Hand use for grasping in a bimanual task: Evidence for different roles?

Article *in* Experimental Brain Research · November 2012

DOI: 10.1007/s00221-012-3325-z · Source: PubMed

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Exp Brain Res (2013) 224:455–467
DOI 10.1007/s00221-012-3325-z

RESEARCH ARTICLE

Hand use for grasping in a bimanual task: evidence for different roles?

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Received: 5 July 2012 / Accepted: 26 October 2012 / Published online: 18 November 2012

Abstract It has been proposed that the two hands play different roles during bimanual object interaction. The right hand takes on an explorative, highly precise, manipulative role while the left hand supports and stabilizes the object. Does this division of labour influence hand use during visually guided grasping? Three experiments were designed to address this question: right-handed individuals put together 3D models using big or small building blocks scattered across a tabletop. Participants were free to build the models; however, it felt comfortable (Experiment 1) or they were required to build on a large (Experiment 2) or small (Experiment 3) base plate. In Experiment 1, the right hand was preferred for grasping while the left hand stabilized the building model. When participants used the large base plate (Experiment 2), right hand use for grasping decreased and left hand use increased. The plate provided freedom to the left hand from having to stabilize the building model, but it also interfered with right/left hand movements directed towards the opposite side of the grasping hand (contralateral movements). To investigate which of these two factors would explain the change in hand use for grasping, a very small base plate was used in the last experiment. Results showed similar right hand use values to those seen in the first experiment (without the use of a plate), even though the left hand was 'released from its stabilizing duties.' The results predict a left-hemisphere right hand advantage in the control of grasping.

Keywords Prehension · Left hemisphere · Hemispheric specialization · Handedness

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Introduction

Many of our everyday actions require interaction of the two hands. For example, peeling an orange, washing the dishes, or pouring a glass of wine all involve the use of both hands to successfully accomplish the task. It has been proposed that each hand performs different, yet complementary roles during asymmetric bimanual object interaction (Fagard and Marks 2000; Guiard 1987; Haaland et al. 2004; Hopkins 1995; Johansson et al. 2006; MacNeilage 1987; Rogow 1987; Serrien et al. 2006; Theorin and Johansson 2010; Wang and Sainburg 2007). Guiard, for example, suggested that the right hand serves the prime acting role, whereas the left hand displays a more supportive, stabilizing role. Therefore, when sawing, writing, or driving a screw, the left hand would hold the material (i.e. cloth, paper or screw) while the right hand performed the action (Guiard 1987). According to this view when peeling an orange, the left hand would hold the orange while the right hand removed the peel. To pick up the orange however, one could use the left hand, which would then stabilize it for the right hand to peel it, or the right hand could grasp the orange and then transfer it to the left hand for stabilization. These possibilities yield opposite patterns of hand use for grasping during bimanual object interaction. In the former case, one would expect objects to be picked up more often using the left hand. In the latter case, objects would be grasped with the right hand and then transported to the left hand. Studies of hand preference for grasping using unimanual tasks have shown that the right hand is preferred when picking up objects. Those studies have asked participants to pick up cards (Bishop 1996; Calvert and Bishop 1998; Carlier et al. 2006), geometrical 3D shapes (Gabbard et al. 2003), toys (Bryden and Roy 2006; Sacrey et al. 2012) or tools (Mamolo et al. 2004, 2005, 2006). They all, however, have asked participants to pick up one object at a time. Therefore, very little is known about hand preference for grasping in tasks that require bimanual interaction.

A task that could be used to investigate hand preference for grasping during bimanual interaction is the block building task (see Fig. 1a; Gonzalez and Goodale 2009; Gonzalez et al. 2007 for a complete description of the task). In this task, a participant sits in front of a table where numerous blocks are distributed randomly across a table-top. Sample models containing 12–15 blocks are handed to the participant (one at a time), and the goal of the task is to reproduce an exact copy of the model using the blocks from the tabletop. To perform the task, participants must pick up a block with one hand and then incorporate it into the model being constructed. The model being constructed is held by one hand while the other hand gathers and inserts the blocks. The interaction of the two hands is essential in order to complete the task. Studies using this task have shown predominant (up to 80 %) use of the right hand for picking up the blocks even in some left-handed individuals (Gonzalez and Goodale 2009). What is not known, however, is if this preference stems from a division of labour between the right and the left hands; or from a right hand/left-hemisphere specialization for grasping as it has been suggested before (Gonzalez et al. 2006, 2007; Goodale 1988; Janssen et al. 2011; Serrien et al. 2006). One could argue, for example, that because the task requires the model being constructed to be held or stabilized with one hand, the prevalence of right hand use for grasping does not reflect left-hemisphere/right hand specialization for grasping but rather right hemisphere/left hand specialization for object stabilization. To address this issue, three experiments were conducted using the block building task. The role of the two hands during bimanual interaction was documented for each of the experiments.

In the first experiment, participants built models freely. This was with no other instruction but to use the blocks from the table to reproduce the models. In the second and third experiments, participants constructed their models using a base plate. The plate was introduced to provide an alternative from having to stabilize the models with one of the hands. Hand preference for grasping was quantified in ipsilateral (same side as the hand) and contralateral (opposite side of the hand) space. The fraction of the total building time during which each hand stabilized the model was also measured. Finally, the hand preferred to pick up the very first block of each model was recorded.

Methods and procedures

Experiment 1: constructing without a base plate

Methods

Participants Fourteen self-reported right-handed individuals (5 males) from the University of Lethbridge between the ages of 18 and 35 participated. No gender differences were found previously in this task (Gonzalez and Goodale 2009), so no action was taken to balance the genders. The studies were approved by the local ethics committee, and all participants gave written informed consent before participating in the study. Participants were naïve to the purposes of the study.

