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Manual preferences for visually- and haptically-guided grasping

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ABSTRACT

Studies have shown that individuals exhibit a right-hand preference for grasping during visually-guided tasks. Recently, we have found that when vision is occluded right-hand preference decreases dramatically. It remains unknown however, if this decrease is a result of visual occlusion or the effects of relying only on haptic feedback. Therefore, in the present study, we sought to explore the contributions of vision and haptics (separately *and* in conjunction) to hand preference for grasping. Right- and left-handed individuals were tested on a block building task under four different visual and haptic conditions: 1) vision/normal haptic feedback (V/H), 2) no vision/normal haptic feedback (NV/H), 3) vision/constrained haptic feedback (V/Constrained-H), and 4) no vision/constrained haptic feedback (NV/Constrained-H). Vision was occluded using a blindfold and haptic feedback was constrained by asking participants to wear textured gloves. Right-handed individuals displayed a right-hand preference when vision was available (V/H and V/Constrained-H groups), but this preference was much greater when haptic feedback was constrained (V/Constrained-H group). When vision was occluded and haptic feedback was used to complete the task (NV/H) no hand preference was found. Finally hand preference was similar between the V/H and the NV/Constrained-H groups. For left-handed individuals, no differences in hand use were found between the different sensory groups, but the NV/H group showed a clear left-hand preference for haptically-guided grasping. The results suggest that haptics plays an important role in hand preference for grasping. Furthermore, they support a left-hand/right-hemisphere specialization for haptically-guided grasping (regardless of handedness) and a right-hand/left-hemisphere specialization for visually-guided grasping (at least in right-handed individuals).

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1. Introduction

Research has shown that vision plays a pivotal role in guiding goal-directed movement. In fact, it has been argued that the primary reason vision evolved was for the distal control of movement (Goodale, 1983). Kinematic analyses have confirmed the importance of visual feedback during goal-directed movement, and in particular, the reach-to-grasp action. When vision is occluded, individuals display larger maximum grip apertures (Jackson, Jackson & Rosicky, 1995; Jakobson & Goodale, 1991; Rand, Lemay, Squire, Shimansky & Stelmach, 2007), slower movement times (Schettino, Adamovich & Poizner, 2003; Winges, Weber & Santello, 2003), and a decrease in task accuracy, to the degree that the hand often collides with the target object (Wing, Turton & Fraser, 1986) or misses the target completely (Babinsky, Braddick & Atkinson, 2012). In contrast, in the presence of vision, individuals show improved endpoint accuracy (Westwood, Heath & Roy, 2003), correct object size scaling (Keefe & Watt, 2009), and enhanced movement regulation (Saunders & Knill, 2003; Tremblay, Hansen, Kennedy & Cheng, 2013). Not surprisingly, vision also plays a critical role in hand preference for grasping. During visually-guided grasping tasks, individuals (even some left-handed) exhibit a clear preference to grasp objects with the right-hand (Bishop, Ross, Daniels & Bright, 1996; Bryden & Roy, 2006; Calvert & Bishop, 1998; Gabbard & Rabb, 2000; Gonzalez & Goodale, 2009; Jacquet, Esseily, Rider & Fagard, 2012; Stone & Gonzalez, 2014a; Stone, Bryant & Gonzalez, 2013). The role of haptics in hand preference for grasping however, has been seldom investigated. Haptics is the perception of combined tactile and kinesthetic inputs during object manipulation and exploration (Grunwald, 2008; Keysers, Kaas & Gazzola, 2010; Lederman & Klatzky, 2009). Kinematic studies of haptically-guided grasping have shown that pre-shaping of the hand could be as accurate as when guided by vision (Karl, Sacrey, Doan & Whishaw, 2012). So although this information suggests that haptics can effectively be used to guide reach-to-grasp movements, the contribution of haptics to hand preference remains unknown. Is there a right-hand preference during haptically-guided grasping as there is during visually-guided grasping?

