

**VISION AND HAPTICS:
HOW SENSORIMOTOR INTERACTIONS INFLUENCE GRASPING**

KAYLA D. STONE
B.Sc. (Psychology), University of Lethbridge, 2013

A Thesis
Submitted to the School of Graduate Studies
of the University of Lethbridge
in Partial Fulfillment of the
Requirements for the Degree

[MASTER OF SCIENCE]

Department of Neuroscience
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

© Kayla D. Stone, 2015

VISION AND HAPITCS:
HOW SENSORIMOTOR INTERACTIONS INFLUENCE GRASPING

KAYLA D. STONE

Date of Defense: July 10, 2015

Claudia Gonzalez Supervisor	Associate Professor	PhD
--------------------------------	---------------------	-----

Jon Doan Thesis Examination Committee Member	Associate Professor	PhD
---	---------------------	-----

Robbin Gibb Thesis Examination Committee Member	Associate Professor	PhD
--	---------------------	-----

Sergio Pellis Thesis Examination Committee Member	Professor	PhD
--	-----------	-----

David Euston Chair, Thesis Examination Committee	Assistant Professor	PhD
---	---------------------	-----

Dedication

For my parents, who have always encouraged me to follow my passion

ABSTRACT

The purpose of this thesis was to investigate the sensory contributions to hand preference for grasping. While numerous studies have investigated this preference for visually-guided grasping (a left-hemisphere specialization), very few have documented it during haptically-guided actions (a right-hemisphere specialization). In a series of four studies, participants (healthy adults, congenitally blind, and children) were asked to replicate 3D-block models from a tabletop of blocks while the hand used for grasping was recorded. Overall the results showed a right-hand preference for grasping independent of age and visual experience (but not sensory modality). Haptics played a modest, yet significant, role in modulating hand preference, as there was a significant reduction in right-hand use in the absence of vision (i.e. during haptically-guided grasping). Because the left hand was never used more than 50% of the time, these findings support the theory of a default right-hand/left-hemisphere specialization for grasping that is modulated by haptics.

ACKNOWLEDGEMENTS

I would like to start by thanking my supervisor, Claudia. Thank you for being such a wonderful mentor and friend. Your patience, wisdom, and unwavering support has been pivotal in my passion to pursue research. You have never failed to surprise, challenge, or entertain me. I feel fortunate to have had such an incredible supervisor.

I also extend sincere gratitude to my committee members: Dr. Doan, Dr. Gibb, and Dr. Pellis. Thank you for your feedback and interesting questions throughout my Master's. Your knowledge and expertise is invaluable.

To all of my lab mates in the Brain in Action lab: thank you for your help with my experiments, editing my work, and simply being my best friends. Thank you to my office mate, Jason, for hiding silly surprises around the office over the last two years and sharing your knowledge about statistics, grammar, and dying grass.

Many thanks to the Natural Sciences and Engineering Research Council of Canada (NSERC) and the University of Lethbridge for funding my project.

Finally, I would like to thank my family and my boyfriend, Chase. Thank you for loving and supporting me unconditionally. Mom and Dad, I can never repay you for the immense amount of emotional and financial support you've given me over the years. I will be forever grateful. Scott, thank you for the hours you've spent explaining MATLAB to me and helping me with every other technology-related incident in my life. Chase, thank you for being the light in my life every day. It is because of all of you that I feel confident going in the direction of my dreams.

TABLE OF CONTENTS

Chapter	page
Thesis Examination Committee	ii
Dedication	iii
Abstract	iv
Acknowledgements	v
1. Preface	1
2. The Contributions of Vision and Touch to Grasping	6
2.1. Introduction	8
2.2. Sensory contributions to hand preference for reaching and grasping: Evidence from healthy and neuropsychological populations	9
2.2.1. Left-hemisphere specialization from visually-guided actions	10
2.2.1.1. Evidence from neuropsychological studies	10
2.2.1.2. Evidence from psychophysics and kinematic studies	11
2.2.1.3. Evidence from neuroimaging studies	14
2.2.1.4. Evidence from natural grasping studies	15
2.2.2. Right-hemisphere specialization for haptic processing	17
2.2.2.1. Evidence from neuropsychological studies	18
2.2.2.2. Evidence from studies involving psychophysics and imaging techniques	19
2.2.2.3. Evidence from natural grasping studies	21
2.3. Sensory contributions to hand preference for reaching and grasping: Evidence from sensory-deprived populations	24
2.3.1. Congenitally Blind individuals	24
2.3.2. Deafferented individuals	28
2.4. Sensory contributions to hand preference for reaching and grasping: Evidence from developmental studies	31
2.4.1. Development of right-hand preference for grasping	31
2.4.2. Development of left-hand preference for haptic processing	32
2.5. Integration of hemispheric specializations	36
2.5.1. Evidence from behavioural studies	36
2.5.2. Evidence from neuroimaging studies	38
2.5.3. Sensory integration for grasping	40
2.5.4. A model of how visuo-haptic integration influences hand preference for grasping	42
2.6. Conclusion	45
References	46
3. Limitations, future directions, and implications	75
References	85
Appendices	
1. Grasping with the Eyes of your Hands: Hapsis and Vision Modulate Hand Preference	88
2. Grasping Without Sight: Insights from the Congenitally Blind	108
3. Manual Preferences for Visually- and Haptically-guided Grasping	133
4. Sensory Modulation of Hand Preference For Grasping in Children	154

5. Waterloo/Edinburg Handedness Questionnaire	172
6. Copyright permissions	175

LIST OF FIGURES

Figure no.	page
Chapter 1. The Contributions of Vision and Touch to Grasping	
Figure 1. The block-building task under three different sensory conditions	23

LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
aIPS	anterior intraparietal sulcus
BA	Brodmann's area
CB	congenitally blind
EEG	electroencephalography
hMT+	human middle temporal area
fMRI	functional magnetic resonance imaging
LOC	lateral occipital cortex
NMR	nuclear magnetic resonance
PPC	posterior parietal cortex
SI	primary somatosensory cortex
SII	secondary somatosensory cortex
TFD	temporary functional deafferentation
TMS	transcranial magnetic stimulation

CHAPTER 1

Preface

The objective of this thesis was to investigate the sensory contributions (vision and haptics) to hand preference for grasping in a series of studies using a natural grasping task. Developmental, kinematic, neuropsychological, neuroimaging, and psychophysical studies have suggested that there is a right-hand/left-hemisphere specialization for visually-guided grasping and a left-hand/right-hemisphere specialization for haptic processing. However, no study to date has investigated if this specialization for haptic processing influences hand preference for grasping. It is possible that when vision is occluded, and one must rely on haptics to guide and complete the action, there is an advantage to use the left hand. Moreover, it remains unknown how hand preference is shaped by the interplay of visual *and* haptic information.

Theory: The four studies were based on a theory that there is a default right-hand/left-hemisphere specialization for grasping that is modulated by sensory information.

The hypotheses and predictions are described next and a brief description of each experiment is included below.

Hypotheses and Predictions:

Hypothesis 1: Vision plays a more powerful role than any other sensory modality in modulating hand preference for grasping.

Prediction 1: If vision plays the most influential role in modulating hand preference, and grasping is a function of the left-hemisphere, then right-hand preference should be greatest when vision is available.

Hypothesis 2: Haptics (a specialization of the left-hand/right hemisphere) plays a small, but significant, role in modulating hand use for grasping.

Prediction 2: If haptics plays a role in modulating hand use for grasping, then there should be a significant increase in left-hand use when vision is not available and the grasp is haptically-guided.

Based on these hypotheses, four experiments were designed.

Study 1 (Appendix 1): *Grasping with the eyes of your hands: Haptics and vision*

modulate hand preference. Healthy individuals were asked to replicate 3D block models from a tabletop of building blocks (i.e. the block-building task) while sighted and while blindfolded (i.e. using haptics). Hand preference for grasping was documented. Starting condition was counterbalanced between participants (Vision first or Haptics first).

Results showed a right-hand preference for grasping while sighted, but a robust decrease in this preference when vision was occluded. Moreover, the results revealed an effect of starting condition: individuals in the vision-first group used their right hands for grasping significantly more while sighted than those in the haptics-first group. This finding suggests that grasping the blocks while blindfolded (or having ‘haptic experience’) influenced hand preference for grasping in the subsequent sighted condition (but not vice-versa). A follow-up experiment was conducted wherein blindfolded participants manipulated building blocks in a container for five minutes prior to completing the block-building task. In this case, right-hand preference was even further reduced suggesting that a haptic experience can influence hand preference for grasping.

Study 2 (Appendix 2): *Grasping without sight: Insights from the congenitally blind.*

Congenitally blind (CB) and visually-unimpaired (VU) individuals completed the block-building task with vision (VU only) and without vision (both groups). As in Study 1, results in VU individuals revealed a right-hand preference for grasping when vision was available and no preference when it was occluded. The CB showed a right-hand preference to the same extent as sighted VU did even though their movements were guided exclusively by haptics. This was surprising as the results of Study 1 suggested that haptic experience can modulate hand preference. Perhaps it is because CB individuals experience cerebral reorganization during development. The development of the sensory specializations for grasping is explored in Study 4. The results of the CB however, do not explain the reduction in right-hand use when vision is occluded. Therefore a third study was designed in which the role of haptics was further examined by limiting its contribution during the grasping task.

Study 3 (Appendix 3): *Manual preferences for visually- and haptically-guided grasping.*

Healthy individuals completed the block-building task under different sensory 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 by using a blindfold and haptic feedback was constrained by asking participants to wear textured, fitted gloves. As in Studies 1 and 2, right-handed participants showed a right-hand preference during the V/H condition and no preference during the NV/H condition. When haptics was constrained and the task was guided by vision (V/Constrained-H), participants almost exclusively used their right hand. When both vision and haptics were

occluded/constrained (NV/Constrained-H), right-hand use was not different from the V/H condition. The results demonstrated, for the first time, that haptics plays a significant role in shaping hand preference.

Study 4 (Appendix 4): *Sensory modulation of hand preference for grasping in children.*

Children between 5-8 years of age completed the block-building task under three sensory conditions: 1) vision/normal haptic feedback (V/H), 2) no vision/normal haptic feedback (NV/H), and 3) vision/constrained haptic feedback (V/Constrained-H). Children showed identical hand preferences for grasping as did the adults in response to the manipulations in sensory information: an increase in right-hand use when haptics was constrained but vision was present, and a decrease in right-hand use when vision was occluded but haptics was present. The results support a hemispheric division of labour for visually- and haptically-guided actions that is evident at five years of age. Moreover, the results suggest that hand preference for grasping develops from an interaction between the visual and haptic systems.

Studies 1-4 are attached as appendices at the end of the thesis. The main body of the thesis (Chapter 2) is a review of the literature pertaining to the visual and haptic contributions to grasping in healthy and neuropsychological populations, in sensory-deprived individuals, and in developing children. The four appended studies are also summarized within the review. Chapter 3 discusses limitations, future directions, and implications of the work summarized in Chapter 2 and appendices 1-4.

CHAPTER 2

The Contributions of Vision and Touch to Grasping*

***Stone K.D.**, Gonzalez C.L.R. (2015 Under review). Manuscript submitted to *Frontiers in Psychology*. Editor assigned: Mirriam Ittyerah

ABSTRACT

This review aims to provide a comprehensive outlook on the sensorimotor contributions to grasping. The focus is on studies in normal and neuropsychological populations, in sensory-deprived individuals, and on developing children. Studies have suggested a right-hand/left-hemisphere specialization for visually-guided grasping and a left-hand/right-hemisphere specialization for haptically-guided object recognition. This poses the interesting possibility that when vision is not available and grasping relies heavily on the haptic system, there is an advantage to use the left hand. We review the evidence for this possibility and dissect the unique contributions of the visual and haptic systems to grasping. We ultimately discuss how the integration of these two sensory modalities shape hand preference.