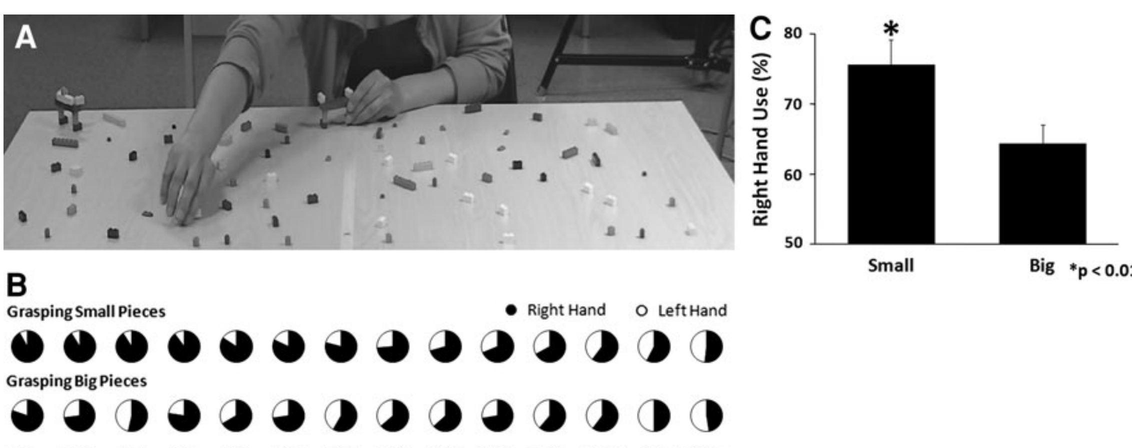

Fig. 1 **a** Photograph of a participant engaging in Experiment 1 (free building condition). Please note that the right hand is grasping while the left hand holds the model. **b** Data demonstrating overall hand use for each participant (P1, P2, etc.) in both the small (*top*) and big (*bottom*) block conditions (expressed as % of the total grasps). **c** The graph demonstrates the average right hand use in percentage for all participants in both the small and big block conditions. Note the significant difference in right hand use between grasping the small and big blocks

Apparatus and stimuli Handedness Questionnaire: a modified version of the Edinburgh (Oldfield 1971) and Waterloo (Brown et al. 2006) handedness questionnaires were given to all participants (see Appendix) at the end of the block building task. This version included questions on hand preference for 22 different tasks. Participants had to rate which hand they prefer on a scale +2 (right always) +1 (right usually), 0 (equal), −1 (left usually) and −2 (left always). Each response was scored as (2, 1, −1, or −2), and a total score was obtained by adding all values. Possible scores range from +44 for exclusive right hand use to −44 for exclusive left hand use.

Block Building Task: A total of ten models built with MEGA BLOKS® (big blocks) and LEGO® (small blocks) were used for the experiment. Five models were built using big blocks (ranging in size from 3.1 L × 3.1 W × 2.0 cm H to 6.3 L × 3.1 W × 2.0 cm H) and five using small blocks (ranging in size from < 0.7 L × 0.7 W × 1.0 cm H to 6.3 L × 1.5 W × 1.0 cm H). Each model contained 10-15 blocks of various colours and shapes. Scattered on a table (122 L × 122 W × 74 cm H with a working space of 70 L × 122 W × 74 cm H) were all the blocks that made up the five models of each size (76 small blocks and 54 big blocks). The models were prepared ahead of time by the experimenter. The same ten models were used with all participants. A clear strip of tape divided the tabletop in half. The same number of blocks was placed on the left and right side of the table.

Procedures Participants were seated in front of the table facing the middle of the display. One model was given to the participant for inspection. After inspection, the model was placed on the far right or left corner (counterbalanced among models) of the table. The model's location on the table did not have any effect on hand use during the block building task. Participants were instructed to replicate the model as quickly and accurately as possible from the blocks given on the table. No other instruction was given. Once the model was replicated, both models were removed from the table, and a new model was given. No blocks were replaced after each model was completed. Each participant built five consecutive models using the small blocks and five consecutive models using the big blocks. Starting size was counterbalanced among participants. The time taken to complete each model was recorded by the investigator using a stop watch. The task was recorded on a JVC HD Everio video recorder approximately 160 cm away from the individual with a clear view of the tabletop, building blocks and participants' hands.

Data analysis All recorded videos were analysed offline. Each grasp was recorded as a left-, right- or two-hand grasp in the participants' ipsilateral or contralateral space. The total number of grasps was calculated to determine a percentage for right hand use (number of right grasps/total number of grasps × 100). The time in which the model being constructed was held by each hand was calculated for each model and expressed as the percentage of the total construction time per model (left/right hand holding/total construction time × 100). For each model, the hand used to grasp the first block was also recorded. This was done for two reasons: first, because there is equal opportunity for the left or the right hand to pick up the first block (i.e. there is nothing to stabilize) and second, because we were interested in knowing which hand would pick up an object that needs to be stabilized afterwards (addressing the dilemma previously described of what hand would pick up an orange if one were to peel it).

Results

Means and standard error are reported in seconds.

Handedness questionnaire All participants self-reported as right-handers, and this was confirmed by the handedness questionnaire. The average score on the questionnaire was +32.9 (±1.2 SE; range +23 to +40) out of the maximum possible score of +44/−44.

Hand use for grasping Figure 1b shows hand use for each participant when picking up the big and the small blocks. Black represents right hand use, while white represents left hand use. Overall, participants used their right hand 64.3 ± 2.6 % of the time to grasp the big blocks and 75.6 ± 3.5 % of the time to grasp the small blocks. The difference between the two values was significant as revealed by a paired-samples t test (t (13) = 4.2; $p < 0.001$). For the big blocks, analysis of contralateral grasps showed that participants used their right hand 19.7 ± 2.3 % of the time for this type of grasp and 5.8 ± 1.2 % of the time with the left hand. The difference between the hands was significant (t (13) = 4.6; $p < 0.001$). When using the small blocks, 27.7 % ± 2.9 of the grasps were in contralateral space for the right hand, and 5.9 ± 1.2 % for the left hand. The difference between the hands was also significant (t (13) = 5.9; $p < 0.001$).

Hand use for stabilization The average time to construct the five models using the big blocks was 168.7 ± 11.6 s. On average, the right hand held the model being constructed 2.2 % of the time (3.5 ± 1.2 s). In sharp contrast, the left hand held the model being constructed 43.4 % of the time (72.6 ± 7.2 s). For models constructed with small blocks, the average construction time was 316.8 ± 20.3 s. The right hand held the model 4.3 % of the time (14.3 ± 4.8 s). In contrast, the left hand held the model 72.2 % of the time (224.4 ± 15.0 s).