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We recently investigated this question using the block building task (Gonzalez & Goodale, 2009; Stone & Gonzalez, 2014a,b; Stone et al., 2013) and found that when individuals are blindfolded and must use only their sense of touch to complete the task (rendering it a haptically-guided task), no hand preference is observed (Stone & Gonzalez, 2014a,b). As haptic discrimination of the building blocks plays a central role in the task, these results pose the question: is this decrease in right-hand use (or increase in left-hand use) due to a left-hand advantage for haptic discrimination? Several studies have shown a left-hand advantage for haptic discrimination. In these studies, individuals have been asked to tactically identify numbers (Heller, Rogers & Perry, 1990) and letters (O'Boyle, Van Wyhe-Lawler & Miller, 1987, including Braille: e.g. Hermelin & O'Connor, 1971; Wilkinson & Carr, 1987) or haptically assess and discriminate between object properties including: thickness (Cormier & Tremblay, 2013), roughness (Tomlinson, Davis, Morgan & Bracewell, 2011), curvature (Squeri et al., 2012), shape (Fagot, Hopkins & Vauclair, 1993a; Fagot, Lacreuse & Vauclair, 1993b), or hardness (Morange-Majoux, 2011) for various objects. For instance, O'Boyle et al. (1987) traced capital letters onto the palms of individuals and found that accuracy was higher when the letter was traced onto the left hand. Also, Heller et al. (1990) found that individuals were more accurate at identifying numbers on a vibrotactile display with the left hand (when compared to the right hand). In fact, evidence for this advantage emerges in infancy. When infants (4 to 6 months of age) are given a cylinder to explore, the left hand spends more time than the right hand touching the object, which was suggested as a left-hand advantage for haptic processing (Morange-Majoux, 2011). Patient studies show that individuals with right- but not left-hemisphere damage show bilateral impairment on tactile tasks, attributing the findings to a left-hand/right-hemisphere advantage for haptic processing (Cannon & Benton, 1969; Fontenot & Benton, 1971; Milner & Taylor, 1972; Zaidel & Sperry, 1973). Together this evidence suggests that the right hemisphere plays a pivotal role in haptic processing.

In Stone and Gonzalez (2014a,b), occluding vision during a grasping task revealed a decrease in right-hand use (inevitably resulting in an increase in left-hand use). Because vision is our dominant source of sensory information (Atkinson, 2000; Rock & Victor, 1964), it is possible that the decrease in right-hand use is exclusively related to the lack of visual feedback. Alternatively, because without vision participants had to rely on haptics to complete the task, the decrease in right-hand use could be due to the left-hand/right-hemisphere specialization for haptic processing. Furthermore, it remains unknown if or how this specialization presents in left-handed individuals. Therefore, in the present experiment, we investigate the contributions of vision and haptics (separately *and* in conjunction) to hand preference for grasping in a right- and a left-handed population.

Right- and left-handed individuals were tested on the block building task (see Gonzalez, Whitwell, Morrissey, Ganel & Goodale, 2007; Stone & Gonzalez, 2014a; Stone et al., 2013). Participants in four different groups (Vision/normal haptic feedback (V/H), No Vision/normal haptic feedback (NV/H), Vision/constrained haptic feedback (V/Constrained-H), No Vision/constrained haptic feedback (NV/Constrained-H)) were asked to replicate 3D models from a tabletop of evenly distributed building blocks. Vision was occluded by using a blindfold and haptics was constrained by using textured fitted gloves. If vision is the primary modulator of hand preference for grasping then manipulating haptic feedback should have little to no effect on this preference. In other words groups V/H and V/Constrained-H should show similar rates of right-hand use. However, if haptic feedback is important for hand selection these two groups should be different. If there is a left-hand advantage for processing haptic information we expect to see a decrease in left-hand use in the V/Constrained-H when compared to the V/H group. Hand preference for grasping was documented in ipsilateral (same side as the hand) and contralateral (opposite side of the hand) space.

2. Experiment One (right-handers)

2.1. Methods and procedures

2.1.1. Participants

Eighty self-reported right-handed individuals (29 males) were recruited for this study. Seventy-eight participants were from the University of Lethbridge between the ages of 18 and 33 and participated in exchange for course credit. Two students were recruited from a local high school (2 females, aged 16 and 17). Twenty participants were randomly assigned to each of the four test groups: Vision/normal haptic feedback (V/H), No Vision/normal haptic feedback (NV/H), Vision/constrained haptic feedback (V/Constrained-H), and No Vision/constrained haptic feedback (NV/Constrained-H). All participants gave written informed consent in accordance with the Declaration of Helsinki and the approval of the University of Lethbridge Human Subjects Research Committee (protocol #2011-22) before participating in the study. Participants were naïve to the purposes of the study and able to withdraw at any time without consequence.

2.1.2. Apparatus and stimuli

2.1.2.1. Handedness questionnaire. A modified version of the Edinburgh (Oldfield, 1971) and Waterloo (Brown, Roy, Rohr & Bryden, 2006) handedness questionnaires were given to all participants at the end of the block building task. This version included questions on hand preference for 22 different tasks (see Appendix 1). Participants had to rate which hand they prefer to use for each task 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.

2.1.2.2. Block building task. A total of three models built with LEGO® blocks were used for the experiment. These blocks ranged in size from <1.5 L × 0.7 W × 1.0 cm H to 3.1 L × 1.5 W × 1.0 cm H. Each model contained 10 blocks of various colors and shapes (see Supplementary material for a picture of models used). 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 three models. The models were prepared ahead of time by the experimenter. The same three models were used with all participants. The same number of blocks was placed on the left and right side of the table. There was a fixed building plate (19 L × 19 cm W) located within arms' length of the participant. Additionally, there was an exact duplicate of this building plate in the front and center of the participant. The far plate had the model to be replicated attached to it, and the near plate was used for the construction of the new model (see Fig. 1 for an example of the display).