2.1. Introduction

Vision is the main sensory system responsible for guiding the majority of our actions (Atkinson, 2002), be it searching for one's keys on a tabletop, navigating through space, recognizing a friend from childhood, or identifying a glass of water to pick it up. But often we forget the pivotal role that haptics plays in completing these actions. Haptics is the perception of combined tactile and kinesthetic inputs during object manipulation and exploration (Grunwald, 2008; Keysers, Kaas, & Gazzola, 2010; Lederman & Klatzky, 2009). For instance, upon grasping a glass of water, haptics not only informs where the arm is in space, but also about object properties (e.g. temperature, hardness, weight, texture, and further information about the shape of the cup), which allows for appropriate interaction with the cup (Sober & Sabes, 2003). As can be appreciated from this example, the integration of visual and haptic feedback is central in ensuring efficacy in everyday goal-directed movements. The right- and left-hands however, do not execute these manual actions to the same extent. Many studies have demonstrated that most individuals have a right-hand preference for visually-guided grasping. A significant number of our everyday grasps however, are haptically-guided (e.g. reaching for your keys in a bag). Very little is known about how hand preference for grasping is affected under different sensory conditions. Studies have suggested a right-hand/left-hemisphere specialization for visually-guided grasping (Flindall & Gonzalez, 2014; C. L. Gonzalez, Ganel, & Goodale, 2006; C. L. Gonzalez & Goodale, 2009; Goodale, 1988; Janssen, Meulenbroek, & Steenbergen, 2011; Radoeva, Cohen, Corballis, Lukovits, & Koleva, 2005; Stone, Bryant, & Gonzalez, 2013; Stone & Gonzalez, 2014a, 2014b) and a left-hand/right-hemisphere specialization for haptic processing (Benton, Levin, & Varney, 1973; Butler et al., 2004; Cannon & Benton, 1969; Cote, 2014; De

Renzi, Faglioni, & Scotti, 1969; Fagot, Hopkins, & Vauclair, 1993; Fagot, Lacreuse, & Vauclair, 1993, 1994; Fontenot & Benton, 1971). This left hand *haptic* advantage might influence hand preference for grasping.

This review will discuss the asymmetrical visual and haptic sensory contributions to hand preference for reaching and grasping. First, we will describe these contributions in: 1) healthy and brain-damaged populations; 2) sensory-deprived individuals (blind and deafferented); and 3) developing children. We conclude by proposing that the integration of the two sensory systems modulates hand preference. A better understanding of the factors that influence our goal-directed actions will advance our knowledge regarding the organization of the sensorimotor system, provide insight into cerebral asymmetries (including handedness) and serve as the basis for the development of therapeutic devices for the sensory-deprived.

2.2. SENSORY CONTRIBUTIONS TO HAND PREFERENCE FOR REACHING AND GRASPING: EVIDENCE FROM HEALTHY AND NEUROPSYCHOLOGICAL POPULATIONS.

Most of the actions we make on a daily basis are visually-guided, such as pointing, pantomiming, gesturing, or grasping objects. Multiple studies have concluded that these visuomotor actions are a specialized function of the left-hemisphere (Esparza, Archambault, Winstein, & Levin, 2003; Fisk & Goodale, 1988; Frey, Funnell, Gerry, & Gazzaniga, 2005; C. L. Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Goodale, 1988; Heilman, Meador, & Loring, 2000; Janssen et al., 2011; Johnson-Frey,

Newman-Norlund, & Grafton, 2005; Radoeva et al., 2005; Roy, Kalbfleisch, & Elliott, 1994; Sainburg, 2014; Serrien, Ivry, & Swinnen, 2006; Serrien & Sovijarvi-Spape, 2015; Stone et al., 2013; Woodworth, 1899). In fact, the relationship between visuomotor control (such as during grasping) and the left-hemisphere is so ingrained that simply *viewing* a graspable object (e.g. a piece of fruit, a tool, a toy) elicits a left-hemisphere response in terms of an increase in neural activity (i.e. left premotor cortex; Proverbio et al., 2013) and decreased reaction times when pressing buttons with the right hand (Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003; Netelenbos & Gonzalez, 2015). The following section will review evidence from neuropsychological, kinematic, psychophysical, and natural grasping studies that support a left-hemisphere specialization for visually-guided actions.

2.2.1. Left-hemisphere specialization for visually-guided actions

2.2.1.1. Evidence from neuropsychological studies

There is a plethora of brain-damaged patient studies that provide support for a left-hemisphere specialization for visuomotor control (Fisk & Goodale, 1988; Flowers, 1975; Freitas, Gera, & Scholz, 2011; Frey et al., 2005; Haaland, Elsinger, Mayer, Durgerian, & Rao, 2004; Haaland & Harrington, 1994; Mani et al., 2013; Perenin & Vighetto, 1988; Radoeva et al., 2005). Usually, damage to the left hemisphere produces more severe visuomotor impairments than similar damage to the right hemisphere. For example, when individuals were asked to move a cylindrical joystick to a 5mm target circle those with left-hemisphere damage had slowed peak velocity and longer deceleration when compared to those with right-hemisphere damage (Haaland et al.,

2004). Furthermore, studies have shown that damage to the left (but not the right) hemisphere can critically impair goal-directed movements of *both* limbs. For example, individuals with left-hemisphere damage displayed significant impairments in tapping speed with *both* the left and the right hands, but individuals with right-hemisphere damage only showed contralateral (left) hand impairments (Wyke 1971). Other studies have reported that patients with left-hemisphere damage show significant impairments including longer execution of the action for target-directed pointing with the ipsilateral hand when compared to those with right-hemisphere damage who displayed only contralateral deficits (Fisk & Goodale, 1988; Perenin & Vighetto, 1988). Moreover, Haaland and Harrington (1994) tested right- and left-hemisphere stroke patients on a task wherein they were asked to alternately tap between two targets using a stylus as quickly and accurately as possible. While the right-hemisphere group did not differ from controls, the left-hemisphere group was significantly slower than both the control and the right-hemisphere stroke groups. In a more recent study, Mani et al. (2013) asked right- and left-hemisphere stroke patients to move their limbs to different visual targets located on a horizontal plane just above their hand. Only the left-hemisphere stroke patients showed significant impairments in movement trajectory and direction. In sum, the general consensus is that when compared to lesions to the right-hemisphere, left-hemisphere damage leads to more severe impairments in visually-guided movement control, in terms of both speed and accuracy, often affecting both limbs.

2.2.1.2. Evidence from psychophysics and kinematic studies

Psychophysical and kinematic studies have confirmed the critical role that vision plays in making appropriate reaching and grasping movements. That is, vision helps to recognize and locate the target, bring the limb to the target, ensure proper reach or grasp configuration, endpoint accuracy, as well as obstacle avoidance (Babinsky, Braddick, & Atkinson, 2012; Chapman & Goodale, 2010a, 2010b; Flowers, 1975; W. D. Hopkins, Hook, Braccini, & Schapiro, 2003; S. R. Jackson, Jackson, & Rosicky, 1995; Jakobson & Goodale, 1991; Keefe & Watt, 2009; Rand, Lemay, Squire, Shimansky, & Stelmach, 2007; Roy et al., 1994; Saunders & Knill, 2003; Schiavetto, Lepore, & Lassonde, 1993; Tremblay, Hansen, Kennedy, & Cheng, 2013; Westwood, Heath, & Roy, 2003). As early as 1899, Woodworth reported a right-hand advantage for minimizing error during high speed aiming movements, leading him to suggest that the right hand is guided by a ‘superior neural motor center’ (Woodworth, 1899). Studies involving psychophysical techniques have also reported a left-hemisphere advantage for visuomotor tasks including: finger tapping (Kim et al., 1993); button pressing (Handy et al., 2003; Netelenbos & Gonzalez, 2015; Serrien & Sovijarvi-Spape, 2015); and reaching and pointing (Elliott, Lyons, Chua, Goodman, & Carson, 1995; Elliott et al., 1993; Fisk & Goodale, 1988; Goodale, 1988; Roy & Elliott, 1986, 1989; Roy et al., 1994; van Doorn, 2008). For example, Flowers (1975) compared simple and complex finger tapping actions and found that the right hand was faster and more accurate during the complex finger tapping task. As the complex tapping task requires more precise movements (and thus visual attention), these results suggest that the left hemisphere is better at processing visual feedback during motor movements. Similar results emerge for pointing: Goodale (1988) asked individuals to reach-to-point at different visual targets while the eyes were

either a) fixated at the center of a screen or b) allowed to freely guide the hand to the target. Individuals were significantly faster at pointing to the target with the right, compared to the left, hand, even when the eyes did not guide the hand to the target. Also, this right-hand advantage is not a product of handedness: in a visuomotor illusion task, C. L. Gonzalez et al. (2006) showed that in both left- and right-handers, the left hand (and not the right) was affected by the presentation of different visual illusions (for both estimating the length of the object *and* actually grasping it). This effect was later reproduced by Adam, Muskens, Hoonhorst, Pratt, and Fischer (2010), who asked left- and right-handers to reach towards targets on a screen with and without the presence of distracters. Results showed that when the distracters were present, the left hand (regardless of the individual's handedness) was not only significantly slower at reaching for the target, but often overshot the end point location of the target. Similarly, these results emerge for grasp planning as well. Janssen et al. (2011) had left- and right-handers grasp CD cases in different orientations and found an advantage in planning for movement with the right hand (not the left) for both populations.

Kinematic studies have shown a right-hand advantage that is contingent on task demand and/or action type (Elliott et al., 1995; Flindall, Doan, & Gonzalez, 2013; Flindall & Gonzalez, 2014; Roy & Elliott, 1989; Roy et al., 1994; van Doorn, 2008). For example, Elliot et al. (1995) asked right-handed individuals to point to small targets, but in some trials, the target suddenly moved to either the left or right side, forcing the individual to correct her/his trajectory. Results showed that participants were better (faster) with their right hand at correcting the movement in response to the target shift. In another study, Flindall et al. (2013) asked right-handed individuals to grasp a glass of

water with each hand. Individuals were faster and more accurate at grasping the glass with the right, compared to the left, hand. In further studies, Flindall and colleagues have included left-handed participants to investigate if handedness significantly influences this kinematic advantage (the previous studies only tested right-handed participants). In this series of studies, the right and left hands of right- *and* left-handed individuals were tested in a grasp-to-eat task (Flindall, Stone, & Gonzalez, 2015) . Participants were asked to grasp for pieces of food to bring to the mouth in order to eat them. The results showed that in both populations, grip aperture was smaller when participants used their right hands. Because smaller grip apertures are typically associated with greater precision, this finding was interpreted as a right-hand advantage for the grasp-to-eat movement regardless of handedness (Flindall et al., 2013; Flindall et al., 2015).

Taken together, these studies highlight the right-hand (left-hemisphere) advantage for visually-guided actions.

