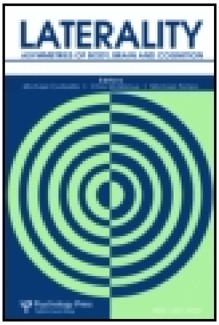

Laterality: Asymmetries of Body, Brain and Cognition
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/plat20

Interlimb coordination during a cooperative bimanual object manipulation task

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Version of record first published: 26 Feb 2013.

Laterality, 2013
http://dx.doi.org/10.1080/1357650X.2012.748060

Routledge
Taylor & Francis Group

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This experiment examined asymmetries in the execution of an object manipulation task that requires the coordinated use of both hands. To this end, twenty right-hand-dominant participants performed a bimanual object manipulation task, which required that they reach for and grasp two objects located on a tabletop, fit the two objects through a hole in a horizontally or vertically oriented fitting board, and then rotate the objects 180° to produce a "beep" tone. Overall, the two hands were highly synchronized at the start, but not at end, of each movement phase. The decrease in interlimb coupling at later stages of the movement phase was primarily driven by the shorter movement time values for the dominant right hand. In addition, degree of left object rotation was greater than the right object, irrespective of board orientation. In sum, the results suggest that manual asymmetries and role assignment are not hardwired constraints, but depend on the overall task constraints and the manner in which the task is conceptualized.

Keywords: Bimanual coordination; Manual asymmetries; Goal-directed.

Handedness is one of the most apparent manifestations of laterality, with approximately nine out of ten individuals exhibiting a right-hand preference

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The authors wish to thank Thorsten Schäfers for building the experimental apparatus. Thanks to Mike Nicholls, David Carey and an anonymous reviewer for helpful comments on the manuscript. This research was funded by the German Research Foundation (DFG; EC 277). Christian Seegelke gratefully acknowledges the financial support from Honda Research Institute Europe.

during manual actions (Levy, 1969). This right-hand preference has been observed in all human cultures and has remained relatively stable over the course of time (Coren & Porac, 1977; Faurie & Raymond, 2004). Although the basis for this right-arm preference is still under debate, a number of studies have demonstrated that the right-hand preference is often accompanied by improved motor skill performance for the right hand (Annett, Annett, Hudson, & Turner, 1979; Peters, 1976; Todor & Kyprie, 1980; Woodworth, 1899). For example, Todor and Kyprie (1980) found shorter average intertap intervals (i.e., a faster tapping rate) and reduced intertap interval variability for the dominant, compared to the non-dominant, hand during unimanual finger tapping. Similarly, Woodworth (1899) showed that movements performed by the dominant right hand were substantially more accurate than those of the non-dominant left in a repetitive line-drawing task. It has also been shown that the degree of manual asymmetry is influenced by the skill level requirements of the task (Steenhuis & Bryden, 1989), the spatial variability of the movement trajectory (Roy, Winchester, Elliott, & Carnahan, 1995), the number of spatial axes in which the movement must be controlled (Roy et al., 1995), and the spatial precision demands of the target (Bryden & Roy, 1999; Bryden, Roy, Rohr, & Egilo, 2007; Roy & Elliott, 1989).

Researchers have also examined manual asymmetries during bimanual actions (Amazeen, Amazeen, Treffner, & Turvey, 1997; Carson, Thomas, Summers, Walters, & Semjen, 1997; Franz, Rowse, & Ballantine, 2002; Peters, 1990; Treffner & Turvey, 1996). This research has indicated that the dominant hand generally leads the non-dominant hand (Amazeen et al., 1997; Franz, et al., 2002), and performs the subtask that requires continuous and precise adjustments of speed and force (Peters, 1990). In addition, when the hands must perform tasks of different difficulty levels, performance is often worse when the non-dominant left arm performs the more demanding movement (Walter & Swinnen, 1990).