2.1.3. Procedures

Participants were seated in front of the table facing the middle of the display which was covered by an opaque tablecloth. To assess how vision and/or haptics affected hand preference for grasping, prior to task initiation, sensory (vision or haptics) availability was manipulated. Individuals either put on a blindfold (NV/H), a pair of Atlas Fit 300™ textured rubber gloves (V/Constrained-H), or a blindfold *and* a pair of textured rubber gloves (NV/Constrained-H). Those in the V/H group did not wear a blindfold or gloves and completed

Fig. 1. Photograph of a participant in the NV/Constrained-H group completing the task. Please note that the participant is wearing a blindfold as well as a pair of gloves. The model to be replicated is located on the clear plate. Using the blocks on the table, the participant will complete a replica of this model on the green plate.

the task under this test condition. Once the instructions were clear for the participant, the opaque tablecloth was removed from the table, revealing the display. Please note that those individuals wearing a blindfold (i.e. NV/H or NV/Constrained-H group) did not see the display at any time. A model was placed on the far building plate and participants were instructed to replicate it as quickly and accurately as possible from the blocks given on the table. 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. 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.

2.1.4. Data analysis

All recorded videos were analyzed offline. Each grasp was recorded as a left- or right-hand grasp in the participants' ipsilateral or contralateral space. The total number of grasps was calculated to determine a percent of right-hand use (number of right grasps / total number of grasps × 100). The time it took participants to construct each model was recorded on a stopwatch and reported in seconds. Data were analyzed using SPSS Statistics 19.0 for Windows (SPSS Inc., Chicago, IL, USA). Tests of normality (Kolmogorov–Smirnov & ShapiroWilk) revealed that the data was normally distributed. An analysis of variance (ANOVA) was performed on the values of right-hand use, as in previous reports using similar tasks and measures (Bryden & Huszczynski, 2011; Bryden & Roy, 2006; Bryden, Pryde & Roy, 2000; Cavill & Bryden, 2003; de Bruin, Bryant & Gonzalez, 2014; Sacrey, Arnold, Whishaw & Gonzalez, 2013; Stone & Gonzalez, 2014a,b; Stone et al., 2013).

2.2. Results

2.2.1. Handedness questionnaire

All participants self-reported as right-handers and this was confirmed by the handedness questionnaire. The average scores for each group out of a total possible score of −44/+44 were as follows: V/H group: +31.4 (±1.3 SE; range +22 to +43); NV/H group: +30.7 (±1.2 SE; range +21 to +40); V/Constrained-H group: +32.9 (±0.8 SE; range +25 to +38); NV/Constrained-H group: +32.5 (±1.1 SE; range +19 to +40). A one-way analysis of variance (ANOVA) revealed no differences among the groups (F (3, 79) = 0.7; p = 0.5).

2.2.2. Build times for models

Given that individuals who had vision for the duration of the task (i.e. V/H, V/Constrained-H) were substantially faster than those who did not (i.e. NV/H, NV/Constrained-H; p < 0.0001), comparisons between the two sets of group were done separately. Groups with vision: An independent samples t-test revealed that on average the V/H group built one model significantly faster than the V/Constrained-H group (M = 24.8 ± 0.8 s versus M = 35.0 ± 1.7 s, (t (38) = −5.3; p < 0.0001)). Groups with no vision: An independent samples t-test revealed that on average the NV/H group built one model significantly faster than the NV/Constrained-H group (M = 160.8 ± 11.5 s versus M = 313.6 ± 14.7 s, (t (38) = −8.1; p < 0.0001)). Thus, it is clear that regardless of visual availability (i.e. vision or no vision) during this grasping task, constraining haptics significantly increased the amount of time it took to complete one model (see Table 1).

2.2.3. Hand use for grasping

A one-way ANOVA with group (V/H, NV/H, V/Constrained-H, NV/Constrained-H) as the independent measure and percentage

Table 1
Means and standard errors for average build times per model for all groups in Experiment One (right-handers) and Experiment Two (left-handers). Asterisks denote significance within visual availability groups.

Visual availability	Group	Mean (sec)	Standard error (sec)
Right-handers			
With vision	V/H	24.8**	±0.8
	V/Constrained-H	35.0	±1.7
Without vision	NV/H	160.8**	±11.5
	NV/Constrained-H	313.6	±14.7
Left-handers			
With vision	V/H	21.2**	±4.8
	V/Constrained-H	31.8	±4.6
Without vision	NV/H	166.3**	±16.1
	NV/Constrained-H	303.6	±24.0