Hand use for initial grasp Three types of grasps were noted when reaching out and grasping the *first* block: right hand, left hand or bimanual. However, most bimanual grasps were led by one hand. In other words, one hand would come in contact first with a block and then was quickly followed by the other hand contacting a second block. For these trials, the pick up order was recorded. For the big blocks, participants picked up the first one with their right hand 48.5 % of the time, their left hand 34.2 % of the time, and 17.1 % grasps were bimanual. These bimanual grasps were led by the right hand 91.6 % of the time. To pick up the first small block, participants used their right hand 57.1 %, their left hand 25.7 %, and both hands 17.1 % of the time. Bimanual grasps were led by the right hand 83.3 % of the time.

Correlation analysis To find out whether there was a relationship between right hand use for grasping and left hand time for holding the model, a correlation analysis between the average data of each participant's right hand use for grasping and left hand use for holding was carried out. The correlation between right hand use for grasping and left hand use for holding the models made of big blocks just failed to reach significance ($r = 0.52$; $p = 0.056$). The correlation for the models made out of small blocks, however, was highly significant ($r = 0.78$; $p < 0.01$).

Discussion

The results showed that the right hand was preferred for grasping both the big and small blocks. This preference was more pronounced for the small blocks, replicating studies that have shown an increase in right hand use for grasping when precision is needed (Fagard and Lockman 2005; Gonzalez and Goodale 2009; Gonzalez et al. 2007). The left hand was used to hold the model a considerable amount of time, particularly when building with the small blocks. In fact, the time spent holding the model with the left hand (72.2 %) closely matched the proportion of time that the right hand was used for picking up the blocks (75.6 %). This serves as strong evidence for a division of labour between the hands during bimanual interaction. Supporting this suggestion, the correlation between right hand use for grasping and time spent by the left hand holding the model was highly significant. The more participants used their right hand for grasping, the more they used their left hand to hold the model. Although a similar correlation using the big blocks was not technically significant ($p = 0.056$), it was strongly suggestive. The results of hand preference using the small and big blocks could be explained in two ways. One, that there is a division of labour between the hands (Guiard 1987), so that the reason why the right hand is preferred for grasping is because the left hand is occupied supporting the model. Two, that there is a left-hemisphere specialization for grasping (Gonzalez et al. 2006, 2007; Goodale 1988; Janssen et al. 2011; Serrien et al. 2006). In this view, the right hand would be preferred to grasp the blocks, regardless of what the left hand was doing (e.g. stabilizing the model). The second experiment was designed to test which of these two views could better explain hand preference. The need to hold the model with the left hand was reduced by introducing a base plate. If hand preference is determined by the division of labour between the hands, then it is expected that the presence of the base plate will increase left hand use for grasping (as the left hand will be free to pick up the objects). Conversely, if right hand preference is a reflection of a hemispheric specialization, then right hand use will remain unchanged (i.e. preferred) even though the left hand is also free to grasp.

Experiment 2: Constructing on a large plate

Methods

Participants Twenty self-reported right-handed individuals (7 males) from the University of Lethbridge between the ages of 18 and 35 participated. The studies were approved by the local ethics committee, and all participants gave written informed consent before participating in the study. Participants were naïve to the purposes of the study.

Apparatus and stimuli All the display material and equipment were the same as Experiment 1, with two exceptions. First, there was a different set of models to build. This array included 98 small blocks or 100 big blocks. Second, there was the implementation of a fixed LEGO® base plate to build the replicated model onto. The plate (38.2 L × 38.2 cm W) was placed on the tabletop, directly in front of the individual (see Fig. 2a).

Procedures All procedures were the same as Experiment 1, but the participant was instructed to build their replica onto the fixed base plate in front of them.

Data analysis Data analysis was the same as Experiment 1.

Results

Handedness questionnaire The average score on the Handedness Questionnaire was +32.7 (±1.4 SE; range: +17 to +41) out of a total possible +44/−44.

Hand use for grasping Figure 2c demonstrates right hand use in percentage when participants built models using big

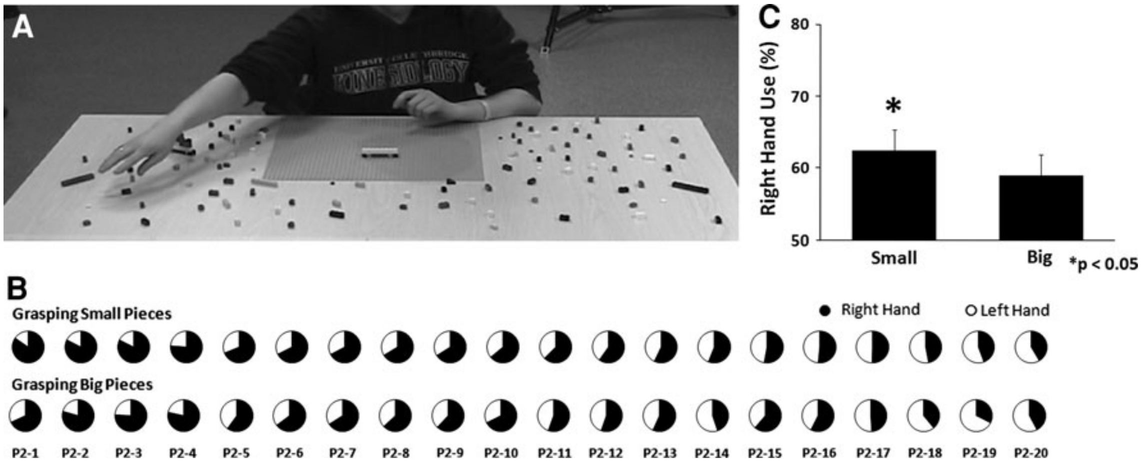

Fig. 2 **a** Photograph of a participant engaging in Experiment 2 (using a large base plate). Please note that the participant is not holding the model. Also note that the base plate is occupying a large portion of the working space. **b** Data demonstrating overall hand use for each participant (P1, P2, etc.) in both the small (*top*) and big (*bottom*) block conditions (expressed as % of the total grasps). **c** The graph demonstrates the average right hand use in percentage for all participants in both the small and big block conditions. Note the significant difference in right hand use between grasping the small and big blocks