The aforementioned manual asymmetries in bimanual coordination have all involved tasks in which the upper limbs were physically independent. In contrast, the manner in which the central nervous system (CNS) controls and coordinates the upper limbs during tasks in which the two hands cooperate with each other to achieve a common goal (e.g., sweeping the floor with a broom, or cutting a steak using a knife and fork) has received much less attention. Much of what is known comes from the drawer-opening studies of Wiesendanger and colleagues (Kazennikov, Perrig, & Wiesendanger, 2002; Serrien & Wiesendanger, 2000; Weiss, Paulignan, Jeannerod, & Freund, 1997). In these studies participants are asked to open a drawer with the one hand, and grasp a small object located inside the drawer with the other hand. The results of those studies revealed that the hands were well synchronized at specific goal-related events at the end of the movement (i.e., "drawer fully opened" and "lifting of peg"), in spite of the large temporal variability of the individual limbs. This temporal goal invariance extends to situations in which a load is applied to the drawer (Perrig, Kazennikov, & Wiesendanger, 1999), the task is performed without visual guidance (Kazennikov & Wiesendanger, 2005; Perrig et al., 1999), and when cutaneous sensation of the index finger and thumb of the drawer-opening hand is blocked (Perrig et al., 1999).

An additional robust finding in the drawer-opening task relates to manual-role assignment. Although participants were free to choose the pulling and grasping hands, all participants used the non-dominant left hand to pull open the drawer, and the dominant right hand to grasp the object within the drawer, even though there were no specific instructions to do so. Thus, the role of "drawer opener" was assigned to the non-dominant left hand, while the role of "peg lifter" was assigned to the dominant right hand (Kazennikov & Wiesendanger, 2005; Serrien & Wiesendanger, 2000).The division of labour suggests that the right hand is not superior to the left hand, but that the two hands are specialized for different functions (Bagesteiro & Sainburg, 2002, 2003; Guiard, 1987; Sainburg, 2002; Sainburg & Kalakanis, 2000; Sainburg & Wang, 2002). For example, the dynamic-dominance hypothesis of Sainburg and colleagues (Bagesteiro & Sainburg, 2002, 2003; Sainburg, 2002; Sainburg & Kalakanis, 2000; Sainburg & Wang, 2002) postulates that the dominant right arm is more adept at the specification of arm trajectories and movement dynamics, while the non-dominant left arm is more adept at obtaining final limb positions and arm postures.

The dynamic-dominance hypothesis has gained increasing acceptance in the motor-control literature, and provides a function-based explanation of upper-limb performance asymmetries. To date the dynamic-dominance hypothesis has been restricted to unimanual tasks. As such, it is not known whether the principles of hemispheric specialization extend to cooperative bimanual movements (but see Dounskaia, Nogueira, Swinnen, & Drummond, 2010 for an investigation of manual asymmetries in torque control during bimanual shape production). Thus, the aim of the current experiment was to examine interlimb coordination and manual-role assignment during a multi-segment cooperative bimanual object-manipulation task. In this task, twenty right-hand-dominant participants reached and grasped two objects located on a tabletop, fitted the two objects together through a hole in a fitting board, and then rotated the objects 180° to produce a "beep" tone. The objects were designed such that the "beep" tone could be produced by symmetric rotation (90° rotation of both objects) or asymmetric (e.g., 180° left-object rotation and 0° right-object rotation, 60° left-object rotation and 120° right-object rotation, etc.). Additionally, in order to examine the influence of task demands on manual asymmetries and role assignment, the orientation of the fitting board was manipulated such that participants had to fit the objects through a hole in a horizontally or vertically oriented fitting board.

Our hypothesis was threefold. First, as Wiesendanger and colleagues suggested (Perrig et al., 1999; Serrien & Wiesendanger, 2000), we expected that temporal asynchrony would be smaller at movement offset than movement onset (Serrien & Wiesendanger, 2000). This would be reflected by relatively lower absolute asynchrony values at the end, than at the start, of both the reach-to-grasp and grasp-to-fit movement phases. Second, it was hypothesized that the role of postural stabilizer is assigned to the non-dominant left hand, while the role of manipulator is assigned to the dominant right hand (Guiard, 1987; Sainburg, 2002). This differentiation in hand assignment would be most evident during the object rotation movement phase, and as such, the degree of object rotation would be greater for the dominant right hand than for the non-dominant left hand. Third, if manual asymmetries and manual role assignment are determined by habitual hand dominance, then movement time and interlimb coupling values should be similar regardless of whether the fitting board is horizontally or vertically oriented.