** $p < 0.0001$.

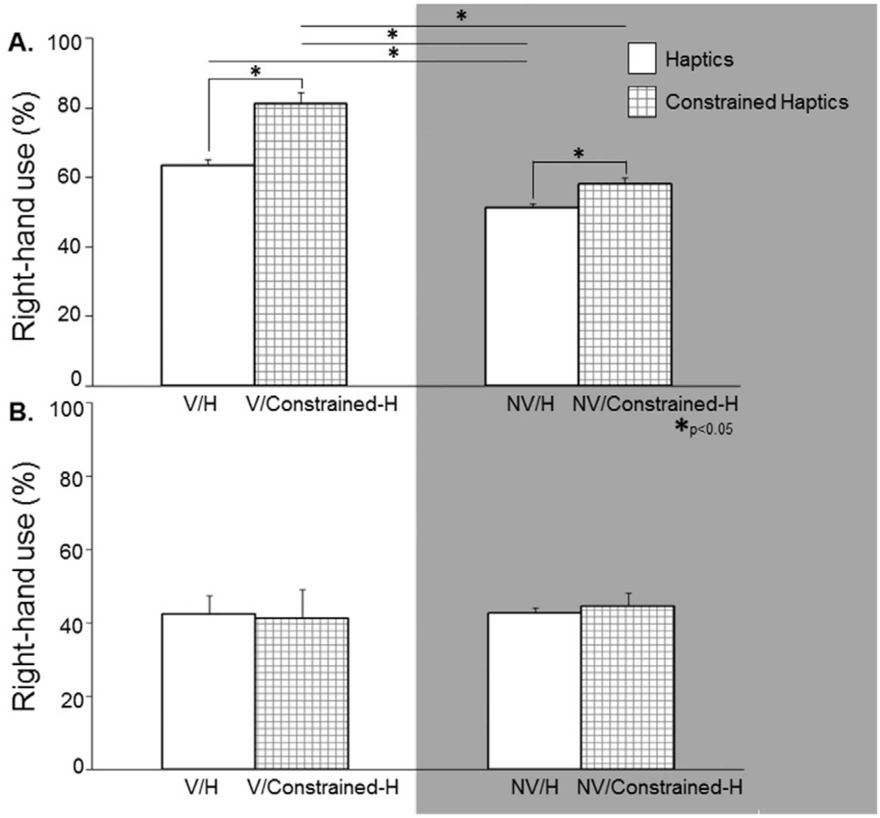

Fig. 2. A) Overall hand use in right-handers: This graph demonstrates right-hand use for all four groups (V/H, V/Constrained-H, NV/H, NV/Constrained-H) in Experiment One. White bars represent the groups who had normal haptics for the duration of the task (V/H, NV/H). The bars filled with the gray grid represent the groups who had constrained haptics for the duration of the task (i.e. wore a pair of gloves; V/Constrained-H, NV/Constrained-H). The left side of the graph (with the white background), represents the two groups who had vision for the duration of the task: V/H and V/Constrained-H. The right side of the graph (with the gray background) represents the groups who did not have vision for the duration of the task (i.e. blindfolded; NV/H, NV/Constrained-H). Note the significant increase in right-hand use within the vision and no vision groups when haptics was constrained. Also note that the only two groups who did *not* differ from one another were the V/H and NV/Constrained-H groups. All other differences are significant. B) Overall hand use in left-handers: This graph demonstrates right-hand use for all four groups in Experiment Two. Note that there are no significant differences within or between sensory groups. Also note that the NV/H group were significantly different from 50%, showing a left-hand preference for grasping.

of right-hand use as the dependent measure was performed. Right-hand use differed significantly across the four groups (F (3, 79) = 35.3; $p < 0.0001$). Levene's test indicated unequal variances ($p < 0.0001$), thus the appropriate post-hoc tests were used. Games-Howell post-hoc comparisons indicated that the V/Constrained-H group used their right-hand for grasping (81.2 ± 3.3%) significantly more than the V/H group (63.5 ± 1.6%), the NV/H group (51.3 ± 1.2%), and the NV/Constrained-H group (58.2 ± 1.7%; $p < 0.0001$ for all comparisons). Also, the V/H group used the right-hand significantly more than the NV/H group ($p < 0.0001$). No significant differences were found between the V/H group and the NV/Constrained-H group ($p = 0.1$). See Fig. 2A for results.

2.2.3.1. Comparison to 50%. To examine if hand use for grasping was significantly different from chance (Gonzalez et al., 2007 and Stone & Gonzalez, 2014a), we compared the results of each group to a value of 50%. Paired samples t-tests revealed that percentage of right-hand use in the V/H, V/Constrained-H, and NV/Constrained-H was significantly different from 50% ($p < 0.0001$ for all comparisons). That is, all groups showed a right-hand preference for grasping. Percentage of right-hand use in the NV/H group (51%) was *not* significantly different from 50% (t (19) = 1.1; $p = 0.2$). In other words, when participants use only haptics for the task, the preference to use the right-hand for grasping is lost. This highlights the role of the left-hand/right-hemisphere during haptically-guided grasping.

