the limbs in extreme joint angles. In contrast, during movements that require 180° rotation, the joints remain within typical anatomical angles throughout the entire movement. That is to say, the cost difference between adopting underhand and overhand grasp postures should be larger when the rotation angle is smaller (90° internal, or 90° external rotation), compared to when the rotation angle is larger (180° rotation). This assumption is confirmed by the ratings of perceived comfort, where the difference in comfort between the overhand and underhand grasp postures was smaller for movements that required 180° rotation (mean comfort rating difference = 0.74), compared to movements that required either 90° internal (mean comfort rating difference = 1.55), or 90° external rotation (mean comfort rating difference = 2.23). Future studies should investigate underlying mechanisms for the reduction in end-state comfort during movements with larger rotation angles.

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