METHOD

Participants

Twenty participants from Bielefeld University (mean age = 24.3, $SD = 2.9$, eight men, twelve women) participated in the present study in exchange for 5€ or course credit. All participants were right-handed, as determined by the revised Edinburgh Handedness Inventory (Dragovic, 2004). All participants had normal or corrected to normal vision, and had no known neuromuscular disorders. The experiment was conducted in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

Apparatus

The apparatus used in the experiment consisted of a fitting board, one start box, and two T-shaped objects (Figure 1a), which were placed on a height-adjustable wooden shelf (200 cm wide, 31.5 cm deep) braced by two legs. Located 8.5 cm from the front edge of the shelf was a clear plexiglass fitting board (35 cm × 35 cm × 2 cm). In the centre of the plexiglass fitting board was a target hole (5 cm diameter) through which the objects could be inserted. The fitting board was attached to a metal stand, which allowed the board to be oriented in either a horizontal or vertical orientation. Prior to the experiment, the shelf was adjusted so that midpoint of the plexiglass fitting board coincided with the solar plexus of the participant.

A PVC start box (30 cm × 10 cm × 2.5 cm) was positioned on a height-adjustable table and arranged to vertically coincide with the participant's body midline. A hole (1.5 cm in depth, 3.1 cm in diameter) was located 10 cm from the lateral edges of the start box and was used to house the objects at the start of each trial. The objects were placed into two holes so that the foot of each object contacted the base of the start box, with the handles facing upwards and in the transverse plane.

Both of the cylindrical PVC objects (object A: 9.5 cm in length and 3.5 cm in diameter, object B: 9.5 in length and 3 cm in diameter) had a circular handle (10 cm in length and 4 cm in diameter) mounted to one end. Each object had a band of green electrical tape (2 cm) wrapped around one end of the handle, which extended down the side of the object. A micro-sensor was embedded into the foot of each object, and produced a "beep" sound when the sensors contacted one another. The objects were designed so that participants had to line up the bands of green tape together in order to fit the foot of object B into the foot of object A (Figure 1). If the green tape bands did not coincide then the foot of object B could not be placed into the foot of object A, and thus the objects could not be rotated and the "beep" tone could not be produced.

Data was recorded using an optical motion-capture system (VICON Motion Systems, Oxford, UK), consisting of ten Bonita cameras with a temporal and spatial resolution of 200 Hz and 1 mm, respectively. Retro-reflective markers (14 mm in diameter) were placed on the distal end of the dorsal third metacarpal (MCP), the styloid process of the ulna (US), and the styloid process of the radius of the left and right hand (RS), and were used to calculate the timing and interlimb coupling variables. Retro-reflective markers were also placed on each end of the object handles and used to calculate the degree of object rotation. Each trial was recorded using a Basler Pilot DV camera (Basler AG, Ahrensburg, Germany) which was

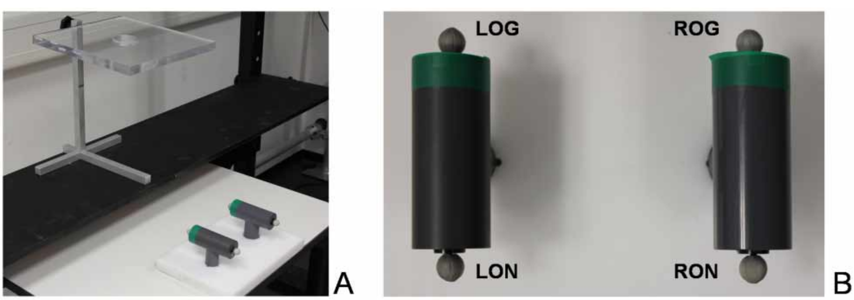

Figure 1. A) Experimental set-up with the board placed in the vertical orientation. B) Start orientation of the objects. Left object green end: LOG; right object green end: ROG; left object non-green end: LON; right object non-green end: RON.

synchronized with the VICON motion capture system. The camera was placed above the apparatus, providing a bird's eye view of the apparatus and the participant.

Task and Procedure

The experimental task required that each participant reach and grasp two objects located on a tabletop, fit the feet of the objects together through a hole in a horizontally or vertically oriented fitting board, and then rotate the objects 180° to produce a "beep" tone. To start each trial, the participant stood with the hands by their sides and indicated to the experimenter that they were ready to begin. The experimenter then gave the verbal command "Los" (German for "Go"), at which point the participant grasped the objects, placed the feet of the objects together through the hole in the plexiglass board, and rotated the objects 180° to produce the required "beep" tone. Upon hearing the beep sound, the participant placed the objects back in the start box and brought both hands to their sides. Participants were instructed to use a power grip (Napier, 1956) to grasp the left object with the left hand, and the right object with the right hand. Participants were told not to change the selected grasps throughout the trial. The instructions also emphasized that participants should avoid contacting the plexiglass board, and should move at a comfortable speed.