2.2.4. Analysis of contralateral grasps

Analysis using a 2 (hand) × 4 (group) repeated measures ANOVA was performed on the percentage of contralateral grasps during the task. Hand (right, left) was a within subject factor and group (V/H, NV/H, V/Constrained-H, NV/Constrained-H) a between subject factor. Levene's test indicated unequal variances for both the right and the left hands ($p < 0.005$), thus the appropriate post-hoc tests were used (Games-Howell). There was a main effect of hand (F (1, 76) = 128.9; $p < 0.0001$, ES = 0.6). Individuals made significantly more right-handed grasps into left contralateral space (12.7 ± 1.0%) than left-handed grasps into right contralateral space (1.0 ± 0.2%). There was also a main effect of group (F (3, 76) = 34.9; $p < 0.0001$, ES = 0.5). Individuals in the V/Constrained-H group made significantly more contralateral grasps (15.4 ± 1.0%) than the V/H (7.7 ± 1.0%), NV/H (1.7 ± 1.0%), and NV/Constrained-H (2.8 ± 1.0%) groups ($p < 0.0001$ for all comparisons). The hand by group interaction was also significant (F (3, 76) = 40.0; $p < 0.0001$, ES = 0.6). Post hoc analysis (independent samples t-tests) revealed that the V/Constrained-H group made significantly more right-handed grasps into left contralateral space (30.3 ± 2.0%) than the V/H (13.8 ± 2.0%), NV/H (2.0 ± 2.0%), and NV/Constrained-H (4.8 ± 2.0%) groups

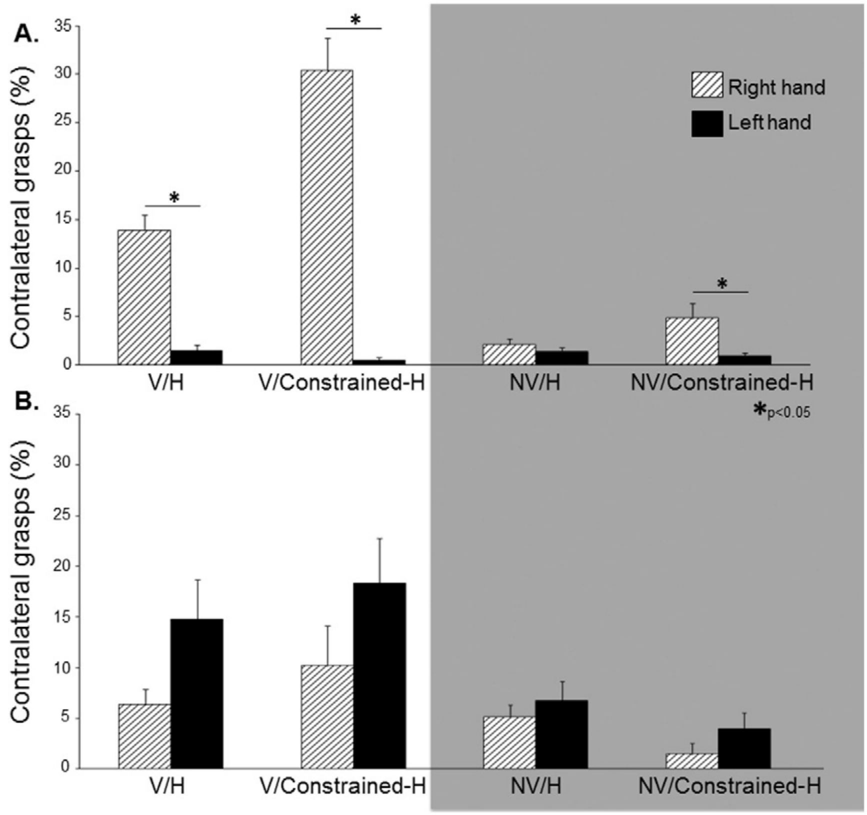

Fig. 3. A) Contralateral grasps in right-handers: The following graphs demonstrate right- and left-handed contralateral grasps for all four groups (V/H, V/Constrained-H, NV/H, NV/Constrained-H) in Experiments One. The bars filled with the diagonal pattern represent the right-hand. The bars filled with black represent the left hand. The left side of the graph (with the white background), represents the two groups who had vision for the duration of the task: V/H and V/Constrained-H. The right side of the graph (with the gray background) represents the groups who did not have vision for the duration of the task (i.e. blindfolded; NV/H, NV/Constrained-H). Note the significant differences between right- and left-handed contralateral grasps for the V/H, V/Constrained-H, and NV/Constrained-H groups. In addition, the V/Constrained-H group made significantly more right contralateral grasps than all other groups. No differences emerged between groups for left-handed contralateral grasps. B) Contralateral grasps in left-handers: This graph demonstrates right- and left-handed contralateral grasps for all four groups in Experiment Two. There were no differences between right- and left-contralateral grasps within each group. The only significant differences were between the V/Constrained-H and the groups without vision.

($p < 0.0001$ for all comparisons). The V/H group made significantly more right-handed grasps into left contralateral space than both the NV/H and NV/Constrained-H groups ($p < 0.0001$ for both comparisons). This difference, however, was not present between the NV/H and NV/Constrained-H t (25.3) = −1.6; $p = 0.1$ (unequal variances assumed). So it appears that not having visions reduces contralateral grasps. See Fig. 3A for these results.