2.2.1.3. Evidence from neuroimaging studies

Fewer imaging studies have investigated the role of each hemisphere in visually-guided actions due to the challenges of movement artefact associated with executing an action. For instance, in one study using electroencephalography (EEG), Proverbio et al. (2013) asked individuals to view objects that afforded either unimanual or bimanual grasps (e.g. a hammer versus a steering wheel). After only 250ms of object viewing, the left premotor cortex showed significant activation for both types of grasps, regardless of object orientation (i.e. the hand afforded for the grasp). No manual actions were performed in this study, however. In a functional resonance magnetic imaging (fMRI)

study, Kuhtz-Buschbeck, Ehrsson, and Forssberg (2001) instructed participants to grasp cubes while inside the scanner. They found that the more precision that was required by the actor to pick up the cube, the stronger the activation of left motor and somatosensory areas. In this study, however, only the right hand was tested. Kim et al. (1993) had individuals tap their thumb against each ipsilateral and contralateral fingers (one at a time) while inside a 4-T Nuclear Magnetic Resonance (NMR) instrument. Results showed an activation of the left motor cortex for ipsilateral taps on *both* the left and right hands. EEG studies show similar results: participants show left-hemisphere superiority for the execution of motor sequences (key presses during a memory-guided task) regardless of hand used or individual handedness (Serrien & Sovijarvi-Spape, 2015). Moreover, fMRI studies have shown preferred left-hemisphere activation for planning an action, observing an action and grasping in both left- and right-handers (Cacioppo, 2005; Gallivan, McLean, & Culham, 2011; Kroliczak & Frey, 2009; Martin, Jacobs, & Frey, 2011). Overall, these studies demonstrate a left-hemisphere bias for the visual control of action.

2.2.1.4. Evidence from natural grasping tasks

Studies on hand preference for grasping have shown a right-hand preference for picking up objects such as cards (Bishop, Ross, Daniels, & Bright, 1996; Calvert & Bishop, 1998; Carrier, Doyen, & Lamard, 2006), geometrical 3D shapes (Gabbard, Tapia, & Helbig, 2003), toys (Bryden & Roy, 2006; Sacrey, Arnold, Whishaw, & Gonzalez, 2013), building blocks (C. L. Gonzalez & Goodale, 2009; Stone et al., 2013; Stone & Gonzalez, 2014a, 2014b) and tools (Mamolo, Roy, Bryden, & Rohr, 2004; Mamolo, Roy,

Rohr, & Bryden, 2006). Furthermore, hand preference tends to remain stable and consistent throughout the lifespan (C. L. Gonzalez, Flindall, & Stone, 2015), save for a slight increase in laterality during adolescence (Bryden & Roy, 2006; Gooderham & Bryden, 2014)

All these studies have controlled for space use in that the objects to be grasped had been equally accessible to either hand. For example Bishop et al. (1996) instructed right-handed individuals to pick up cards arranged in a semi-circle and place them into a box at the midline. A right-hand preference for picking up the cards was observed, even when reaching for the cards in left space. This behaviour, although biomechanically costly, is not unusual for right-handed individuals and has been observed in many other studies (Bryden & Huszczyński, 2011; Bryden & Roy, 2006; C. L. Gonzalez et al., 2007; Leconte & Fagard, 2004; Mamolo et al., 2006; Stone et al., 2013).

Interestingly, this right-hand preference for grasping does not appear to be linked to handedness. Several studies have shown no hand preference or even a right-hand preference for grasping in left-handers (Gallivan et al., 2011; C. L. Gonzalez et al., 2006; C. L. Gonzalez & Goodale, 2009; C. L. Gonzalez et al., 2007; Main & Carey, 2014; Stone et al., 2013). For instance, Stone et al. (2013) asked right- and left-handed individuals to grasp for different building blocks from a scattered array on a tabletop in order to replicate a 3D block model (i.e. the block-building task; see Stone et al. 2013; Gonzalez et al. 2007). They found that 50% of their left-handed sample showed a preference for grasping with their non-dominant right hand. Similar results have been found by Gonzalez and colleagues (2007, 2009), who have categorized these left-handers

as ‘right-left-handers.’ In other words, some left-handers behave indistinguishably from right-handers in terms of hand selection for grasping.

This prevalent right-hand preference for grasping that includes some (self-identified) left-handers has been attributed to the aforementioned left-hemisphere specialization for visuomotor control (Fisk & Goodale, 1988; Frey et al., 2005; C. L. Gonzalez et al., 2006; C. L. Gonzalez et al., 2007; Goodale, 1988; Janssen et al., 2011; Kimura, 1977; Radoeva et al., 2005; Sainburg, 2014; Serrien et al., 2006; Stone et al., 2013; Wang & Sainburg, 2007). But often we grasp objects in the absence of vision. What do we know about the contributions of haptics to hand preference? In the absence of vision one must rely primarily on the sense of touch (and kinesthesia) to complete a task. It is possible that one might prefer to use the left hand given the known left-hand advantage for haptic processing (De Renzi et al., 1969; Fagot, Hopkins, et al., 1993; Franco & Sperry, 1977; Lacreuse, Fagot, & Vauclair, 1996; D. F. Witelson, 1976; S. F. Witelson, 1974). The role of the right-hemisphere in haptic processing and haptically-guided grasping is discussed next.

2.2.2. Right-hemisphere specialization for haptic processing

Even when we are unaware of it, we use haptics for the identification and manipulation of objects (e.g. reaching for keys in a bag, reaching for your cell phone in your pocket, typing on a keyboard, bringing food to the mouth). Similar to visually-guided movements, when the movement is haptically-guided, an individual must find a way to identify and manipulate the object appropriately. Kinematic studies show that when reaching for an object while blindfolded, sighted individuals show larger peak grip

apertures (Flindall & Gonzalez, 2014; S. R. Jackson et al., 1995; Jakobson & Goodale, 1991; Rand et al., 2007), slower movement times (Schettino, Adamovich, & Poizner, 2003; Winges, Weber, & Santello, 2003), and a decrease in task accuracy, sometimes knocking over (Wing, Turton, & Fraser, 1986) or missing the target completely (Babinsky et al., 2012). Furthermore, hand pre-shaping may not occur until tactile contact has been made with the object (Karl, Sacrey, Doan, & Whishaw, 2012; Karl & Whishaw, 2013). These studies however, have only investigated haptically-guided grasping with the right hand. In one study that compared the kinematics of the left and right hands for grasping when vision is occluded have shown no differences between the hands (Grosskopf & Kutzt-Buschbeck, 2006).

So while there is a dearth of kinematic studies that could inform us on manual asymmetries for haptically-guided actions, evidence from other sources has shown a left-hand/right-hemisphere specialization for this type of action. This evidence is reviewed below.

2.2.2.1. Evidence from neuropsychological studies

Studies in brain-damaged patients provide compelling support for a right-hemisphere specialization for haptic processing (Fontenot & Benton, 1971; Franco & Sperry, 1977; Kumar, 1977; Milner & Taylor, 1972). Kumar (1977) had patients with hemispheric disconnection (i.e. split-brain) complete a tactile version of the Memory for Designs test (see Graham and Kendall, 1960) . Using one hand at a time, participants were asked to haptically inspect objects of various shapes and then, using the same hand, to draw whatever shape they had just felt. Participants made significantly fewer errors after inspecting with the left hand. The same result is found when patients actively

encode geometrical shapes (Franco and Sperry, 1977). Franco and Sperry asked split-brain patients to complete a geometrical shape-matching task. The individuals sat at a table with a curtain in front of them that occluded vision to their hands. Objects were placed in front (within view) and behind the curtain (out of view) and the patient's job was to haptically match the object behind the curtain with those in front. Results showed that patients were faster and more accurate when they used the left- versus the right-hand. Furthermore, patients with right-hemisphere lesions show bimanual impairments when coding vibrotactile information, whereas left-hemisphere damage leads to only contralesional impairments (Fontenot and Benton, 1971). Taken together, these brain-damaged patient studies reveal a robust left hand/right-hemisphere advantage for haptic processing.

2.2.2.2. Evidence from studies involving psychophysics and imaging techniques

Studies involving psychophysics and neuroimaging have also demonstrated a right-hemisphere advantage for haptic processing in both humans (Benton et al., 1973; Butler et al., 2004; Cormier & Tremblay, 2013; De Renzi et al., 1969; Dodds, 1978; Fagot, Hopkins, et al., 1993; Fagot, Lacreuse, et al., 1993; Fagot et al., 1994; Harada et al., 2004; Loayza, Fernandez-Seara, Aznarez-Sanado, & Pastor, 2011; Milner & Taylor, 1972; Morange-Majoux, 2011; O'Boyle, Van Wyhe-Lawler, & Miller, 1987; Riege, Metter, & Williams, 1980; Stone & Gonzalez, 2014a, 2014b; Tomlinson, Davis, Morgan, & Bracewell, 2011; Wilkinson & Carr, 1987) and non-human primates (Lacreuse & Frigaszy, 1996; Lacreuse & Frigaszy, 1999). For most of these studies, individuals have been asked to haptically explore, differentiate, or detect geometrical shapes (Cormier &

Tremblay, 2013; Franco & Sperry, 1977; Stone & Gonzalez, 2014a, 2014b), non-sense shapes (Dodds, 1978; Fagot, Hopkins, et al., 1993; Fagot, Lacreuse, et al., 1993; Fagot et al., 1994), vibrations (Heller, Rogers, & Perry, 1990; Rhodes & Schwartz, 1981; Weinstein, 1978; Wiles, Pearce, Rice, & Mitchell, 1990), or object orientation (Benton et al., 1973; Brizzolara, De Nobili, & Ferretti, 1982; Cannon & Benton, 1969; Varney & Benton, 1975). For instance, Fagot and colleagues had individuals haptically explore different cubes either unimanually or bimanually and measured accuracy during a recognition test. When both hands were used, individuals were more accurate at identifying the cubes explored more with the left, rather than the right hand (Fagot, Lacreuse, et al., 1993; Lacreuse et al., 1996). When one hand was used, it was found that individuals used the left hand to cover more surface area per cube and touched more cubes overall during this haptic recognition task (Fagot, Hopkins, et al., 1993; Fagot et al., 1994). Furthermore, even when the experimenter moves an object across the palms of the participant (rather than the participant actively exploring it), the left hand is more accurate at detecting differences between stimuli (Benton et al., 1973). Aligned with these findings, in a more recent study, individuals were asked to assess the curvature of different virtual contours (Squeri et al., 2012). While grasping the handles of a manipulandum, the hands were passively moved along a curved pathway “as if exploring the smooth surface of a round object.” Results showed that the left hand was more sensitive to detecting differences in curvature. The authors conclude that the left hand produces more precise haptic estimates than does the right hand. Finally, it appears that the right-hemisphere specialization for haptic processing is not dependent on individual handedness. A study found that the left thumb is more accurate than the right thumb (for

both left- and right-handers) in terms of detecting sense position, which requires the processing of haptic feedback (Riolo-Quinn, 1991).

Imaging studies have shown support for the theory of a right-hemisphere specialization for haptics. Using fMRI, Harada et al. (2004) found that regardless of hand, when an individual's fingers were passively moved across Braille letters there was increased activation in the right hemisphere (frontal and parietal areas) when compared to the left hemisphere. Loayza et al. (2011) applied vibrations to the left and right hands of participants while undergoing an fMRI scan. Results revealed increased right-hemisphere activation (fronto-parietal areas) for detecting stimulus location on the hand, regardless of the hand that was stimulated. Furthermore, Cormier and Tremblay (2012) showed that right-handers exhibit increased corticomotor excitability in the right-hemisphere when haptically judging the thickness of a metal plate with the left hand (compared to the left-hemisphere/right-hand). Together, these studies illustrate the unique role of the right hemisphere in haptic processing.