and small blocks onto a fixed plate. Their right hand was used 58.9 ± 2.8 % of the time to grasp the big blocks, and 62.4 ± 2.8 % of the time to grasp the small blocks. A pair-samples t test revealed that the difference between the two values was significant (t (19) = 2.5; $p < 0.02$). Contralateral grasps were made 14.5 ± 2.3 % of the time with the right hand and 5.7 ± 12 % of the time with the left hand when grasping the big blocks. The difference between the hands was significant (t (19) = 3.6; $p < 0.01$). When using the small blocks, the right hand grasped in contralateral space 18.3 ± 2.1 % of the time and the left hand 4.2 ± 0.7 % of the time. The difference between the hands was also significant (t (19) = 4.8; $p < 0.001$).

Hand use for stabilization The building plate dramatically reduced the need to use one hand for holding the models. Average times were greater than in Experiment 1 because there were many more blocks in the model set. The average time to construct the five models using the big blocks was 438.1 ± 22.1 s. On average, the right hand held the model being constructed 0.6 % of the time (3.1 s ± 1.3 s). The left hand held the model being constructed 4.6 % of the time (20.4 ± 5.1 s). For models constructed with small blocks, the average construction time was 413.1 ± 17.1 s. The right hand held the model 1.1 % of the time (4.6 ± 1.3 s). The left hand held the model 9.5 % of the time (39.9 ± 10.1 s).

Hand use for initial grasp Right hand, left hand and bimanual grasps were observed. For the big blocks, 62.0 % of initial grasps were made with the right hand, 22.0 % with the left hand, and 16.0 % with both hands. These bimanual grasps were led by the right hand 68.7 % of the time. For the small blocks, 61.0 % of initial grasps were made with the right hand, 21.0 % with the left hand, and 18.0 % with both hands. Bimanual reaches were led by the right hand 83.3 % of the time.

Correlation analysis Because the left hand rarely held the model (especially when using the big blocks), there were multiple values of zero that went into the computation. Therefore, the results of the correlation analysis between right hand use for grasping and left hand use for stabilization must be taken with caution. There was positive significant correlation between right hand use for grasping and left hand holding for the models made with big blocks ($r = 0.66$; $p < 0.01$) and small blocks ($r = 0.47$; $p < 0.05$).

Comparison between Experiment 1 and Experiment 2 A one-way ANOVA with Experiment (i.e. 1 and 2) as the between subjects factor and right hand use for grasping as the within subjects factor was conducted to assess the effects of the plate on hand preference. The plate did not have a significant effect on right hand preference for grasping the big blocks ($F(1,32) = 1.7$, $p = 0.19$). However, it significantly reduced right hand preference for grasping the small blocks ($F(1,32) = 8.5$, $p < 0.01$). Similar analysis was carried out on the time that the left hand held the model. A significant effect was found for both the big ($F(1,32) = 131.1$, $p < 0.001$) and the small blocks ($F(1,32) = 172.8$, $p < 0.001$). In both cases, introducing the base plate significantly reduced the amount of time the left hand held the model.

Discussion

The purpose of the second experiment was to investigate whether hand use for grasping is determined by the division of labour between the hands during bimanual interaction or by a possible left-hemisphere specialization for grasping. The role of the left hand for object stabilization was minimized by asking participants to build their models on a base plate. There was a major reduction in the amount of time participants used their left hand to stabilize the model. As a consequence, participants increased the use of their left hand when grasping the small blocks. This resulted in a decrease of right hand use when compared to the first experiment. It was noted by a few participants, however, that the plate separated the working space (see Fig. 2a) and interfered with contralateral reaches (particularly those made by the right hand). Contralateral grasps were compared between Experiment 1 and Experiment 2. Results showed a small (<10 %) but significant decrease in right hand contralateral grasps ($F(1, 32) = 6.6$ $p < 0.02$). In Experiment 3, participants built on a very small base plate to provide stabilization for the model and to also reduce the chances that the plate acted as a divider or obstacle. Furthermore, in order to increase the generalization of our findings to the entire population, we included a sample of left-handed individuals and compared their hand preferences to that of right-handers.

Experiment 3: Constructing on a small plate

Methods

Participants Twenty-one self-reported right-handed individuals (5 males) and twelve self-reported left-handed individuals (4 males) from the University of Lethbridge between the ages of 18 and 35 participated. The studies were approved by the local ethics committee, and all participants gave written informed consent before participating in the study. Participants were naïve to the purposes of the study.

Apparatus and stimuli All the display material and equipment were the same as Experiment 1 and 2, but the fixed base plate was one-ninth the size of the big plate (12.8 L × 12.8 cm W). Because the purpose of this experiment was to provide a plate in which the model could be built onto, yet reduce the chances of it acting as an obstacle, participants only engaged in the grasping task with the small blocks.

There were six new models made of a total array of 110 small blocks (see Fig. 3a).

Procedures All procedures were the same as Experiment 2 with the participant instructed to build their replica onto the fixed base plate in front of them.

Data analysis Data analysis was the same as Experiments 1 and 2.

Results

Handedness questionnaire For right-handers, the average score on the Handedness Questionnaire was +32.9 (±1.1 SE; range: +22 to +43) of a total possible score of +44/−44. For left-handers, the average was −20.25 (±3.2 SE; range −5 to −38).