2.2.5. Discussion and rationale for Experiment Two

Results revealed a robust increase in right-hand use when haptics was constrained regardless of visual availability. This finding lends support to the idea of a left-hand/right-hemisphere specialization for haptic processing. Yet, individuals in the NV/Constrained-H group did not differ from the V/H group, both displaying a preference to use the right-hand for grasping. So, when both vision and haptics were occluded, a right-hand preference remained. Is this right-hand preference because participants were right-handed, or because grasping is a specialized function of the left hemisphere? This question provided the rationale for our second experiment. In Experiment Two, we tested left-handed individuals on the same task under the same sensory conditions. If the use of the right-hand in NV/Constrained-H and V/H trials is affected by handedness, then left-handed individuals should show a preference for their dominant left hand during these trials. If however, left-handers do not display a left-hand preference during these trials, then the results of the right-handers could be attributed to a right-hand/left-hemisphere specialization for grasping (Castiello, 2005; Gonzalez & Goodale, 2009; Gonzalez, Ganel & Goodale, 2006; Gonzalez et al., 2007; Goodale, 1988; Janssen, Meulenbroek & Steenbergen, 2011; Netelenbos & Gonzalez, 2015; Serrien, Ivry & Swinnen, 2006; Stone et al., 2013).

3. Experiment Two (left-handers)

3.1. Methods and procedures

3.1.1. Participants

Sixty self-reported left-handed individuals (16 males) between the ages of 17 and 30 years old were recruited from the University of Lethbridge and participated in exchange for course credit. Fifteen participants were randomly assigned to each of the four test groups: Vision/normal haptic feedback (V/H), No Vision/normal haptic feedback (NV/H), Vision/constrained haptic feedback (V/Constrained-H), and No Vision/constrained haptic feedback (NV/Constrained-H). All participants gave written informed consent in accordance with the Declaration of Helsinki and the approval of the University of Lethbridge Human Subjects Research Committee (protocol #2011-22) before participating in the study. Participants were naïve to the purposes of the study and able to withdraw at any time without consequence.

3.1.2. Apparatus and stimuli

All the display material and equipment were the same as in Experiment One.

3.1.3. Procedures

All procedures were identical to those used in Experiment One.

3.1.4. Data analysis

Data analysis was the same as Experiment One.

3.2. Results

3.2.1. Handedness questionnaire

All participants self-reported as left-handers and this was confirmed by the handedness questionnaire. The average scores for each group out of a total possible score of −44/+44 were as follows: V/H group: −18.8 (±3.0 SE; range −38 to −5); NV/H group: −18.0 (±4.4 SE; range −42 to +19); V/Constrained-H group: −20.8 (±3.8 SE; range −42 to +5); NV/Constrained-H group: −18.3 (±3.9 SE; range −42 to +19). A one-way ANOVA revealed no differences between the groups (F (3, 59) = 0.1; $p = 0.9$).

3.2.2. Build times for models

Again, since individuals who had vision for the duration of the task (i.e. V/H, V/Constrained-H) were substantially faster than those who did not have vision (i.e. NV/H, NV/Constrained-H; $p < 0.0001$), comparisons between the two sets of group were done separately. Groups with vision: An independent samples t-test revealed that on average the V/H group built one model significantly faster than the V/Constrained-H group (M = 21.2 ± 4.8 s versus M = 31.8 ± 4.6 s, (t (28) = −6.0; $p < 0.0001$)). Groups with no vision: An independent samples t-test revealed that on average the NV/H group built one model significantly faster than the NV/Constrained-H group (M = 166.3 ± 16.1 s versus M = 303.6 ± 24.0 s, (t (28) = −4.7; $p < 0.0001$)). Thus, similar to right-handed individuals (Experiment One), constraining haptics significantly increased the amount of time it took to complete one model regardless of visual availability. See Table 1 for results.

3.2.3. Hand use for grasping

A one-way ANOVA was performed on percentage of right-hand use between all four groups (V/H, NV/H, V/Constrained-H, NV/Constrained-H). In contrast to the results in right-handers, no significant differences in right-hand use were found in left-handers across the four groups (F (3, 59) = 0.07; $p = 0.9$). See Fig. 2B for results.

3.2.3.1. Comparison to 50%. Again, to examine if hand use for grasping was significantly different from chance, we compared the results of each group to values of 50%. Paired samples t-tests revealed that percentage of right-hand use in the V/H, V/Constrained-H, and, NV/Constrained-H was not different from 50% ($p > 0.1$ for all comparisons). Right-hand use in the NV/H group (41%) however, *was* significantly different from 50% (t (14) = −5.3; $p < 0.001$). This result suggests that consistent with the findings in right-handers, when the task is solely guided by haptics there is an increase in left-hand use.