2.2.2.3. Evidence from natural grasping studies

Because vision is unavailable during haptically-guided tasks, individuals will use exploratory procedures (EP) to extract relevant information about the object(s) or stimuli. EPs are stereotyped patterns of hand movements used to extract object properties and features during haptic object recognition (Lederman & Klatzky, 1987, 2009). There are six observable types of EPs, each specialized for encoding specific haptic properties. These include: lateral motion (for texture); unsupported holding (for weight); pressure (for hardness); enclosure (for global shape and volume); contour following (for global

shape and exact shape); and static contact (for temperature). It has been concluded that the most effective way to haptically process an object is to grasp it, which at minimum combines enclosure, static contact, and unsupported holding (Lederman & Klatzky, 1990, 2009). If grasping is the most effective method to use for haptic object recognition, then grasping could be used as a model to investigate hemispheric specialization for haptic processing. Yet, this is rarely the case. In a series of studies, Stone and Gonzalez (2014a, b; see Appendices 1 and 2) asked right-handed individuals to grasp building blocks in order to replicate different 3D models (i.e. the block-building task) while sighted (see Figure 1A) and while blindfolded (see Figure 1C). The hand selected for picking up each block was assessed. Although a right-hand preference was observed during the visually-guided portion of the task, there was a significant increase in left-hand use when the task was haptically-guided (i.e. while blindfolded; see Figure 1D). Because without vision, individuals must use haptics to guide their actions (and in turn manipulate and discriminate between the different types of building blocks), the authors attributed their finding to a left-hand/right-hemisphere specialization for haptic processing. What is more, if participants haptically manipulated the building blocks in a container five minutes prior to the block-building task, they showed an even greater preference for the left hand when completing the task. It appears that five minutes of an added 'haptic experience' increases the preference to use the left hand. If this is the case, how would a lifetime of haptic experience affect hand preference for grasping? To address this question, investigations involving congenitally blind individuals are discussed in the following section.

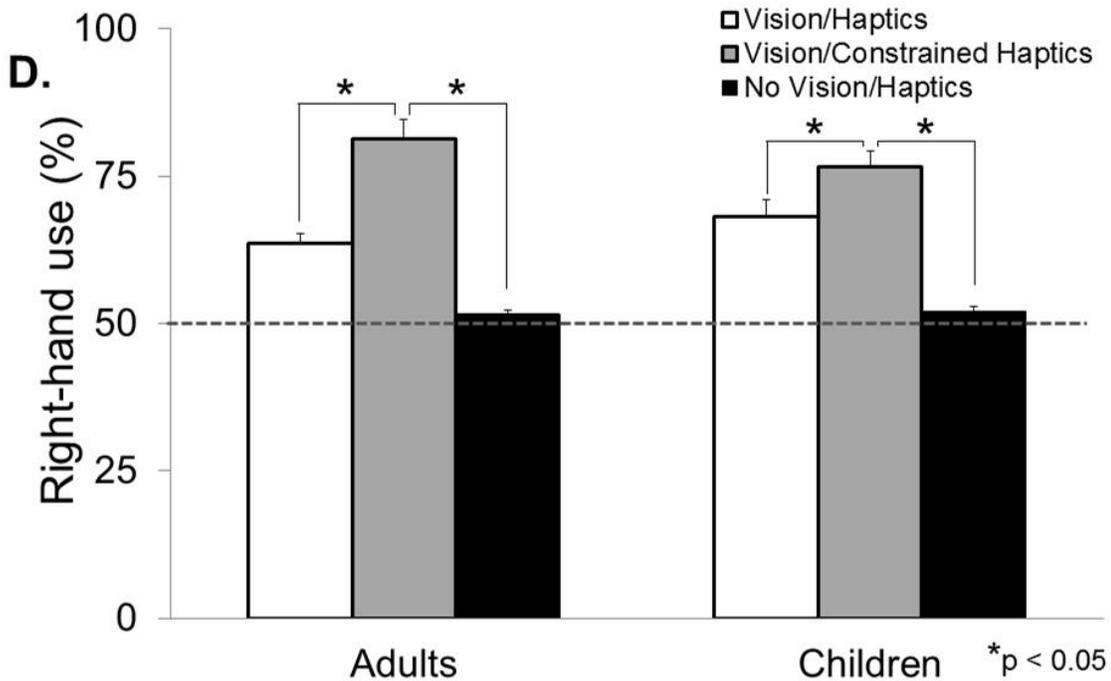


Fig 1. Experimental set-up and results from Stone & Gonzalez (2014a,b; 2015a, b). Photographs of participants completing (A) the Vision/Haptics condition (B) the Vision/Constrained-Haptics condition (note that the participant is wearing a pair of gloves) and (C) the No Vision/Haptics condition (note that the participant is wearing a blindfold) (D) Graph demonstrating right-hand use for grasping in percentage for the three sensory conditions in children and adults. White bars represent the Vision/Haptics condition. Grey bars represent the Vision/Constrained-Haptics condition. Black bars represent the No Vision/Haptics condition. The grey dashed line denotes 50% right-hand use (or equal use of each hand). Note the significant difference within sensory conditions.

2.3. SENSORY CONTRIBUTIONS TO HAND PREFERENCE FOR REACHING AND GRASPING: EVIDENCE FROM SENSORY-DEPRIVED POPULATIONS

2.3.1. Congenitally Blind individuals

One population that inarguably has a lifetime of haptic experience is congenitally blind (CB) individuals. CB are those who were born without sight, or lost sight shortly thereafter, and therefore have no recollection of having a visual experience (Thinus-Blanc & Gaunet, 1997). Most cases of congenital blindness are due to dysfunctional development of the retina and/or optic nerve (McColm & Fleck, 2001). In turn, the CB rely on their other senses (mainly haptics and audition) to guide their movements. Many studies have compared haptics in CB versus sighted individuals (Collignon & De Volder, 2009; Heller, Calcaterra, Burson, & Tyler, 1996; Hermelin & O'Connor, 1971; Ittyerah, 2000, 2009; Ittyerah & Marks, 2007; Millar, 1974; Theurel, Frileux, Hatwell, & Gentaz, 2012; Theurel, Witt, Claudet, Hatwell, & Gentaz, 2013). For example, Theurel et al. (2012) asked CB and blindfolded-sighted individuals to haptically discriminate between different geometrical shapes including common (square, triangle, rectangle) and nonsense shapes. The CB were more efficient in their exploratory procedures for identifying the shapes, and could identify non-sense shapes just as easily as the common shapes. Blindfolded-sighted individuals, on the other hand, were only proficient at identifying common shapes. These results align with Postma, Zuidhoek, Noordzij, and Kappers (2007) who found that, in comparison to blindfolded controls, blind individuals were more accurate in a cut-out shape identification and matching task. Neither of these studies however, assessed hand differences for haptics. For the most part, participants were asked

to use their dominant hand or both hands to complete the task. This scenario does not provide any information about differences in haptic ability between the two hands in blind individuals.

Hand preference in CB individuals has been seldom investigated. The few studies that have assessed hand preference in the CB have been subjective (i.e. through the use of questionnaires or interviews) and/or have focused mainly on children. Ittyerah (2000, 2009), for example, had CB children between the ages of 6 and 15 years of age complete a multitude of tasks such as putting beads in a jar, cutting paper with scissors, picking up a pen, or throwing a ball. Both CB and blindfolded-sighted children displayed a preference (of similar extent) to use the right hand. The children were also asked to sort items such as cards, buttons, tokens, and paper clips, and it was revealed that CB children were significantly faster at sorting the objects with the left hand. These results highlight that although there may be a preference for the right hand for certain tasks, the left hand still plays a critical role in haptically identifying objects (i.e. in this case, to sort). Yet, another study by Caliskan and Dane (2009) showed that CB children between the ages of 7 and 12 years were more likely to be left-handed than were sighted children, though these results were based on a questionnaire. Using questionnaires, studies have also reported CB adults to be right-handed (Argyropoulos, Sideridis, & Papadimitriou, 2014; Nava, Gunturkun, & Roder, 2013). None of the adult studies specifically assessed hand preference for *grasping*. Closing this gap, Stone and Gonzalez (2014b; see Appendix 2) asked CB, sighted, and blindfolded-sighted individuals to complete the block-building task and recorded hand selection for grasping the blocks. As in Stone and Gonzalez (2014; Appendix 1), the blindfolded-sighted group used their left hand significantly more

than the sighted group highlighting the difference in hand use between visually-guided and haptically-guided grasping. Interestingly, the CB group showed a right-hand preference for grasping that was indistinguishable from that of the sighted participants. So even though the CB had a lifetime of haptic experience, they did not demonstrate a left-hand preference for grasping. Instead, their behaviour was similar to that of sighted individuals. The question remains: why is this the case if sighted and CB rely on different sensory modalities to complete the task?

One possibility might be related to similar processing in the ventral and dorsal visual streams found in sighted and CB individual. These pathways project from primary visual cortex to the inferior temporal lobe (the ventral stream) and to the posterior parietal cortex (PPC; the dorsal stream; Goodale and Milner, 1992). The ventral (vision-for-perception) stream is responsible for object identification, or knowing ‘what’ an object is, whereas the dorsal (vision-for-action) stream is responsible for the visuomotor transformation and control of actions, or knowing ‘where’ the object is in space and ‘how’ to interact with it (e.g. manipulate and grasp). Although CB individuals have a lifetime without visual input, surprisingly, their dorsal and ventral “visual” streams are preserved (Amir Amedi et al., 2007; Collignon et al., 2011; Fiehler, Burke, Bien, Roder, & Rosler, 2009; Mahon, Anzellotti, Schwarzbach, Zampini, & Caramazza, 2009; Pietrini et al., 2004; Poirier et al., 2006; Reich, Szwed, Cohen, & Amedi, 2011; Renier et al., 2010; Ricciardi et al., 2009; Striem-Amit, Dakwar, Reich, & Amedi, 2012). The lateral occipital complex (LOC) is an area located in the ventral stream that is responsible for both the visual and haptic identification of object shape (A. Amedi, Malach, Hendler, Peled, & Zohary, 2001; T. W. James et al., 2002; T. W. James, Kim, & Fisher, 2007;

Pietrini et al., 2004; Stilla & Sathian, 2008; Zhang, Weisser, Stilla, Prather, & Sathian, 2004). In an fMRI study, sighted and CB individuals were asked to identify different common objects (e.g. shoe, water bottle) using both hands. Both groups showed robust activation of area LOC during haptic recognition, even though the CB had never visually experienced the object before (Pietrini et al., 2004). Moreover, hearing auditory properties (e.g. ‘crinkling’ and ‘crumbling’) of material objects also elicit ventral stream activation in the CB (Arnott, Cant, Dutton, & Goodale, 2008). These results demonstrate that object recognition in the ventral visual stream remains functionally specialized even without visual experience. Similarly, the dorsal visual stream is also functionally specialized in CB individuals. In an fMRI study, CB and blindfolded-sighted participants were asked to trace different line patterns using a stylus in their right hand to investigate brain activation during movement of the limbs and hands (Fiehler, Burke, Engel, Bien, & Rosler, 2008). The same dorsal stream areas were activated in both groups during this task, primarily the anterior intraparietal sulcus (aIPS) and superior parietal lobe. Moreover, the human middle temporal area (area hMT+), a portion of the dorsal stream that is responsible for processing motion, shows overlapping activation in sighted and blind individuals, be it for visual or tactile motion (Ricciardi et al., 2007).

Because similar visual areas are activated in both CB and sighted individuals for perception and action, it makes sense that the CB group behaved similarly to the sighted group in terms of hand selection during the grasping task (Stone & Gonzalez, 2014b; see Appendix 2). Further supporting this notion, kinematic studies have shown that like sighted individuals, CB showed: size-appropriate grip scaling when grasping different sized objects (Castiello, Bennett, & Mucignat, 1993) and similar hand orientation in a

posting task (Gosselin-Kessiby, Kalaska, & Messier, 2009). In sum, early loss of vision in humans appears to result in reorganization that affords similar grasping profiles as those observed among normally-sighted individuals.