Hand use for grasping *Right-handers*: Fig. 3b, c demonstrates right hand use in percentage when participants built models using small blocks onto a small base plate. Their right hand was used 72.2 ± 2.7 % of the time to grasp the blocks. Analysis of contralateral grasps showed 20.2 ± 2.6 % use for the right hand and 1.1 ± 0.2 % use for the left hand. A pair-samples *ttest* revealed that the difference between the hands was significant ($t\ (20) = 6.9$; $p < 0.001$). *Left-Handers*: overall, they used their left dominant hand 59.0 %. Figure 4a, b demonstrates hand use in percentage. As previously reported (Gonzalez and Goodale 2009) based on the hand that they preferred to pick up blocks, two separate populations of left-handers appeared: "right–left-handers" who overall used their left hand less than 50 % of the time; and "left–left-handers" who used their left hand more than 50 % of the time. Right–left-handers used their non-dominant right hand 59.8 % of the time, whereas left–left-handers only used their right hand 21.9 % of the time. As previously reported (Gonzalez and Goodale 2009), an ANOVA with three groups (right-handers, right–left-handers and left–left-handers) and the scores of right hand use for grasping revealed differences in performance. Figure 4 shows that when picking up the blocks, left–left-handers used their right hand significantly less than the right-handers and than right–left-handers ($F(2,32) = 40.9$; $p < 0.001$). Post hoc analysis (Bonferroni correction) showed that right–left-handers differed from right-handers ($p < 0.001$) and from left–left-handers ($p < 0.001$). These last two groups did not differ from each other ($p > 0.1$).

Hand use for stabilization *Right-handers:* the average time to construct the six models was 639.6 ± 31.8 s. On average, the right hand held the model being constructed 0.3 % of the time (2.5 ± 0.9 s). The left hand held the model being constructed 11.5 % of the time (69.9 ± 11.9 s). *Left-handers:* The average time to construct was 547.9 ± 38.8 s. On average, the model being constructed was held 9.1 % (50.3 ± 14.7 s) of the time with the right hand and 4.1 % (22.8 ± 9.4 s) of the time with the left hand. However, when divided into the two groups, right–left-handers held the model 3.3 % of the time

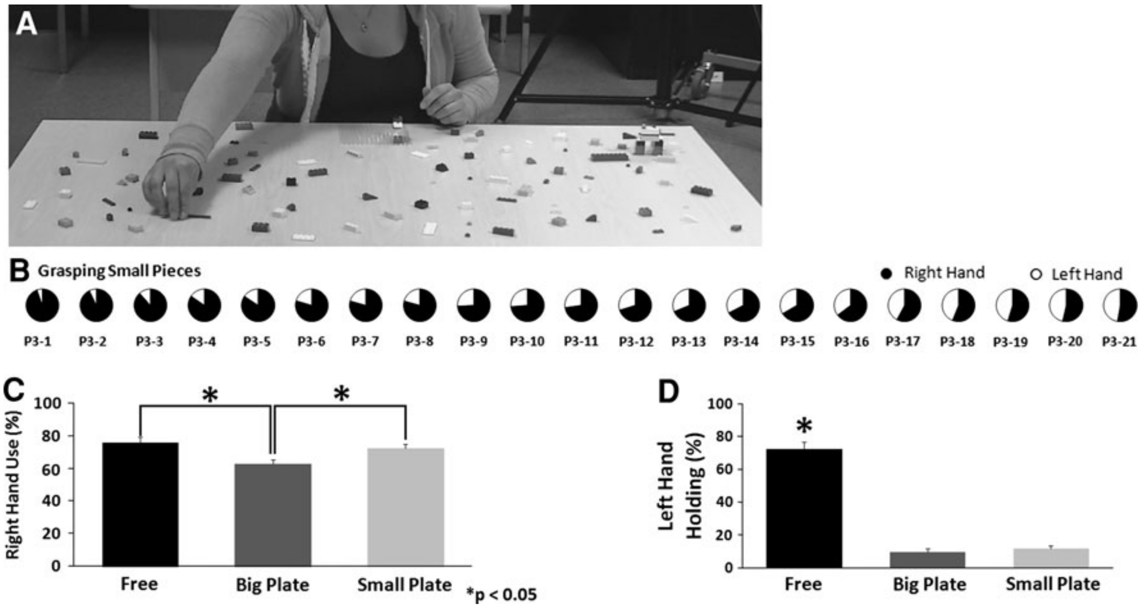

Fig. 3 **a** Photograph of a participant engaging in Experiment 3 (using a small base plate). Please note the change in size compared to the plate used in Experiment 2. Also note that the participant is not holding the model. **b** Data demonstrating overall hand use for each participant (P1, P2, etc.) in the small block condition (expressed as % of the total grasps). **c** Graph demonstrating average right hand use in percentage for all participants across all three experiments (for the small block condition only). **d** Graph demonstrating average use of the left hand to hold the model (as expressed as a % of total building time). Please note the significant decrease in left hand holding when building onto a base plate

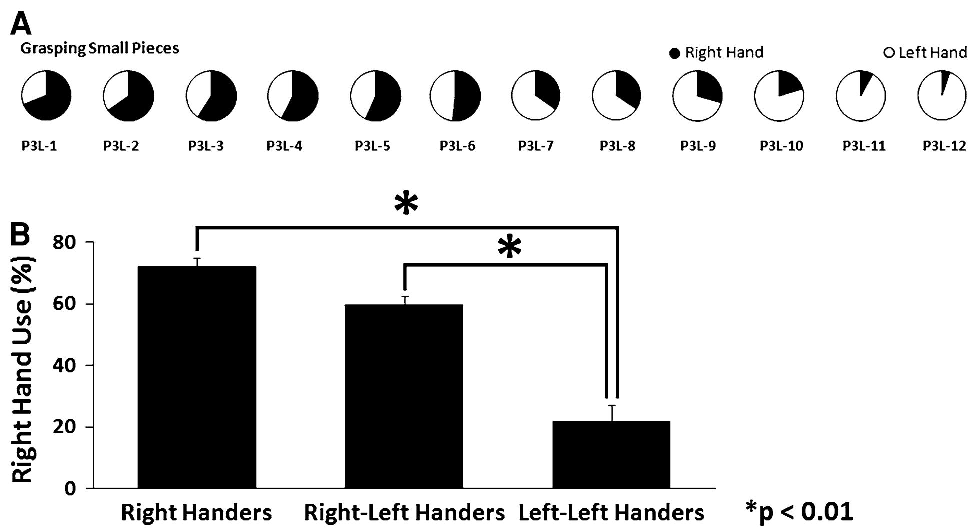

Fig. 4 **a** Data demonstrating overall hand use for each left-handed participant (P1, P2, etc.) in the small block condition (expressed as % of the total grasps). **b** Graph demonstrating average right hand use for the right-handers, right–left-handers, and left–left-handers in Experiment 3. Please note the significant reduction in right hand use for the left–left-handers