3.2.4. Analysis of contralateral grasps

Analysis using a 2 (hand) × 4 (group) repeated measures ANOVA was performed on the percentage of contralateral grasps during the task. Hand (right, left) was a within subject factor and group (V/H, NV/H, V/Constrained-H, NV/Constrained-H) a between subject factor. Levene's test indicated unequal variances for both the right and the left hands ($p < 0.002$), thus the appropriate post-hoc tests were used (Games-Howell). There was a main effect of hand (F (1, 56) = 4.9; $p = 0.03$, ES = 0.08). Individuals made significantly more left-handed grasps into right contralateral space (10.9 ± 1.5%) than right-handed grasps into left contralateral space (5.7 ± 1.1%). There was also a main effect of group (F (3, 56) = 11.7; $p < 0.0001$, ES = 0.3). Individuals in the V/Constrained-H group made significantly more contralateral grasps (14.2 ± 1.4%) than the NV/H (5.8 ± 1.4%) and NV/Constrained-H (2.7 ± 1.4%) groups ($p = 0.006$ and $p < 0.0001$, respectively), but not the V/H (10.5 ± 1.4%) group ($p = 0.4$). The hand by group interaction was not significant (F (3, 56) = 0.5; $p = 0.6$, ES = 0.03). See Fig. 3B for results.

4. General discussion

In the present study we sought to investigate the contributions of vision and haptics (separately *and* in conjunction) to hand preference for grasping. We asked 80 right-handed and 60 left-handed individuals to replicate LEGO© models while under one of the following test conditions: 1) sighted (V/H group), 2) blindfolded (NV/H group), 3) sighted, but wearing a pair of gloves (V/Constrained-H group), or 4) blindfolded, *and* while wearing a pair of gloves (NV/Constrained-H group). The purpose of wearing a pair of gloves was to constrain haptic feedback. Results of the right-handed participants showed that the right-hand was used most often (>80% of the time) when they had vision but constrained haptic feedback, and least often (only 50% of the time) when vision was occluded but haptic feedback was intact. Puzzling, hand preference for grasping when both sensory systems were available (V/H group) was similar to hand preference when both were absent or constrained (NV/Constrained-H). We reasoned that this could be attributed to the natural tendency of right-handers to prefer their dominant hand for grasping and thus tested a population of left-handers. Left-handers, however, failed to show a hand preference (except for the NV/H group) and demonstrated little to no change in hand use under the different sensory modalities. The only group that was affected by manipulating sensory feedback was the NV/H group who showed consistent left-hand use during the task. This last finding together with the results of the right-handers (which comprise ~90% of the population), suggest a double dissociation between the left and right hemispheres for visually- and haptically-guided grasping. That is, a left-hemisphere/right-hand advantage for visually-guided grasping (which was most evident when there was no contribution of haptics), and a right-hemisphere/left-hand advantage for haptically-guided grasping (which was most evident when there was no contribution of vision).

Some studies have suggested that vision plays a role in hand preference (Michel, 1981; Ocklenburg et al., 2010), whereas others have concluded otherwise (Carey & Hutchinson, 2013; Ittyerah, 1993, 2009). For instance, Ocklenburg et al. (2010) tested over 100 children with congenital torticollis and found that those individuals who had a fixed head tilt to the left (and thus extensive visual information concerning actions of the right-hand) were significantly more likely to be right-handed than individuals who had a fixed head tilt to the right *and* individuals with no head tilt at all (controls). Yet, Ittyerah (1993, 2009) found that hand preference in congenitally blind children (who have never had a visual experience) is not significantly different from sighted children. These studies, however, were not examining hand preference *for grasping* per se. In recent investigations, Stone and Gonzalez (2014a,b) have found that occluding vision during a natural grasping task decreases the preference to use the right-hand, suggesting that vision plays a role in hand preference for grasping. Yet these studies did not investigate if such increase was the result of participants relying on haptics, being deprived of vision, or both. So, in the current study we predicted that if vision was the sole contributor to this hand preference, then the V/H and the V/Constrained-H groups should display similar rates of hand use. The results of Experiment One showed differently. The V/H group demonstrated a significantly lower average in right-hand use (63.5%) when compared to the V/Constrained-H group (81.2%). Furthermore, analysis of contralateral grasps revealed that the V/Constrained-H group was significantly more likely than any other group to reach across space with their dominant right-hand to grasp a block. The findings of the visually-guided grasping groups support the view of a left-hemisphere/right-hand specialization for grasping, as has been argued before (Castiello, 2005; Gonzalez & Goodale, 2009; Gonzalez et al., 2006, 2007; Goodale, 1988; Janssen et al., 2011; Netelenbos & Gonzalez, 2015; Serrien et al., 2006; Stone et al., 2013).