At the start of the experiment, participants performed 20 practice trials to familiarize themselves with the general task procedures and ensure that they were able to fit the objects together in order to produce the "beep" tone. The familiarization trials were performed without the plexiglass fitting board, and were not included in future analysis. After the familiarization trials, there was a three-minute rest period, and then the experimental session was initiated.

The experimental trials were divided into two blocks of 50 trials, separated by a two-minute rest period. Within each block, participants performed 25 trials to each board orientation condition (horizontal, vertical). Board orientation was blocked and counterbalanced across participants. The entire testing session, including informed consent, lasted approximately 40 minutes.

Data analysis

Trials were counted as errors when participants picked up one or both objects then placed them back down and changed the way they grasped the object, contacted the plexiglass fitting board with one or both objects, or the objects were not rotated 180° and failed to produce the "beep" sound. The trials rejected due to error accounted for less than 1% of the data, and were equally distributed across conditions and participants. These trials were not included in analysis. Given the low number of errors, condition mean substitution was used to replace missing data.

The 3D coordinates of the reflective markers placed on the hands and objects were reconstructed and missing data were interpolated using a cubic spline and filtered using a Woltring filter, with a predicted mean square error value of 5 mm^2 (Vicon Nexus 1.5). The Woltring filter is a squintic cubic spline routine and is equivalent to a double Butterworth filter (Hughes, Seegelke, Reißig, & Schütz, 2012; Woltring 1986).

Prior to kinematic analysis, the wrist joint centre (WJC) was calculated midway between the marker placed on the styloid process of the ulna (US) and the marker placed on the styloid process of the radius (RS). Kinematic variables were calculated using custom-written MatLab programs (Mathworks, Version 7.0).

For each trial, the time series was divided into the reach-to-grasp phase, grasp-to-fit phase, and object rotation phase (Figure 2). The reach-to-grasp phase was defined as the time period between when the hand WJC left the body to the time the hand WJC contacted the object. The grasp-to-place phase was defined as the time period between when the object left the start board to the time the objects contacted one another. Movement onset for each phase was determined as the time of the sample in which the resultant velocity of the hand WJC exceeded 5% of peak velocity of the corresponding phase (Seegelke, Hughes, & Schack, 2011). Movement offset was determined as the time of the sample in which the WJC resultant velocity dropped and stayed below 5% of peak velocity of the corresponding phase. The object rotation phase was defined as the time period between when the objects contacted one another to the time the objects were rotated 180° and the "beep" sound was produced.

Reach-to-grasp time was defined as the time period between reach-to-grasp phase onset and reach-to-grasp phase offset. Grasp-to-fit time was defined as the time period between grasp-to-fit phase onset and grasp-to-fit time offset. Movement velocity for the reach-to-grasp and grasp-to-fit phase was calculated using a first order central difference technique, and normalized to 100 data points prior to calculation of peak velocity and time to peak velocity. Movement onset of the rotation phase was defined as the time of the sample where the Euclidean distance between LOG and ROG was minimal. Movement offset of the rotation phase was defined as the time of the sample where the Euclidean distance between LOG and RON was minimal. Potential differences in reach-to-grasp and grasp-to-place time were examined using a repeated measures analysis of variance (RM ANOVA) with the factors hand (left, right) and board orientation (horizontal, vertical).

Interlimb coupling during the reach-to-grasp and grasp-to-fit movement segments were quantified using three methods. First, to examine whether the