2.3.2. Deafferented individuals

Another population that could provide insight into the contributions of sensory information to grasping is individuals with deafferentation. Deafferentation is a rare condition that occurs from the degeneration or loss of the large afferent nerve cells that convey information about touch and/or position sense (Cole & Sedgwick, 1992; Proske & Gandevia, 2012). Motor control in the deafferented has been previously investigated (Cole & Sedgwick, 1992; Cooke, Brown, Forget, & Lamarre, 1985; Forget & Lamarre, 1987; Gentilucci, Toni, Chieffi, & Pavesi, 1994; Hermsdorfer, Elias, Cole, Quaney, & Nowak, 2008; Nowak, Glasauer, & Hermsdorfer, 2004; Rothwell et al., 1982; Sens et al., 2013; Travieso & Lederman, 2007). A seminal investigation on deafferentation and motor control was conducted in 1982 with patient GO, who had severe peripheral sensory neuropathy induced by influenza (Rothwell et al., 1982). Patient GO had an extreme reduction in vibration and temperature detection, reduced response to skin pricks, and severe impairments in light touch recognition. Although GO's hands were "relatively useless to him in daily life" (Rothwell et al., 1982, p. 515) he was still able to complete a multitude of manual actions. For instance, he was able to accurately produce different levels of force on his thumb pad when asked. He was also able to accurately complete simple finger movements (e.g. outline shapes, tap his fingers, or wave his hands). These manual actions, however, were guided entirely by vision. After approximately 30 seconds

without visual *or* haptic input, he could no longer complete these types of tasks. Because GO was a right-handed man, most of the testing focused on the use of his right hand, thus not allowing for an analysis of possible asymmetries in the contribution of haptics to manual actions. With respect to the few studies that have investigated reach-to-grasp movements, it has been reported that deafferented individuals show overall longer movement times and immense variability in their movements, in terms of endpoint accuracy, time to peak velocity, and movement initiation (Gentilucci et al., 1994; G. M. Jackson et al., 2000; G. M. Jackson, Jackson, Newport, & Harvey, 2002). G. M. Jackson et al. (2002) investigated grasping in a deafferented individual (patient DB) with no sense of touch in her left arm, yet her proprioception was intact. Patient DB was asked to reach for wooden dowels using one hand or both hands. Immediately after the reach was initiated, vision was occluded via liquid crystal goggles. Results revealed that during unimanual trials, DB's left and right hands took the same amount of time to reach the target. However, during the bimanual trials, the left hand (when compared to the right hand) took significantly longer and was considerably more variable in reaching for its left-side target. This is in contrast to controls who showed no difference in movement time between the limbs for bimanual actions. When the task was visually-guided, her movement was virtually unimpaired (G. M. Jackson et al., 2000). Yet only DB's left arm was affected by her deafferented condition; perhaps if both arms were affected manual asymmetries might emerge for motor actions. Gentilucci et al. (1994) assessed reach-to-grasp movements in a bilaterally-deafferented individual (who had no sense of touch *or* proprioception from her shoulders down). She took significantly longer than controls to close her fingers over the target (a sphere), while also displaying immense variability in

these movements. Only the right hand was tested however, not allowing for a comparison between the hands. Nonetheless, these studies highlight the importance of haptic feedback during reach-to-grasp movements.

One method of inducing deafferentation in healthy individuals is via Temporary Functional Deafferentation (TFD), which creates a pharmacological blockade of peripheral nerve transmission (Opsommer, Zwissig, & Weiss, 2013; Sens et al., 2012). For the most part, this method has been used in stroke rehabilitation (Opsommer et al., 2013; Sens et al., 2013; Sens et al., 2012; Weiss et al., 2011; Werhahn, Mortensen, Kaelin-Lang, Boroojerdi, & Cohen, 2002), however some studies have documented the effects of TFD in healthy individuals. In stroke rehabilitation, using an anesthetic cream on the affected arm enhances performance on a variety of tactile and motor tasks (Sens et al., 2013). In healthy individuals, a few studies have shown enhanced sensorimotor performance with anesthetic-cream based TFD (Bjorkman, Rosen, & Lundborg, 2004; Bjorkman, Weibull, Rosen, Svensson, & Lundborg, 2009; Petoe, Jaque, Byblow, & Stinear, 2013) whereas one study showed no effect of TFD on sensorimotor performance (Sens et al., 2013). It should be noted that in these studies, TFD cream was applied to the forearm and not to the hands. As argued by Bjorkman et al. (2004) the enhanced sensorimotor function may be due to an expansion of cortical sensory representation of the hand which is adjacent to the forearm. With respect to the hands, however, it has been shown that *tourniquet*-induced anesthesia of the right hand improves sensorimotor function (i.e. grip strength, tactile discrimination, tactile acuity) of the left hand (Bjorkman et al., 2004; Werhahn et al., 2002). This last result demonstrates that hand function can be enhanced by temporarily inducing deafferentation in the contralateral arm (as the

previous studies tested the ipsilateral arm). No study to our knowledge has used this method of transient deafferentation applied to both of the hands to investigate hand preference and/or performance for grasping or other sensorimotor tasks.

Although motor control has been assessed in the deafferented, there is a dearth of information on *hand preference* for grasping in this population. We speculate, however, that bilaterally-deafferented patients would favor the right hand for grasping. If haptics is a specialization of the left hand, then in the absence of that sense, one would resort to using the right hand because, as argued in the previous section, when grasping with vision the right hand is preferred for grasping. Consistent with this speculation, a recent study found that constraining haptics (i.e. by asking participants to wear a pair of textured, fitted gloves; see Figure 1B) during a grasping task, results in a decrease of left-hand use to the point that the right hand is used almost exclusively (Stone and Gonzalez, 2015; see Figure 1D and Appendix 3).

Together, studies in the sensory deprived (i.e. congenitally blind and deafferented) provide a glimpse into the asymmetric contributions of the visual and haptic systems to sensorimotor control, and by no means are the results conclusive. There is ample opportunity to further this knowledge using these populations, and by including related populations, such as late blind individuals or patients with tactile agnosia, tactile apraxia, or autotopagnosia.

2.4. SENSORY CONTRIBUTIONS TO HAND PREFERENCE FOR REACHING AND GRASPING: EVIDENCE FROM DEVELOPMENTAL STUDIES

A window of opportunity to gain further insight into how vision and haptics shape hand preference for grasping is through developmental studies. These are discussed below.

2.4.1. Development of right-hand preference for grasping

It has been suggested that our inclination to use the right hand for manual actions derives from the development of an “asymmetric neuromotor system” in which the left hemisphere develops earlier than the right hemisphere (J. Fagard, 2013; P. F. MacNeilage, Rogers, & Vallortigara, 2009). Studies in utero have shown that the left hemisphere is larger than the right hemisphere as early as 20 weeks gestation (J. Fagard, 2013; Hering-Hanit, Achiron, Lipitz, & Achiron, 2001). By 30 weeks gestation, the temporal lobe, the superior sulcus, and the corticospinal tract are larger on the left side than on the right (Dubois et al., 2009; Kasprian et al., 2011; Liu et al., 2010). This asymmetry persists into the first few weeks of life (Gilmore et al., 2007). Furthermore, it has been suggested that postural asymmetries *in utero*, such as a rightward head-turning preference, also encourage right-hand preference (Michel, 1981; Ververs, de Vries, van Geijn, & Hopkins, 1994). It has been speculated that when the head is turned to the right, it is easier for the fetus to bring the right hand to the mouth rather than the left (J. Fagard, 2013), speculation that could find support from a study showing right-hand preference for sucking as early as 15 weeks gestation (Hepper, McCartney, & Shannon, 1998) which correctly predicted right-handedness into adolescence (Hepper, Wells, & Lynch, 2005). It is possible that the combination of a more developed left hemisphere and postural preferences in utero may influence right-hand preference for manual actions.

Postnatally, studies have documented a right-hand preference for grasping between 6-18 months of age (Carlson & Harris, 1985; Corbetta & Thelen, 1999; Jacqueline Fagard, 1998; Jacqueline Fagard & Lockman, 2005; Ferre, Babik, & Michel, 2010; Hinojosa, Sheu, & Michel, 2003; Jacobsohn, Rodrigues, Vasconcelos, Corbetta, & Barreiros, 2014; Jacquet, Esseily, Rider, & Fagard, 2012; McCormick & Maurer, 1988; Michel, Ovrut, & Harkins, 1985; Michel, Tyler, Ferre, & Sheu, 2006; Morange-Majoux, Peze, & Bloch, 2000; Nelson, Campbell, & Michel, 2013; Ronnqvist & Domellof, 2006; Sacrey et al., 2013). Yet, it appears that consistent preference for the right hand is not robust until around 4 years of age (Bryden & Roy, 2006; Gesell & Ames, 1947; C. L. Gonzalez et al., 2015; Hill & Khanem, 2009; McManus et al., 1988; Sacrey et al., 2013). Although debate remains regarding *when* this right-hand preference is established, it is clear that the left-hemisphere specialization for visuomotor control develops early in life, and begins to shape hand preference as early as one year of age.

Previous studies have recorded hand preference for grasping while infants and children picked up items such as toys (Jacqueline Fagard & Marks, 2000; Ramsay, 1980), building blocks (C. L. Gonzalez et al., 2015; C. L. Gonzalez et al., 2014; Sacrey et al., 2013), food (Kastner-Koller, Diemann, & Bruckner, 2007; Marschik et al., 2008; Sacrey et al., 2013), geometrical shapes (Kotwica, Ferre, & Michel, 2008), or tools (Marschik et al., 2008; McManus et al., 1988). Noteworthy, in all of these studies infants and children were tested with visual availability, therefore much less is known about hand preference for haptically-guided grasping. One study reported that blindfolded-sighted children preferred the use of their right hand for a multitude of actions but the rate of this preference was not reported (Ittyerah 2000). In the only study (of which we are aware)

investigating hand preference for haptically-guided grasping, 5-8 year old children wore a blindfold when completing the block-building task (Stone et al., 2013). Results showed a marked decrease in right-hand use that was comparable to that seen in adults (Stone and Gonzalez, 2015b; see Appendix 4). So perhaps the hemispheric specializations for visually- and haptically-guided grasping is evident as early as five years of age.

2.4.2. Development of left-hand preference for haptic processing

The human hand is sensitive to touch (i.e. cutaneous stimulation) as early as 10.5 weeks gestation (Humphrey, 1978). Moreover, by 14 weeks gestation, reflex responses are elicited by stimulation of most of the body surface (Humphrey, 1978). As early as 25 weeks, preterm infants will show cortical evoked responses to cutaneous stimulation and by 26 weeks, they will demonstrate reflexive withdrawal of the foot and leg when stimulated (Andrews & Fitzgerald, 1994). Remarkably, premature infants at 28 weeks demonstrate haptic ability for recognizing novel shapes placed in their left hand (Marcus, Lejeune, Berne-Audeoud, Gentaz, & Debillon, 2012). By three months postnatal, fMRI reveals that the cortex and thalamus show a clear, contralateral response to passive cutaneous information presented to each hand (Erberich et al., 2006). Taken together, these reports highlight the early functional development of the somatosensory system.