with their right hand, and 8.6 % of the time with their left hand. This pattern closer resembles the performance of right-handers. Conversely, left–left-handers held the model 14.2 % of the time with their right hand and 0.2 % with their left hand, showing the opposite behaviour from right- and right–left-handers. In fact, an ANOVA with the three groups and the amount of time the right hand was used for holding the model revealed significant group differences ($F(2,32) = 32.2$; $p < 0.001$). Post hoc analysis (Bonferroni correction) showed that right–left-handers used their right hand for holding significantly more than right-handers ($p < 0.001$) and than right–left-handers ($p < 0.001$). These last two groups did not differ from each other ($p > 0.1$).

Hand use for initial grasp *Right-handers:* for all initial grasps, 65.0 % were made with the right hand, 30.9 % with the left, and 3.9 % with both hands. In these few bimanual reaches, the right hand led the grasps 60.0 % of the time. *Left-handers*: Overall 37.5 % of initial grasps were made with the right hand, 61.1 % with the left hand, and 1.3 % with both hands. When analysed by subgroups, right–left-handers used their right hand 44.4 %, their left 52.7 % and both hands 2.7 % of the time. Left–left-handers used their right hand 30.6 % and their left 69.4 % of the time to pick up the first piece. An ANOVA with the three groups (right-handers, right–left-handers and left–left-handers) revealed significant differences ($F(2,32) = 5.8$; $p < 0.01$) among the groups. Post hoc analysis showed that left–left-handers were significantly different from the right-handed group ($p < 0.01$) but not from the right–left-handed group ($p > 0.1$). Right-handers and right–left-handers did not differ from each other ($p > 0.1$).

Correlation analysis *Right-handers:* there was a positive significant correlation between right hand use for grasping and left hand use for holding the models ($r = 0.69$; $p < 0.01$).

Left-handers: we did not separate this group into right- and left–left-handers given the small number of participants in each subgroup. Overall, there was a positive significant correlation between right hand use for grasping and left hand use for holding the models ($r = 0.61$; $p < 0.05$). There was also a negative significant correlation between right hand use for grasping and right hand use for holding the models ($r = -0.9$; $p < 0.01$). These results demonstrate the heterogeneity in behaviour exhibited by left-handers.

Comparison among Experiments 1, 2 and 3 *Handedness Questionnaire:* Analysis of variance showed that the average score for the handedness questionnaire was very similar among the three experiments ($F(2,52) = 0.01$, $p = 0.99$). *Hand use for grasping:* Fig. 3c demonstrates the differences in right hand use for right-handers across all three experiments (in the condition using the small blocks). A one-way ANOVA with experiment (i.e. 1, 2 and 3) as the between subjects factor and right hand use for grasping as the within subjects factor was conducted to assess the effects of the two plates on hand preference. There was a significant effect of experiment ($F(2,52) = 5.0$, $p = 0.01$). Post hoc analysis (Bonferroni correction) showed a significant reduction in right hand use when the big plate was used ($p = 0.01$). When the small plate was used, there was no difference in right hand use ($p = 1.0$). Importantly, there was also a significant difference in right hand use between Experiment 2 and Experiment 3 ($p = 0.05$). This finding suggests that the size of the building plate had a significant effect on hand use for grasping. *Analysis of contralateral grasps:* a one-way ANOVA showed a significant effect of hand use in contralateral grasps ($F(2,52) = 3.4$, $p < 0.05$). Post hoc analysis (Bonferroni correction) showed a significant reduction in right hand contralateral grasping when the big plate was used ($p < 0.05$), but not when the small plate was used ($p = 0.13$), when compared to the condition where no plate was used (Experiment 1). *Hand use for holding the model:* a similar analysis was carried out on the time that the left hand held the model (see Fig. 3d). A significant effect of experiment was found ($F(2,52) = 129.0$, $p < 0.001$). Post hoc analysis (Bonferroni correction) showed a significant decrease in the time the left hand spent holding the model between Experiment 1 and Experiment 2 ($p < 0.001$) and between Experiment 1 and Experiment 3 ($p < 0.001$). No difference was found between Experiment 2 and Experiment 3 ($p = 1.0$).

Discussion

The results of Experiment 3, building on a small plate, showed that for right-handers, the right hand was preferred for grasping to the same extent as when building with no plate (Experiment 1). Furthermore, the number of contralateral grasps was not different than those observed in the first experiment. This suggests that the big plate used in Experiment 2 indeed acted as a divider or obstacle, which interfered with contralateral reaches. Most importantly, Experiment 3 showed minimal left hand use for holding the model yet quite prominent right hand use for grasping. For left-handers, we replicated previous findings of hand use for grasping and furthered this knowledge to show that in most respects of hand use (i.e. grasping, holding), right–left-handers are just like right-handers, whereas left–left-handers are the mirror opposite of right-handers. These results are further discussed in the next section.

General discussion

While hand preference for grasping has been documented using unimanual tasks, this study assessed hand preference in a bimanual task. Furthermore, this study characterized the different roles that each hand plays during bimanual asymmetric object interaction. Participants reached out and grasped blocks scattered on a tabletop to construct 3D models. Interaction of both hands was essential to successfully complete the task. The models were built on a tabletop surface (free building condition) or onto a base plate. Hand use for grasping the blocks and for holding the models during construction was examined. The results of the free building condition demonstrate predominant right hand use for grasping and predominant left hand use for object stabilization. When equal opportunity was given to both hands to grasp and there was no need to hold the model, the right hand was still used more often. In other words, the right hand preference for grasping can be dissociated from the left hand preferred role for object stabilization.