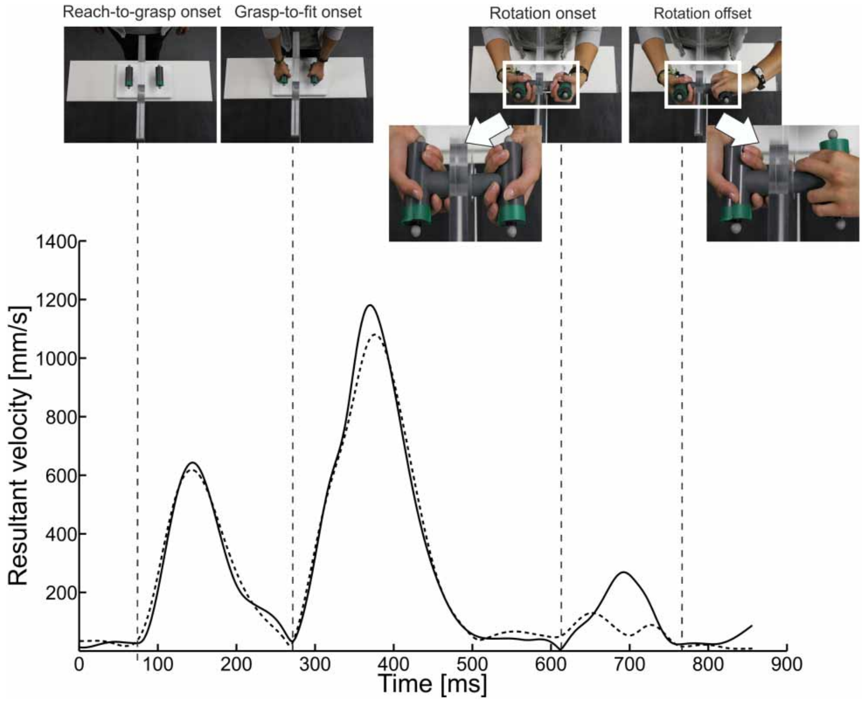

Figure 2. Typical velocity profiles indicating the reach-to-grasp phase, the grasp-to-fit phase, and the object rotation phase.

non-dominant left hand or the dominant right hand consistently initiated or completed its movements before the other, the signed asynchrony difference was computed for the reach-to-grasp and grasp-to-fit movement phases. For each phase, signed onset was determined by subtracting the time of left-hand onset from the time of right-hand onset. Negative signed values indicate a left-hand lead, whereas positive signed values indicate a right-hand lead. Signed offset was determined by subtracting the time of left-hand offset from the time of right-hand offset. Positive values indicate that the left hand completed the movement first, whereas negative values indicate that the right hand completed the movement first.

Second, absolute onset and offset asynchrony difference was calculated to examine the magnitude of asynchrony irrespective of hand lead or lag (Hughes & Franz, 2007, 2008). To this end, the absolute difference for each trial was calculated, and the individual trials were then averaged to provide a mean value for each condition. Large values indicate that the performance of the two hands were dissimilar and not close in synchrony, whereas values close to zero indicated a tight degree of coupling between the two hands.

Third, we calculated the RMS velocity difference between the hands to investigate the strength of the interlimb coupling throughout the reach-to-grasp and grasp-to-fit movement phases. In contrast to signed and absolute asynchrony measures, RMS velocity difference provides information regarding magnitude differences between the movements of the two hands over time (Hughes, Haddad, Franz, Zelaznik, & Ryu, 2011; Hughes, Reißig, & Seegelke, 2011; Hughes et al., 2012). Lower RMS velocity difference values indicate similar spatial trajectories indicative of strong interlimb synchrony. Mean values in each condition for the interlimb coupling variables outlined above were submitted to separate 2×2 RM ANOVAs, with the factors of board orientation (horizontal, vertical) and time (onset, offset).

Manual asymmetries during the object rotation movement phase of the movement were examined by calculating the degree of rotation (°) for each object. To this end, we calculated direction vectors at rotation phase onset and rotation phase offset, pointing from LOG to LON ($VLO_{onset} = LON_{onset} - LOG_{onset}$; $VLO_{offset} = LON_{offset} - LOG_{offset}$) for the left object, and from ROG to RON ($VRO_{onset} = RON_{onset} - ROG_{onset}$; $VRO_{offset} = RON_{offset} - ROG_{offset}$) for the right object. The degree of object rotation was calculated as

$$LOrotation = \cos^{-1}\left(\frac{\mathrm{VLOonset} \cdot \mathrm{VLOoffset}}{|\mathrm{VLOonset}| * |\mathrm{VLOoffset}|}\right)$$

and

$$ROrotation = \cos^{-1}\left(\frac{\mathrm{VROonset} \cdot \mathrm{VROoffset}}{|\mathrm{VROonset}| * |\mathrm{VROoffset}|}\right)$$

for the left and the right object, respectively.

Differences in the degree of manual asymmetry during the object rotation phase of the movement were analyzed using a 2×2 RM ANOVA with the factors board orientation (horizontal, vertical) and object (left, right).

RESULTS

Reach-to-grasp phase

In general, reach-to-grasp times were similar for the horizontal (1022 ms) and vertical (996 ms) board orientations, $F(1,19) = 2.366$, $p = .140$. Reach-to-grasp times were, however, influenced by hand, with shorter average reach-to-grasp time values for the dominant right hand (987 ms), than the non-dominant left hand (1031 ms), $F(1,19) = 7.946$, $p = .011$. The interaction between hand and board orientation was not significant.