It has been suggested that there is a division of labour between the hands as early as 4 months of age: a right-hand specialization for fine motor movements and left-hand specialization for processing spatial arrangements and haptic information (Morange-Majoux, 2011; Morange-Majoux, Cougnot, & Bloch, 1997). Studies on infants and children have shown a left-hand advantage for haptically identifying objects such as

wooden cylinders, tactile letters, non-sense or geometrical shapes (Kalenine, Pinet, & Gentaz, 2011; Morange-Majoux, 2011; D. F. Witelson, 1976; S. F. Witelson, 1974). In one study, 4-6 month old infants were observed manipulating wooden cylinders. The results showed that the left hand spent more time touching and passively exploring the cylinders than did the right (Morange-Majoux, 2011). It has been suggested that the increased time spent touching the object is due to deeper haptic information processing ability of the left hand (Lhote & Streri, 1998). In fact, infants as young as 2 months of age show the ability to retain haptic information better when that information is exposed to the left hand than when exposed to the right hand (Lhote & Streri, 1998). This result in infants aligns with other studies in early childhood that reported that 2-year-olds display an advantage for visually recognizing novel geometrical shapes that were previously haptically manipulated with the left (but not the right) hand (Rose, 1984). This left-hand advantage for novel object recognition has also been reported in older children (6-12 year olds; Witelson, 1974; Witelson, 1976). In addition to shape recognition, developmental studies have also demonstrated a robust left-hand advantage for haptically discriminating between different orientations (Brizzolara et al., 1982), as well as for utilizing proprioceptive feedback in a trajectory-matching task (Goble, Lewis, Hurvitz, & Brown, 2005). In sum, a right-hemisphere specialization for haptics is present and robust early in development. The combination of the left- and right-hemisphere specializations for sensory control during development might modulate hand selection for grasping into adulthood. The integration of these specializations are discussed next.

2.5. INTEGRATION OF HEMISPHERIC SPECIALIZATIONS

Overall, the literature suggests a left-hemisphere specialization for visually-guided movements and a right-hemisphere specialization for haptic processing. These specializations tend to be developed in childhood, and possibly even infancy. On a moment-to-moment basis, vision and haptics work together to create a perception of the world and the ability to act upon it. It has been argued that concurrent use of visual and haptic information provides the best means to recognize an object (Woods & Newell, 2004). Many studies have investigated the relationship between these two sensory systems and have demonstrated their interconnectedness at both the behavioural and neural levels (Held, 2009; Hupp & Sloutsky, 2011; Lacey & Sathian, 2011, 2014; Lawson, Boylan, & Edwards, 2013; Millar & Al-Attar, 2005; Norman, Clayton, Norman, & Crabtree, 2008; Norman, Norman, Clayton, Lianekhammy, & Zielke, 2004; Reales & Ballesteros, 1999; Rognini et al., 2013; Sadato, Okada, Honda, & Yonekura, 2002; Volcic, Wijntjes, Kool, & Kappers, 2010; Wallraven, Bulthoff, Waterkamp, van Dam, & Gaissert, 2013; Wesslein, Spence, & Frings, 2014; Woods & Newell, 2004; Xu, O'Keefe, Suzuki, & Franconeri, 2012).

2.5.1. Evidence from behavioural studies

One way to understand the imbricated relationship between vision and haptics to manual actions is to investigate facilitation or interference effects when the senses are combined or isolated. Millar and Al-Attar (2005) explored the extent to which vision facilitates haptic processing. Using the right index finger, participants were asked to remember spatial landmarks on a tactile map while visual availability was manipulated (i.e. no

vision, tunnel vision, peripheral vision, or full vision). Results showed that having vision increased performance on the task, even if it was just tunnel or peripheral vision. Moreover, Tipper et al. (1998) found that having vision of the hand (via a computer screen) during a tactile recognition (i.e. vibration) task significantly improved participant's response time. This finding has been replicated in other studies (Sambo et al., 2012; Wesslein et al., 2014), which together support the theory of an integrated visual and haptic system. In a study that investigated the bidirectional contributions of vision and haptics to grasping, participants were asked to reach-to-grasp various sized wooden blocks using the right hand (Pettypiece, Goodale, & Culham, 2010). Concurrently, participants gripped a wooden block with the left hand that was either the same (congruent) or a different (incongruent) size as the block they were instructed to grasp with the right hand. When the object in the left hand was incongruent (larger), participants opened their right hand significantly wider prior to grasp onset. That is, even though the participant could *see* the object they were grasping, haptic information in the left hand interfered with the kinematics of the right. Therefore, although vision enhances performance on a haptic task, haptic information can also affect performance on a visual task.

One theory supporting this integrated relationship is known as the 'optimal integration theory' or sometimes referred to as 'the sensory weighting hypothesis' (Ernst & Banks, 2002; Helbig & Ernst, 2007; Spence & Walton, 2005). This theory posits that during a task that involves sensory competition (such as the presence of both vision and touch), humans will rely on whichever domain provides optimal information to complete the task. For example, if you are looking for your cup of coffee in a well-lit room, vision

will arguably provide more relevant information than haptics. In contrast, if the room is poorly-lit, haptics might assume a more dominant role in identifying the cup. In one study, Ernst and Banks (2002) presented individuals with two bars and asked them to indicate which bar was taller. Participants explored the bars either visually and haptically. The visual scene was manipulated in order to investigate when individuals would switch to relying on one sense versus the other. They found that when the visual scene was “noisy” (i.e. with distractors), performance tended to rely more on the haptic domain, demonstrating that humans integrate sensory information in a statistically optimal fashion (Ernst & Banks, 2002). Further support for optimal integration of visual and haptic cues is evident in a recent report by Kandula, Hofman, and Dijkerman (2015). They reported that individuals were faster to respond to tactile stimuli when it was congruent (rather than incongruent) with incoming visual stimuli. Participants watched a video of a hand coming towards their face while vibrotactile stimulation was applied to the cheek. When the stimulation matched that of the projected hand path coming towards the cheek, participants were significantly faster at responding to the vibration. Similar results with respect to congruent/incongruent visual and haptic stimulation were reported by Gray and Tan (2002). These behavioural studies highlight an integrated, inter-sensory relationship between the visual and haptic systems.

2.5.2. Evidence from neuroimaging studies

This integrated relationship has also been shown at the neural level in areas including the occipital and parietal cortices. For instance, transcranial magnetic stimulation (TMS) to the occipital cortex of healthy individuals not only impairs visual perception (e.g.

Beckers and Homberg, 1991) but also tactile processing (Zangaladze, Epstein, Grafton, & Sathian, 1999). In fact, patient DF, an individual with ventral visual stream damage (mainly in the occipital areas) causing visual-form agnosia, shows extreme impairments in visual as well as in haptic object recognition (Thomas W James, James, Humphrey, & Goodale, 2006). fMRI studies in healthy individuals have shown activation of the middle and lateral occipital areas during visual and haptic recognition of 3D non-sense objects (T. W. James et al., 2002). The lateral occipital complex (LOC) has been coined a ‘visuo-haptic shape identification’ area (A. Amedi et al., 2001; Grill-Spector, Kourtzi, & Kanwisher, 2001; Lacey, Tal, Amedi, & Sathian, 2009). For instance, in an fMRI study, Amedi and colleagues asked individuals to visually and haptically identify different 3D common objects (e.g. fork, syringe). Results showed significant object-related activation in area LOC for both visual and haptic identification (A. Amedi et al., 2001). Furthermore, the right LOC shows greater activation when haptic processing is completed with the left hand, compared to activation of the left LOC when using the right hand (Yalachkov, Kaiser, Doehrmann, & Naumer, 2015). Taken together, these studies highlight the role of occipital areas in visuo-tactile processing.

The parietal cortex also plays a key role in multisensory processing. In fact, simply observing someone else being touched has been shown to activate areas such as the secondary somatosensory cortex (SII; Keysers et al., 2004) and the PPC (Chan and Baker, 2015). The PPC is implicated in both the visual (Goodale & Milner, 1992) and haptic (Dijkerman & de Haan, 2007) dorsal streams, which are responsible for how we interact with objects. The visual dorsal stream, which projects from primary visual cortex to PPC, aids in the visuomotor transformation and control of actions. The haptic dorsal

stream which projects from SI and SII also to the PPC assists in the haptic-motor transformation of information for action. Both the dorsal-visual and the dorsal-haptic streams are responsible for transforming information about an object's features (e.g. size, orientation, location) for appropriate grasp and manipulation. With respect to integration of vision and haptics, fMRI studies have shown activation in the anterior intraparietal sulcus (aIPS), an area implicated in grasping (e.g. Binkofski et al., 1998; Grezes et al., 2003; Castiello, 2005; Frey et al., 2015; Gallivan and Culham, 2015) during both visual and tactile object recognition (Grefkes, Weiss, Zilles, & Fink, 2002; Tal & Amedi, 2009). Overall, it is clear that parietal areas play a role in the integration of vision and touch.

Not surprisingly, these same occipito-parietal areas responsible for visual and haptic integration have also been implicated in grasping. Studies investigating this sensory integration for grasping are discussed below. We conclude by proposing a model of how vision and haptics shape hand preference for grasping.

2.5.3. Sensory integration for grasping

The combined role of *both* vision and haptics during reach-to-grasp movements has been investigated in few studies (Buckingham, Ranger, & Goodale, 2012; Chang, Flanagan, & Goodale, 2008; Endo, Wing, & Bracewell, 2011; Kritikos & Beresford, 2002; Pettypiece et al., 2010). In one study, using the size-weight illusion (an illusion in which objects of similar size differ in weight, and objects of identical weight differ in size) participants were asked to lift with one hand objects that were resting on the palm of the other hand or on a tabletop. Results showed more accurate lifting forces when the object rested on the hand (objects only rested in the left hand) presumably because the

left hand provided helpful haptic feedback to guide the lift made by the right hand (Chang et al., 2008) . This study unfortunately only tested the right hand for lifting (left hand for resting). In a different study that tested both hands, Kritikos and Beresford (2002) investigated the effects of visual and haptic information on grasp formation. Individuals were asked to make a visually-guided grasp towards a target object (rubber ball) with one hand while the other hand held an unseen distractor object (that was either smaller, larger, or the same size as the target object). Because the distractor was not seen but instead only felt, the authors were able to investigate if irrelevant haptic information in one hand affected the grasping parameters of the other. Intriguingly, grasp kinematics were only affected when the left hand held the distractor object. The authors concluded that irrelevant haptic information has an influence on visuomotor control and argued that the left-handed kinematics were not affected by holding an object in the right hand because the left-handed kinematics were already quite variable. Alternatively, one could speculate that because the left hand is better at haptic processing, holding an object in the left hand would have a greater influence on the actions of the right hand than would the opposite. If this hypothesis were correct, the results would suggest that the left-hemisphere specialization for visually-guided grasping can be easily influenced by the right-hemisphere specialization for haptics. This possibility, and whether haptically-guided grasping could be influenced by visual information, warrants further investigation.

2.5.4. A model of how visuo-haptic integration influences hand preference for grasping

In the only study (to our knowledge) that has investigated how vision *and* haptics modulate hand preference for grasping, right- and left-handed adults were asked to complete the block-building task under four conditions: Vision/Haptics, No Vision/Haptics, Vision/Constrained Haptics, No Vision/Constrained Haptics (Stone & Gonzalez, 2015a; Appendix 3). In the No Vision conditions participants wore a blindfold and in the Constrained Haptics they wore a pair of textured, fitted gloves (see Figure 1B). Results showed a right-hand preference (~65%) for grasping when vision and haptics were both available (Vision/Haptics), replicating numerous other studies (Bryden, Pryde, & Roy, 2000; Cavill & Bryden, 2003; C. L. Gonzalez et al., 2015; C. L. Gonzalez & Goodale, 2009; C. L. Gonzalez et al., 2007; Main & Carey, 2014; Stone et al., 2013; Stone & Gonzalez, 2014a, 2014b). When vision was occluded, and the task was haptically-guided (No Vision/Haptics condition), there was a significant increase in *left*-hand use, to the point where the right and left hands were used to the same extent (~50% left-hand use). This result also replicated the findings of Stone & Gonzalez (2014a, 2014b). Interestingly, when vision was available but haptics was constrained (Vision/Constrained Haptics), the right hand was used almost exclusively (~80%, see Figure 1D). These results strongly suggest the interconnectedness of the visual and haptic systems in shaping hand preference for grasping in which both sensory systems, albeit in opposite directions, contribute to this preference. What is more, similar results were also found in children as early as five years of age (Stone and Gonzalez, 2015b; Appendix 4)

suggesting that vision and haptics have a modulatory effect on hand preference since early development.