Studies have investigated how constraining haptics can affect one's ability to haptically identify and/or discriminate between objects. In these studies, individuals without visual feedback wore thick mittens (Klatzky, Loomis, Lederman, Wake & Fujita, 1993; Lakatos & Marks, 1999), splinted gloves (Lakatos & Marks, 1999), finger sheaths or splints (Klatzky et al., 1993; Lederman & Klatzky, 2004), or were restricted in the number of fingers that they could use during these tasks (Lederman & Klatzky, 2004). For instance, in Klatzky et al. (1993), individuals identified numerous common objects (e.g. ball, stapler, cup) under different conditions of reduced haptic feedback. Participants were slower and less accurate in these conditions than when using their bare hands. Similar results were found in the other studies that have constrained haptic feedback. Our study aligns with these findings with respect to build times: participants were faster at completing the task when haptic feedback was available than when it was constrained. None of the previous studies however, documented hand use. It has been suggested that grasping an object is the most efficient method to process and extract object properties during haptic discrimination (Lederman & Klatzky, 2009; Lederman, Klatzky, Chataway & Summers, 1990). In the current investigation, we predicted that if haptic feedback was the major contributor to hand preference for grasping, then similar rates of hand use should be seen in the V/H and the NV/H group. This was not the case. While the V/H group showed a right-hand preference, the NV/H group displayed no preference at all (51.3% right-hand use). These findings support the view of a right-hemisphere/left-hand specialization for haptic processing as has been argued before (Benton, Levin & Varney, 1973; De Renzi, Faglioni & Scotti, 1969; Dodds, 1978; Fagot, Hopkins & Vauclair, 1993a; Fagot, Lacreuse & Vauclair, 1993b; Harada et al., 2004; Milner & Taylor, 1972; O'Boyle et al., 1987; Riege, Metter & Williams, 1980; Tomlinson et al., 2011).

One puzzling finding of the current study is that the NV/Constrained-H group used their right hands to a similar extent as the V/H group. That the latter group exhibited a right-hand preference was not surprising given the abundant literature showing a right-hand preference for grasping and specifically when completing the block building task. However, that the NV/Constrained-H group also displayed a right-hand preference is surprising. We speculate that because the majority of our grasping actions are executed with vision, in the absence of both vision *and* haptics hand selection would rely on the more practiced system: right-hand/left-hemisphere. Together the results of all four groups suggest first, that vision and haptics do not contribute equally but also, and perhaps more importantly, that hand preference is more than the additive effect of the two systems. When vision was not contributing to the task and haptics was guiding the action (NV/H), right-hand use was 50%, restoring vision only brought this preference up to ~60%, and removing haptics to ~80%. This suggests that hand preference for grasping is modulated by a dynamic system that is influenced not only by vision and haptics, but possibly also by other interoceptive or exteroceptive factors.

Left-handers, on average, displayed a modest and insignificant left-hand preference for grasping under all sensory conditions (~58%). Research has shown that left-handers represent a very heterogeneous population (Annett, 1970; Bryden & Huszczynski, 2011; Calvert & Bishop, 1998; Flindall, Stone & Gonzalez, 2014; Gonzalez et al., 2007; Judge & Stirling, 2003; Stone et al., 2013; Tapley & Bryden, 1985; Willems, Van der Haegen, Fisher & Francks, 2014; Yahagi & Kasai, 1999). In fact, in the current study left-hand use values ranged from 4% to 96% when vision was available, illustrating the high variability in manual preference of left-handers (compared to right-handers who ranged from 51% to 100%). The only group that showed a consistent and significant left-hand preference was NV/H group, wherein the variability (standard deviation) of hand use was 5.2% (similar to that of the right-handed NV/H group: 5.4%). With respect to the other groups, the variability in left-handers was 21.2% (but only 10% in right-handers) further illustrating the heterogeneity of hand use in left-handed individuals. The consistent preference to use the left hand when the task was solely guided by haptics offers support to the theory of a left-hand specialization for haptic processing. Nonetheless, in the other groups we failed to observe modulation of hand preference according to sensory modality. One might argue that this is due to the between-subject nature of the comparisons. In a pilot study, we tested a group of left-handers using a within study design (not reported). Similar to the between-subject design, results showed no modulation in hand use under the different sensory conditions. Together, these results lend support to previous research showing atypical cerebral organization in left-handers (Bryden, Hecaen & DeAgostini, 1983; Gur, Gur, Obrist, et al., 1982; Levy & Reid, 1978; Mazoyer, Zago, Jobard, et al., 2014; Steinmetz, Volkmann, Jancke & Freund, 1991; Szaflarski et al., 2002; Willems et al., 2014).

In conclusion, the results of the current study uncover how the visual and haptic systems contribute to and shape hand preference for grasping in both right- and left-handed individuals. Furthermore, they highlight the integrated yet divided roles of the left and right hemispheres for sensory-guided movements. Future studies could complement or refine these findings using imaging or electrophysiological techniques.

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Appendix 2. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.actpsy.2015.06.004.

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Appendix 1. Waterloo/edinburg handedness questionnaire

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 non-dominant hand? If so, please explain:

____
____
____

Appendix 1. (*continued*)

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