Mean onset and offset asynchrony values for horizontal and vertical board-orientation conditions during the reach-to-grasp phase are shown in Figure 3. Analysis of signed asynchrony indicated that hand lead was similar for the horizontal and vertical board orientations (horizontal = 17 ms, vertical = −4 ms), $F(1,19) = 1.936$, $p = .180$. The main effect of time was non-significant, with similar absolute asynchrony values at the start (signed onset = −5 ms) and end (signed offset = 18 ms) of the reach-to-grasp phase, $F(1,19) = 2.740$, $p = .114$.

Analysis of absolute asynchrony indicated that interlimb coupling was similar for the horizontal and vertical board orientations (82 ms and 102 ms, respectively), $F(1,19) = 3.181$, $p = .090$. The main effect of time was non-significant, with similar absolute asynchrony values at the start (absolute onset = 88 ms) and end (absolute offset = 102 ms) of the reach-to-grasp phase, $F(1,19) = 0.661$, $p = .426$. Further, the movements of the two hands were initiated within 50 ms of one another in 65% of all trials, and ended within 50 ms of each other in 46% of total trials. As with the measures of absolute asynchrony, board orientation did not influence the degree of coupling between onset and offset (RMS velocity difference: horizontal = 142 mm/s, vertical = 138 mm/s), $t(19) = 0.635$, $p = .533$.

In sum, the movements of the two hands were highly synchronized at both the start and the end of the reach-to-grasp phase, with neither the left nor

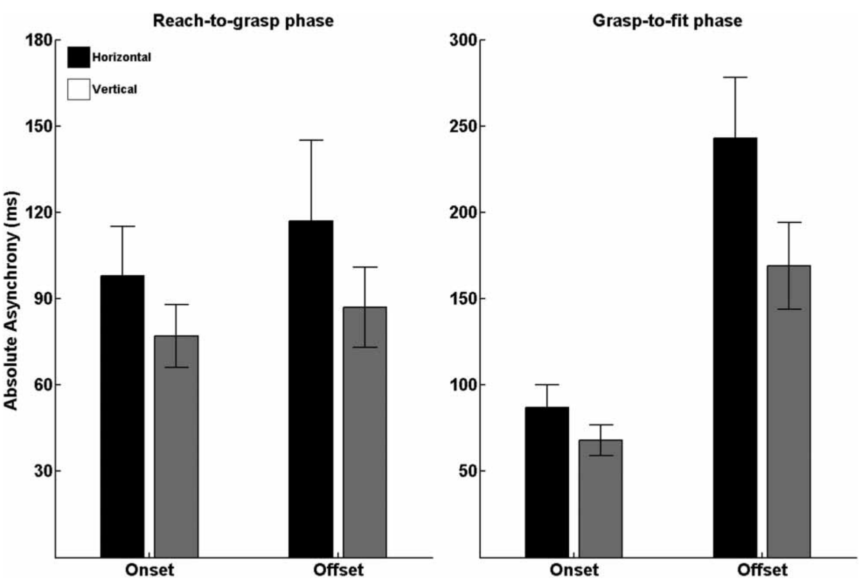

Figure 3. Average interlimb coupling variables for horizontal and vertical board orientation during the reach-to-grasp and grasp-to-fit phases of the movement. Error bars represent standard errors.

right hand consistently initiating or completing its movements before the other. Further, concurrent with previous research (Franz, 1997; Kelso, Southard, & Goodman, 1979; Spijkers & Heuer, 1995) the spatio-temporal trajectories of the hands were highly similar, and were not influenced by board orientation.

Grasp-to-fit phase

Average grasp-to-fit times were similar for the horizontal (1137 ms) and vertical board orientations (1157 ms), $F(1,19) = 0.407$, $p = .531$. Mean grasp-to-fit times were however highly influenced by hand, with shorter average grasp-to-fit time values for the dominant right hand (906 ms) than the non-dominant left hand (1389 ms), $F(1,19) = 42.242$, $p < .001$.