If vision and haptics both contribute to shaping hand preference for grasping (from opposite hemispheres), why do individuals still present with a right-hand preference (~65%)? One possibility is that handedness plays a role. However, numerous studies have shown that left-handers are not the mirror image of right-handers and in fact, as a population left-handers do not show a hand preference for grasping in some studies (Bryden, Mayer, & Roy, 2011; Main & Carey, 2014; Mamolo, Roy, Bryden, & Rohr, 2005; Stone et al., 2013; Stone & Gonzalez, 2015a). Moreover, hand preference remained unchanged for left-handers in response to the visual and haptic manipulations in Stone & Gonzalez (2015b). This finding is supported by Tomlinson et al. (2011) who found that left-handers show much weaker lateralization during a haptic task than right-handers, as well as by Pool, Rehme, Eickhoff, Fink, and Grefkes (2015) who found that left-handers have significantly lower interhemispheric functional connectivity between sensorimotor areas. Another possibility is that higher rates of right-hand use in the presence of both vision and haptics are a reflection of the type of grasping actions that we execute. Studies have shown kinematic differences in seemingly similar actions that only differ in the ultimate goal of the action (e.g. grasp-to-place vs grasp-to-throw (Armbruster & Spijkers, 2006); grasp-to-place versus grasp-to-eat (Flindall & Gonzalez, 2014; Flindall et al., 2015). It remains to be shown if haptically-guided grasping movements that require only identification of an object (i.e. grasp-to-identify) generate higher rates of left-hand use. In our studies using the block-building task, participants are not only required to haptically identify the blocks that constitute the sample model, but are also required to manipulate

and assemble the pieces to successfully construct a replica (grasp-to-construct). It is possible that hand preference would be different for these two very different types of grasps (i.e. grasp-to-identify versus grasp-to-construct). Observations from our lab may lend support to this idea. Although not specifically investigated, in Stone and Gonzalez (2015a; Appendix 3) participants made more grasp-to-identify movements with the left hand than they did with the right hand. This suggests that hand preference is sensitive to the intent behind a grasp. Experiments specifically testing this suggestion are underway.

Finally, a viable model to explain hand preference for grasping would be to frame it around an evolutionary scenario. Studies have shown that non-human primates exhibit a left-hand preference for haptic discrimination (Fagot, Drea, & Wallen, 1991; Lacreuse & Fragaszy, 1996; Lacreuse & Fragaszy, 1997, 1999; Laska, 1996; Parr, Hopkins, & de Waal, 1997; G. Spinozzi & Cacchiarelli, 2000) and a right-hand preference for visually-guided reaching and grasping (Diamond & McGrew, 1994; W. D. Hopkins, 1995; W. D. Hopkins, Bennett, Bales, Lee, & Ward, 1993; Peter F MacNeilage, Studdert-Kennedy, & Lindblom, 1987). For example Lacreuse and Fragaszy (1999) observed Capuchins searching for sunflower seeds in the crevices of 12 clay objects using haptics, similar to a ‘grasp-to-identify’ action. Capuchins showed a robust preference to use the left hand during this task. The authors suggested that “the left-hand preference for the haptic task may reflect a hemispheric specialization to integrate the spatial and motor components of an action” (Lacreuse and Fragaszy, 1999; p. 65). Conversely, during a visually-guided reach-to-eat task, Giovanna Spinozzi, Castorina, and Truppa (1998) showed that Capuchins show a preference to grasp with the right hand, a preference found in

chimpanzees as well (W.D. Hopkins & Fernández-Carriba, 2000; W. D. Hopkins, Gardner, Mingle, Reamer, & Schapiro, 2013). So it is plausible that these specializations were present in our common ancestors and thus passed through our lineage. Since the majority of grasps in primates are not specifically to identify an object (vision usually enables object identification) then recruitment of the left hand for grasping occurs less frequently.

2.6. Conclusion

The literature suggests a left-hemisphere specialization for visuomotor control, particularly for visually-guided grasping and a right-hemisphere specialization for haptic processing. We speculate that these sensory-modality specific asymmetries integrate to contribute to hand preference during grasping (even early in development). During visually-guided grasping, a right-hand/left-hemisphere specialization presents but during haptically-guided grasping, a trend to rely increasingly on the left-hand/right-hemisphere emerges. Taken together, the interplay of these two systems allows for effective sensorimotor control.

References

- Adam, J. J., Muskens, R., Hoonhorst, S., Pratt, J., & Fischer, M. H. (2010). Left hand, but not right hand, reaching is sensitive to visual context. *Exp Brain Res*, *203*(1), 227-232. doi: 10.1007/s00221-010-2214-6
- Amedi, A., Malach, R., Hendler, T., Peled, S., & Zohary, E. (2001). Visuo-haptic object-related activation in the ventral visual pathway. *Nature Neuroscience*, *4*(3), 324-330. doi: 10.1038/85201
- Amedi, A., Stern, W. M., Camprodon, J. A., Bermpohl, F., Merabet, L., Rotman, S., . . . Pascual-Leone, A. (2007). Shape conveyed by visual-to-auditory sensory substitution activates the lateral occipital complex. *Nature Neuroscience*, *10*(6), 687-689. doi: 10.1038/nm1912
- Andrews, K., & Fitzgerald, M. (1994). The cutaneous withdrawal reflex in human neonates: Sensitization, receptive fields, and the effects of contralateral stimulation. *Pain*, *56*(1), 95-101. doi: [http://dx.doi.org/10.1016/0304-3959\(94\)90154-6](http://dx.doi.org/10.1016/0304-3959(94)90154-6)
- Argyropoulos, V., Sideridis, G. D., & Papadimitriou, V. (2014). Hand preference of individuals with blindness in everyday activities: The effects of age of sight loss, age, and gender. *Research in Developmental Disabilities* doi: 10.1016/j.ridd.2014.03.027
- Armbruster, C., & Spijkers, W. (2006). Movement planning in prehension: Do intended actions influence the initial reach and grasp movement? *Motor Control*, *10*(4), 311-329.
- Arnott, S. R., Cant, J. S., Dutton, G. N., & Goodale, M. A. (2008). Crinkling and crumpling: An auditory fMRI study of material properties. *Neuroimage*, *43*(2), 368-378. doi: 10.1016/j.neuroimage.2008.07.033
- Atkinson, J. (2002). *The developing visual brain*. Oxford: Oxford University Press.
- Babinsky, E., Braddick, O., & Atkinson, J. (2012). The effect of removing visual information on reach control in young children. *Exp Brain Res*, *222*(3), 291-302. doi: 10.1007/s00221-012-3216-3

- Beckers, G., & Homberg, V. (1991). Impairment of visual perception and visual short term memory scanning by transcranial magnetic stimulation of occipital cortex. *Exp Brain Res*, 87(2), 421-432. doi: 10.1007/BF00231859
- Benton, A. L., Levin, H. S., & Varney, N. R. (1973). Tactile perception of direction in normal subjects: Implications for hemispheric cerebral dominance. *Neurology*, 23(11), 1248-1250. doi: 10.1212/WNL.23.11.1248
- Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., & Freund, H. J. (1998). Human anterior intraparietal area subserves prehension: A combined lesion and functional MRI activation study. *Neurology*, 50(5), 1253-1259. doi: 10.1212/WNL.50.5.1253
- Bishop, D. V., Ross, V. A., Daniels, M. S., & Bright, P. (1996). The measurement of hand preference: A validation study comparing three groups of right-handers. *British Journal of Psychology*, 87 (Pt 2), 269-285. doi: 10.1111/j.2044-8295.1996.tb02590.x
- Bjorkman, A., Rosen, B., & Lundborg, G. (2004). Acute improvement of hand sensibility after selective ipsilateral cutaneous forearm anaesthesia. *Eur J Neurosci*, 20(10), 2733-2736. doi: 10.1111/j.1460-9568.2004.03742.x
- Bjorkman, A., Weibull, A., Rosen, B., Svensson, J., & Lundborg, G. (2009). Rapid cortical reorganisation and improved sensitivity of the hand following cutaneous anaesthesia of the forearm. *Eur J Neurosci*, 29(4), 837-844. doi: 10.1111/j.1460-9568.2009.06629.x
- Brizzolara, D., De Nobili, G. L., & Ferretti, G. (1982). Tactile discrimination of direction of lines in relation to hemispheric specialization. *Perceptual and Motor Skills*, 54(2), 655-660. doi: 10.2466/pms.1982.54.2.655
- Bryden, P. J., & Huszczyński, J. (2011). Under what conditions will right-handers use their left hand? The effects of object orientation, object location, arm position, and task complexity in preferential reaching. *Laterality*, 16(6), 722-736. doi: 10.1080/1357650x.2010.514344
- Bryden, P. J., Mayer, M., & Roy, E. A. (2011). Influences of task complexity, object location, and object type on hand selection in reaching in left and right-handed children and adults. *Developmental Psychobiology*, 53(1), 47-58. doi: 10.1002/dev.20486

- Bryden, P. J., Pryde, K. M., & Roy, E. A. (2000). A performance measure of the degree of hand preference. *Brain and Cognition*, *44*(3), 402-414. doi: 10.1006/brcg.1999.1201
- Bryden, P. J., & Roy, E. A. (2006). Preferential reaching across regions of hemispace in adults and children. *Developmental Psychobiology* *48*(2), 121-132. doi: 10.1002/dev.20120
- Buckingham, G., Ranger, N. S., & Goodale, M. A. (2012). Handedness, laterality and the size-weight illusion. *Cortex*, *48*(10), 1342-1350. doi: 10.1016/j.cortex.2011.09.007
- Butler, A. J., Fink, G. R., Dohle, C., Wunderlich, G., Tellmann, L., Seitz, R. J., . . . Freund, H. J. (2004). Neural mechanisms underlying reaching for remembered targets cued kinesthetically or visually in left or right hemispace. *Human Brain Mapping*, *21*(3), 165-177. doi: 10.1002/hbm.20001
- Caliskan, E., & Dane, S. (2009). Left-handedness in blind and sighted children. *Laterality*, *14*(2), 205-213. doi: 10.1080/13576500802586251
- Calvert, G. A., & Bishop, D. V. (1998). Quantifying hand preference using a behavioural continuum. *Laterality*, *3*(3), 255-268. doi: 10.1080/713754307
- Cannon, A., & Benton, A. L. (1969). Tactile perception of direction and number in patients with unilateral cerebral disease. *Neurology*, *19*(6), 525. doi: 10.1212/wnl.19.6.525
- Carlier, M., Doyen, A. L., & Lamard, C. (2006). Midline crossing: Developmental trend from 3 to 10 years of age in a preferential card-reaching task. *Brain and Cognition*, *61*(3), 255-261. doi: 10.1016/j.bandc.2006.01.007
- Carlson, D. F., & Harris, L. J. (1985). Development of the infant's hand preference for visually directed reaching: Preliminary report of a longitudinal study. *Infant Mental Health Journal*, *6*(3), 158-174. doi: 10.1002/1097-0355(198523)6:33.0.CO;2-X
- Castiello, U. (2005). The neuroscience of grasping. *Nature Reviews Neuroscience*, *6*(9), 726-736. doi: 10.1038/nrn1744