Numerous studies have investigated hand preference for grasping and how this preference relates to handedness. A pegboard task using one hand at a time (unimanual task) has demonstrated the superiority of the right hand for removing the pegs from a board (Annett et al. 1979; Bryden et al. 1994). Similarly, subjects have shown a preference (almost 100 %) for the right hand when picking up tools or simpler objects (i.e. cube) located at the midline or on the right side of space (ipsilateral space). When grasping in contralateral space, the right hand use decreases (40 %) for tools, but it remains preferred (60 %) for simpler objects (Gabbard and Rabb 2000; Mamolo et al. 2004, 2005, 2006). All these studies have tested each hand separately. The vast majority of human everyday manual acts, however, require the interaction of both hands and therefore could be considered bimanual asymmetric (Buckingham et al. 2010; Johansson et al. 2006; Perrig et al. 1999). Some examples include: cutting bread, pouring a glass of wine, playing an instrument (i.e. guitar, violin, flute), a multitude of sports (e.g. baseball, basketball, golf), and even writing (because one hand holds the pen while the other holds the paper). Our study utilized a bimanual asymmetric task to assess the role of each hand during object interaction. It was found that the right hand was preferred for grasping even after the need to stabilize the object was reduced. This finding is in line with the proposal from unimanual and bimanual studies of a left hemispheric specialization for visually guided actions (Gonzalez et al. 2006, 2007; Goodale 1988; Janssen et al. 2011; Serrien et al. 2006).

The analysis of the initial grasps, that is, of grasps where construction had not begun and there was equal opportunity for either hand to grasp the first piece, also revealed a right hand preference for grasping. If we consider the example given earlier about picking up an orange, our results would suggest that the right hand would pick up the orange and then it would be transported to the left hand for stabilization. This is puzzling for two reasons: first, if the role of the left hand is to stabilize the object (as shown here), then it would make more sense, for at least biomechanical reasons, to use that hand to pick it up. This way, the object is already in the hand that would be used to stabilize it. Second, it has been reported that right-handed participants will spontaneously use their left hand to hold an object during a 'real-life' bimanual task. In one task, participants reached for, pulled and maintained open a drawer with one hand while the other hand reached for the drawer to pick up a small peg with a precision grip. It was observed that all participants chose to use their left hand to open the drawer and their right hand to grasp the small peg (Kazennikov et al. 2002; Perrig et al. 1999). It is possible that the block building and the pull-and-grasp task differ, at least, on the demands placed on the left hand. In the pull-and-grasp task, in order to retrieve the peg, the left hand must open the drawer and maintain a holding position. In the block building task, the tabletop or the base plate could be used for support at least during the initial grasp. If a quasi-finished model had to be picked up with one hand while the other is used to insert only one last piece, it is possible that all participants would prefer to use their left hand to pick up the model.

The results of the analysis of initial grasps were insightful in another way. Three kinds of grasps were identified: right hand, left hand and bimanual. It has been shown that during a bimanual grasp, there is a temporal coupling between the hands. In other words, when both hands move together, they do so in a synchronized fashion, starting and ending the movement at the same time (Jackson et al. 1999; Kelso et al. 1979; Mason 2008; Perrig et al. 1999). In our sample of bimanual grasps, we found that these were rather asymmetric and, in the majority, the right hand contacted the object first. This would suggest that during bimanual reaches, one hand (i.e. the right) takes the lead. This finding is supported by kinematic studies showing that during bimanual grasping, the left hand is yoked to the right hand (Buckingham et al. 2010). For that study, participants were asked to bimanually reach for two separate targets on one side of space (i.e. right or left). It was found that the right hand facilitated the behaviour of the left hand. That is, the left hand increased its speed so that it reached the end target with the right hand. The right hand, however, did not display this behaviour to the same degree. These results, together with the results of the present study, provide evidence that the right hand plays a 'leading' role in bimanual action.

In relation to the role of the left hand, the results of Experiment 1 showed a clear left hand preference for object stabilization which has been previously shown in infants and non-human primates (Fagard and Marks 2000; Flament 1975; Hopkins 1995). Toddlers, for example, will use their left hand to stabilize an object (i.e. a container) in order to extract another object or to unscrew a lid. Similarly, adults will prefer to use their left hand to open and hold open the lid of a box while the right hand reaches inside the box to grasp and extract a toy (Birtles et al. 2011). Interestingly, the results of Experiments 2 and 3 showed that by building on the base plate, the amount of time the left hand was used for support was drastically reduced, yet its use for grasping only increased marginally. If the left hand was not grasping nor holding the model, the question arises: what was the left hand doing during this time? We observed two common behaviours: hovering and resting (see Fig. 5). During shovering, the participant's left hand would 'cloud' above the model in progress without actually touching it. This behaviour was observed in *all* participants when building on both the big and small base

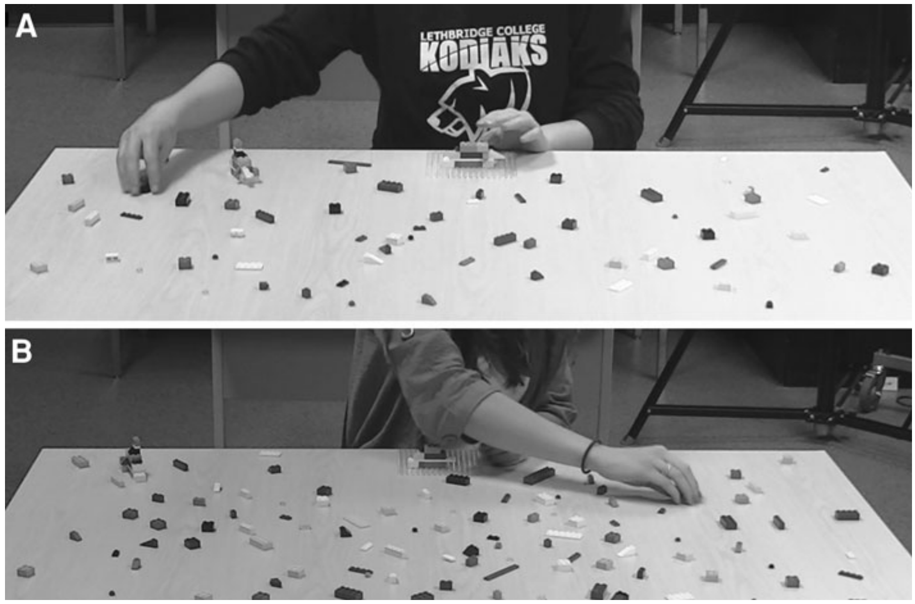

Fig. 5 **a** Photograph of a participant grasping with the right hand while hovering over the model with the left hand. **b** Photograph of a participant grasping with the right hand while the left hand rests on the table