Mean onset and offset asynchrony values for horizontal and vertical board-orientation conditions during the grasp-to-fit phase are shown in Figure 3. Signed asynchrony analysis indicated that hand lead was similar for both board orientations (horizontal = 2 ms, vertical = 9 ms), $F(1,19) = 0.128$, $p = .725$. Analysis also revealed a non-significant effect of time (signed onset = −4 ms, signed offset = 15 ms), $F(1,19) = 0.609$, $p = .445$. The movements of the two hands were initiated within 50 ms of one another in 61% of all trials. Further, although the two hands completed the grasp-to-fit phase within 50 ms of each other in 32.5% of total trials, there were also a number of trials (28%) in which the offset asynchrony was greater than 200 ms.

Analysis of absolute asynchrony indicated that the hands were more coupled when the board was oriented vertically (118 ms), than when it was oriented horizontally (166 ms), $F(1,19) = 14.806$, $p < .001$. Interlimb coupling was also significantly lower at the end (206 ms), compared to the start of the grasp-to-fit phase (78 ms), $F(1,19) = 18.745$, $p < .001$. The interaction between board orientation and time was also significant, $F(1,19) = 4.291$, $p = .05$. The hands were more coupled at the start, compared to the end, of the grasp-to-fit phase for both the vertical (onset = 68 ms, offset = 169 ms) and horizontal board orientation (onset = 87 ms, offset = 244 ms). However, this difference was more pronounced for the horizontal board orientation (onset/offset difference = 157 ms) than the vertical board orientation condition (onset/offset difference = 101 ms).The influence of board orientation was also observed throughout the movement, with significantly higher RMS velocity difference values for the horizontal (223 mm/s), compared to the vertical board orientation (134 mm/s), $t(19) = 9.310$, $p < .001$.

Similar to the reach-to-grasp phase of the movement, signed asynchrony analysis revealed that neither the left nor right hand consistently initiated or completed its movements before the other. However, the results of the grasp-to-fit phase differed from the reach-to-grasp phase in two ways. First, the degree of interlimb coupling was higher at grasp-to-fit onset, compared to grasp-to-fit phase offset. Second, the effect of board orientation on interlimb coupling was significant, with the hands being more coupled when the board was oriented in the vertical, compared to the horizontal orientation.

Object rotation phase

In general, the degree of object rotation was significantly larger for the left object (99.4°, 55.2%) compared to the right object (68.9°, 32.2%), $F(1,19) = 12.535$, $p = .002$. The interaction between board orientation and object was not significant ($p = .437$), such that object rotation was greater for the left object regardless of whether the board was oriented in a horizontal (left = 95°, right = 71°) or vertical fashion (left = 104°, right = 67°).

DISCUSSION

The purpose of the current experiment was to examine interlimb coordination and manual-role assignment during a multi-segment bimanual object manipulation task. We observed shorter reach-to-grasp and grasp-to-fit times for the dominant right hand, compared to the non-dominant left hand. The right-hand advantage in movement execution has been consistently observed in a number of paradigms (Annett et al., 1979; Carson, Goodman, Chua, & Elliott, 1993; Roy & Elliott, 1989), and is thought to arise from differences in the processing of visual feedback (Flowers, 1975; Honda, 1982), a left hemisphere specialization for the organization and control of sequential movements (Todor, Kyprie, & Price, 1982) and/or the timing of forces required to accelerate and decelerate the hand toward a target (Roy & Elliott, 1989), or the susceptibility of the non-dominant hand to noise in the motor system (Carson, Chua, Elliott, & Goodman, 1990; Carson et al., 1993).

Based on previous research (Perrig et al., 1999; Serrien & Wiesendanger, 2000), we hypothesized that the spatial trajectories of the individual limbs would be variable, but that there would be a high degree of interlimb coupling at critical goal-related events. During the reach-to-grasp phase, the movements of the two hands were highly synchronized at both onset and offset, and were moderately coupled throughout the reach-to-grasp phase. In contrast, the hands were less coupled when placing the object through the fitting board (i.e., a critical goal-related event), and were not well coupled throughout the grasp-to-fit movement phase. These results are counter to what would be expected based on the drawer-opening studies which generally indicate that the hands are highly coupled at critical goal-related events. Furthermore, we did not replicate the finding that temporal asynchrony is smaller at movement offset than movement onset (Serrien & Wiesendanger, 2000), as the hands were more coupled at the start, compared to the end, of the grasp-to-fit movement phase.