plates. This finding suggests that even though there was no need to stabilize the model, the left hand could not disengage from its natural supportive role. With respect to resting, it could be argued that by introducing a building plate, we inadvertently shifted the task from primarily bimanual to a more unimanual task. Analysis showed that although the left hand was used for holding only 11.5 % of the time, this was significantly correlated to the right hand's use for grasping suggesting that both hands are still working together to achieve the common goal. Another possibility is that during resting, the left hand is 'waiting in readiness' to assist the right hand. Support for this possibility is demonstrated in our findings: one-third of the initial grasps were made with the right hand, and as soon as this block was placed on the table or building plate, the left hand would come to assist by holding the block. It is also possible that the resting position has, in fact, a functional role. It has been argued that there are no truly unimanual behaviours in real life, and that all manual activities could be considered bimanual (see Guiard 1987 for a complete explanation of this argument). During writing, for example (a task considered exclusively unimanual), one hand holds the pen while the other hand holds the page. Under this view, it is possible that the left hand, even when resting, provides some postural support that facilitates the right hand's performance. Finally, one could speculate that during resting, part of the left hand's job is to provide some sort of spatial reference or context for the motion of the right hand. Because the left hand is primarily controlled by the right hemisphere, this idea would find support in the body of literature demonstrating the right hemisphere's pivotal role in spatial processing (see Bartolomeo 2006; Vallar 1997; Vogel et al. 2003 for reviews). Future research could look at whether changing the spatial demands of the task would have an impact on hand use. If the right hemisphere is more specialized for spatial processing, then one would expect an increase in left hand use on a highly demanding spatial task.

With respect to left-handers, our results support previous findings showing that this population is more likely to use their non-dominant hand for grasping and other manual tasks when compared to right-handers (Calvert and Bishop 1998; Gabbard et al. 1997; Steenhuis and Bryden 1999). Furthermore, within our small sample, we replicated Gonzalez and Goodale 2009. We found that left-handers can be subdivided into right- and left–left-handers depending on their hand preference for grasping. Right–left-handers did not differ from right-handers in their right hand use for grasping or their left hand use for holding the model. The fact that grasping behaviour in a population of left-handers (albeit not all) closely resembles that of right-handers suggests a common neural mechanism responsible for this behaviour (see Begliomini et al. 2008 for evidence supporting this suggestion).

In conclusion, the present study demonstrated a right hand preference for grasping and a left hand preference for object stabilization. Right hand preference for grasping, however, can be dissociated from the left hand's role for object stabilization. Importantly, the results from each analysis: big blocks, small blocks, building with or without a plate, initial reaches, bimanual reaches, all demonstrated a right hand preference for grasping even in some left-handed individuals. These results speak strongly in favour of a left-hemisphere specialization for the visual control of grasping.

Appendix

Each of the questions below offers five possible responses:
-2 (left always), -1 (left usually), 0 (equal), +1 (right usually), and +2 (right always).

1. Which hand would you use to spin a top?
-2____ -1____ 0____ +1____ +2____

2. With which hand would you hold a paintbrush to paint a wall?
-2____ -1____ 0____ +1____ +2____

3. Which hand would you use to pick up a Cheerio?
-2____ -1____ 0____ +1____ +2____

4. With which hand would you use a spoon to eat soup?
-2____ -1____ 0____ +1____ +2____

5. Which hand would you use to pick up a piece of paper?
-2____ -1____ 0____ +1____ +2____

6. Which hand would you use to insert and turn a key in a lock?
-2____ -1____ 0____ +1____ +2____

7. Which hand would you use to insert a plug into an electrical outlet?
-2____ -1____ 0____ +1____ +2____

8. Which hand would you use to throw a ball?
-2____ -1____ 0____ +1____ +2____

9. Which hand would you use to pick up a marble?
-2____ -1____ 0____ +1____ +2____

10. Which hand would you use to saw a piece of wood with a hand saw?
-2____ -1____ 0____ +1____ +2____

11. Which hand would you use to open a drawer?
-2____ -1____ 0____ +1____ +2____

12. Which hand would you turn a doorknob with?
-2____ -1____ 0____ +1____ +2____

13. Which hand would you use to hammer a nail?
-2____ -1____ 0____ +1____ +2____

14. Which hand do you use for writing?
-2____ -1____ 0____ +1____ +2____

15. Which hand would you turn the dial of a combination lock with?
-2____ -1____ 0____ +1____ +2____

16. Which hand would you use to sign your name?
-2____ -1____ 0____ +1____ +2____

17. With which hand would you use scissors?
-2____ -1____ 0____ +1____ +2____

18. With which hand would you use a toothbrush?
-2____ -1____ 0____ +1____ +2____

19. With which hand would you use a broom (upper hand)?
-2____ -1____ 0____ +1____ +2____

20. Which hand would you use to strike a match?
-2____ -1____ 0____ +1____ +2____

21. Which foot would you use to kick a ball?
-2____ -1____ 0____ +1____ +2____

22. Which hand would you use to swing a bat (upper hand)?
-2____ -1____ 0____ +1____ +2____

21. Is there any reason (e.g. injury) why you have changed your hand preference for any of the above activities?
YES (Explain) NO

22. Have you ever been given special training or encouragement to use a particular hand for certain activities?
YES (Explain) NO

1. Do you consider yourself:

Right-handed Left-handed Ambidextrous (both hands)

2. Is there anyone in your immediate family who is Left-handed? Yes or No

If yes, who____

3. Did you ever change handedness? Yes or No

If yes, please explain____
____
____

4. Is there any activity not on this list that you do consistently with your left hand? If so, please explain:
____
____
____

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