Taken together, these results indicate that there is a tendency for the hands to be tightly coupled at critical events during goal-directed movements, but that the degree of interlimb coupling is influenced by task demands and context. For example, in the current experiment, the objects were designed such that they had to be fit together prior to object rotation. This design may have biased participants toward a movement strategy in which they first positioned one object (e.g., object A) in front of the hole in the plexiglass board, and then inserted the other object (e.g., object B) into it (e.g., object A). Furthermore, participants were free to choose whether to perform the task symmetrically or asymmetrically in the current experiment, whereas the drawer-opening task required that participants choose one hand to pull open the drawer, and the other hand to grasp the object within the drawer. Given these potentially influential factors, it would be worthwhile investigating how individuals perform various bimanual cooperative tasks with differing task demands and contexts. One would expect to observe differences in interlimb coupling between tasks if task demands and context is a driving factor in bimanual cooperative actions. However, if goal synchronization is a primary constraint in bimanual cooperative actions then we would expect that the hands would be highly coupled at the end of the movement, and that the degree of interlimb coupling would be similar across tasks.

Counter to our original expectations, we found that participants rotated the left object more than the right object, indicating that the role of manipulator was assigned to the non-dominant left hand, while the role of postural stabilizer was assigned to the dominant right hand. This finding directly contrasts with our hypothesis that the role of postural stabilizer would be assigned to the non-dominant left hand, while the role of manipulator would be assigned to the dominant right hand (Guiard, 1987; Sainburg, 2002). As such, the results of the present study suggest that that manual asymmetry and role assignment are not fixed constraints that are determined by habitual hand dominance, but are flexibly and functionally guided by the type of activity, and the demands of the task.

Flexible manual role assignment can be seen in many everyday bimanual cooperative actions. Take, for example, the task of opening a bottle of water. When the task requires that the bottle be opened by removing the cap, individuals are more likely to grasp the bottle with the non-dominant left hand and use the dominant right hand to twist and remove the bottle cap. However, when the task requires that the bottle be opened and drank from, individuals generally grasp the bottle with the dominant right hand and use the non-dominant left hand to remove the bottle cap (Theorin, 2009).

Assigning the roles in this manner allows the bottle to be lifted to the mouth with the more spatially and temporally accurate dominant right hand (Annett et al., 1979; Roy & Elliott, 1989; Woodworth, 1899), which decreases the likelihood of spilling the contents of the bottle. Thus, even though both tasks require the grasping of the bottle and the removal of the cap, the roles assigned to the two hands differ depending on overall task demands (i.e., future actions).

Additional support for flexible manual role assignment comes from the work of Johansson and colleagues (Johansson et al, 2006; Theorin & Johansson, 2010) In Johansson et al. (2006), participants were asked to move a cursor (displayed on a computer screen) into successively displayed target areas by applying linear and torque forces to the handles of an unsupported rectangular object. During bimanual conditions, there were two mapping rules that related linear and torque forces to the cursor movements. For the left-hand mapping rule, the cursor moved in the direction of the forces applied by the left hand, whereas for the right-hand mapping rule, the cursor moved directionally with the forces applied by the right hand. Johansson et al., (2006) found that the choice of prime actor (i.e., manipulator) was not fixed, but depended on the mapping rule: the left hand was the prime actor when the cursor moved directionally with the left-hand forces, and the right hand was the prime actor when the cursor moved directionally with the right-hand forces. When the empirical and observational data are considered together, there is evidence that the functional roles of the hands during bimanual object manipulations depend strongly on the overall task constraints.

As a final comment regarding the influence of board orientation on bimanual cooperative actions, recall the hypothesis that movement time and interlimb coupling values should be similar regardless of board orientation if manual asymmetries and manual role assignment are determined by habitual hand dominance. We found that board orientation did not influence timing (i.e., reach-to-grasp time, grasp-to-place time) or object rotation. Board orientation did, however, influence the degree of interlimb coupling. Specifically, the hands were more coupled when the board was oriented in a vertical position, compared to when the board was oriented in a horizontal position. This finding provides further support that manual asymmetries are not driven solely by hand dominance. Rather, we hypothesize that differences in interlimb coupling arises from the fact that homologous muscles are activated during the vertical board orientation condition, whereas non-homologous muscles are activated during the horizontal board orientation. This hypothesis coincides with previous research demonstrating that movements in which homologous muscle groups are simultaneously activated are more stable and result in higher interlimb coupling than movements in which non-homologous muscles are activated (Serrien & Swinnen, 1997a, 1997b, 1998; Swinnen, Dounskaia, Verschueren, Serrien, & Daelman, 1995).

Manuscript received 25 June 2012
Revised manuscript received 3 November 2012
First published online 19 February 2013

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