- Castiello, U., Bennett, K. M., & Mucignat, C. (1993). The reach to grasp movement of blind subjects. *Exp Brain Res*, *96*(1), 152-162. doi: 10.1007/BF00230448
- Cavill, S., & Bryden, P. (2003). Development of handedness: Comparison of questionnaire and performance-based measures of preference. *Brain and Cognition*, *53*(2), 149-151. doi: 10.1016/S0278-2626(03)00098-8
- Chan, A. W., & Baker, C. I. (2015). Seeing is not feeling: Posterior parietal but not somatosensory cortex engagement during touch observation. *The Journal of Neuroscience*, *35*(4), 1468-1480. doi: 10.1523/jneurosci.3621-14.2015
- Chang, E. C., Flanagan, J. R., & Goodale, M. A. (2008). The intermanual transfer of anticipatory force control in precision grip lifting is not influenced by the perception of weight. *Exp Brain Res*, *185*(2), 319-329. doi: 10.1007/s00221-007-1156-0
- Chapman, C. S., & Goodale, M. A. (2010a). Obstacle avoidance during online corrections. *Journal of Vision*, *10*(11), 17. doi: 10.1167/10.11.17
- Chapman, C. S., & Goodale, M. A. (2010b). Seeing all the obstacles in your way: The effect of visual feedback and visual feedback schedule on obstacle avoidance while reaching. *Exp Brain Res*, *202*(2), 363-375. doi: 10.1007/s00221-009-2140-7
- Cole, J. D., & Sedgwick, E. M. (1992). The perceptions of force and movement in a man without large myelinated sensory afferents below the neck. *Journal of Physiology-London*, *449*, 503-515. doi: 10.1113/jphysiol.1992.sp019099
- Collignon, O., & De Volder, A. G. (2009). Further evidence that congenitally blind participants react faster to auditory and tactile spatial targets. *Canadian Journal of Experimental Psychology*, *63*(4), 287-293. doi: 10.1037/a0015415
- Collignon, O., Vandewalle, G., Voss, P., Albouy, G., Charbonneau, G., Lassonde, M., & Lepore, F. (2011). Functional specialization for auditory-spatial processing in the occipital cortex of congenitally blind humans. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(11), 4435-4440. doi: 10.1073/pnas.1013928108
- Cooke, J. D., Brown, S., Forget, R., & Lamarre, Y. (1985). Initial agonist burst duration changes with movement amplitude in a deafferented patient. *Exp Brain Res*, *60*(1), 184-187. doi: 10.1007/BF00237030

- Corbetta, D., & Thelen, E. (1999). Lateral biases and fluctuations in infants' spontaneous arm movements and reaching. *Developmental Psychobiology*, *34*(4), 237-255. doi: 10.1002/(SICI)1098-2302(199905)34:23.3.CO;2-R
- Cormier, J. M., & Tremblay, F. (2013). Asymmetry in corticomotor facilitation revealed in right-handers in the context of haptic discrimination. *Laterality*, *18*(3), 365-383. doi: 10.1080/1357650x.2012.701631
- Cote, C. A. (2014). Haptic exploration in elementary school age children. *OTJR: Occupation, Participation and Health* *34*(1), 4-11.
- De Renzi, E., Faglioni, P., & Scotti, G. (1969). Impairment of memory for position following brain damage. *Cortex*, *5*(3), 274-284. doi: 10.1016/S0010-9452(69)80035-3
- Diamond, A. C., & McGrew, W. C. (1994). True handedness in the cotton-top tamarin (*Saguinus oedipus*)? *Primates*, *35*(1), 69-77. doi: 10.1007/BF02381487
- Dijkerman, H. C., & de Haan, E. H. (2007). Somatosensory processes subserving perception and action. *Behavioral and Brain Sciences*, *30*(2), 189-201; discussion 201-139. doi: 10.1017/s0140525x07001392
- Dodds, A. G. (1978). Hemispheric differences in tactuo-spatial processing. *Neuropsychologia*, *16*(2), 247-250. doi: 10.1016/0028-3932(78)90115-X
- Dubois, J., Hertz-Pannier, L., Cachia, A., Mangin, J. F., Le Bihan, D., & Dehaene-Lambertz, G. (2009). Structural asymmetries in the infant language and sensori-motor networks. *Cerebral Cortex*, *19*(2), 414-423. doi: 10.1093/cercor/bhn097
- Elliott, D., Lyons, J., Chua, R., Goodman, D., & Carson, R. G. (1995). The influence of target perturbation on manual aiming asymmetries in right-handers. *Cortex*, *31*(4), 685-697. doi: 10.1016/S0010-9452(13)80020-2
- Elliott, D., Roy, E. A., Goodman, D., Carson, R. G., Chua, R., & Maraj, B. K. (1993). Asymmetries in the preparation and control of manual aiming movements. *Canadian Journal of Experimental Psychology*, *47*(3), 570. doi: 10.1037/h0078856

- Endo, S., Wing, A. M., & Bracewell, R. M. (2011). Haptic and visual influences on grasp point selection. *Journal of Motor Behavior*, 43(6), 427-431. doi: 10.1080/00222895.2011.621996
- Erberich, S. G., Panigrahy, A., Friedlich, P., Seri, I., Nelson, M. D., & Gilles, F. (2006). Somatosensory lateralization in the newborn brain. *Neuroimage*, 29(1), 155-161. doi: <http://dx.doi.org/10.1016/j.neuroimage.2005.07.024>
- Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, 415(6870), 429-433. doi: 10.1038/415429a
- Esparza, D. Y., Archambault, P. S., Winstein, C. J., & Levin, M. F. (2003). Hemispheric specialization in the co-ordination of arm and trunk movements during pointing in patients with unilateral brain damage. *Exp Brain Res*, 148(4), 488-497. doi: 10.1007/s00221-002-1325-0
- Fagard, J. (1998). *Changes in grasping skills and the emergence of bimanual coordination during the first year of life*. Londres: Mac Keith Press.
- Fagard, J. (2013). The nature and nurture of human infant hand preference. *Annals of the New York Academy of Sciences*, 1288, 114-123. doi: 10.1111/nyas.12051
- Fagard, J., & Lockman, J. J. (2005). The effect of task constraints on infants' (bi)manual strategy for grasping and exploring objects. *Infant Behavior & Development*, 28(3), 305-315. doi: <http://dx.doi.org/10.1016/j.infbeh.2005.05.005>
- Fagard, J., & Marks, A. (2000). Unimanual and bimanual tasks and the assessment of handedness in toddlers. *Developmental Science*, 3(2), 137-147. doi: 10.1111/1467-7687.00107
- Fagot, J., Drea, C. M., & Wallen, K. (1991). Asymmetrical hand use in rhesus monkeys (*Macaca mulatta*) in tactually and visually regulated tasks. *Journal of Comparative Psychology*, 105(3), 260-268. doi: 10.1037//0735-7036.105.3.260
- Fagot, J., Hopkins, W. D., & Vauclair, J. (1993). Hand movements and hemispheric specialization in dichhaptic explorations. *Perception*, 22(7), 847-853. doi: 10.1068/p220847

- Fagot, J., Lacreuse, A., & Vauclair, J. (1993). Haptic discrimination of nonsense shapes: Hand exploratory strategies but not accuracy reveal laterality effects. *Brain and Cognition*, *21*(2), 212-225. doi: 10.1006/brcg.1993.1017
- Fagot, J., Lacreuse, A., & Vauclair, J. (1994). Hand-movement profiles in a tactual-tactual matching task: Effects of spatial factors and laterality. *Perception & Psychophysics*, *56*(3), 347-355. doi: 10.3758/BF03209768
- Ferre, C. L., Babik, I., & Michel, G. F. (2010). Development of infant prehension handedness: A longitudinal analysis during the 6- to 14-month age period. *Infant Behavior & Development*, *33*(4), 492-502. doi: 10.1016/j.infbeh.2010.06.002
- Fiehler, K., Burke, M., Bien, S., Roder, B., & Rosler, F. (2009). The human dorsal action control system develops in the absence of vision. *Cerebral Cortex*, *19*(1), 1-12. doi: 10.1093/cercor/bhn067
- Fiehler, K., Burke, M., Engel, A., Bien, S., & Rosler, F. (2008). Kinesthetic working memory and action control within the dorsal stream. *Cerebral Cortex* *18*(2), 243-253. doi: 10.1093/cercor/bhm071
- Fisk, J. D., & Goodale, M. A. (1988). The effects of unilateral brain damage on visually guided reaching: Hemispheric differences in the nature of the deficit. *Exp Brain Res*, *72*(2), 425-435. doi: 10.1007/BF00250264
- Flindall, J. W., Doan, J. B., & Gonzalez, C. L. (2013). Manual asymmetries in the kinematics of a reach-to-grasp action. *Laterality*, *19*(4), 489-507. doi: 10.1080/1357650x.2013.862540
- Flindall, J. W., & Gonzalez, C. L. (2014). Eating interrupted: The effect of intent on hand-to-mouth actions. *Journal of Neurophysiology*, *112*(8), 2019-2025. doi: 10.1152/jn.00295.2014
- Flindall, J. W., Stone, K. D., & Gonzalez, C. L. (2015). Evidence for right-hand feeding biases in a left-handed population. *Laterality*, *20*(3), 287-305. doi: 10.1080/1357650x.2014.961472
- Flowers, K. (1975). Handedness and controlled movement. *British Journal of Psychology*, *66*(1), 39-52. doi: 10.1111/j.2044-8295.1975.tb01438.x

- Fontenot, D. J., & Benton, A. L. (1971). Tactile perception of direction in relation to hemispheric locus of lesion. *Neuropsychologia*, *9*(1), 83-88. doi: 10.1016/0028-3932(71)90065-0
- Forget, R., & Lamarre, Y. (1987). Rapid elbow flexion in the absence of proprioceptive and cutaneous feedback. *Human Neurobiology*, *6*(1), 27-37.
- Franco, L., & Sperry, R. W. (1977). Hemisphere lateralization for cognitive processing of geometry. *Neuropsychologia*, *15*(1), 107-114. doi: 10.1016/0028-3932(77)90120-8
- Freitas, S. M., Gera, G., & Scholz, J. P. (2011). Timing variability of reach trajectories in left versus right hemisphere stroke. *Brain and Cognition*, *1419*, 19-33. doi: 10.1016/j.brainres.2011.08.039
- Frey, S. H., Funnell, M. G., Gerry, V. E., & Gazzaniga, M. S. (2005). A dissociation between the representation of tool-use skills and hand dominance: Insights from left- and right-handed callosotomy patients. *Journal of Cognitive Neuroscience*, *17*(2), 262-272. doi: 10.1162/0898929053124974
- Frey, S. H., Hansen, M., & Marchal, N. (2015). Grasping with the press of a button: Grasp-selective responses in the human anterior intraparietal sulcus depend on nonarbitrary causal relationships between hand movements and end-effector actions. *Journal of Cognitive Neuroscience*, *27*(6), 1146-1160. doi: 10.1162/jocn_a_00766
- Gabbard, C., Tapia, M., & Helbig, C. R. (2003). Task complexity and limb selection in reaching. *The International Journal of Neuroscience*, *113*(2), 143-152. doi: 10.1080/00207450390161994
- Gallivan, J. P., & Culham, J. C. (2015). Neural coding within human brain areas involved in actions. *Current Opinion in Biology*, *33*, 141-149. doi: 10.1016/j.conb.2015.03.012
- Gallivan, J. P., McLean, A., & Culham, J. C. (2011). Neuroimaging reveals enhanced activation in a reach-selective brain area for objects located within participants' typical hand workspaces. *Neuropsychologia*, *49*(13), 3710-3721. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2011.09.027>

- Gentilucci, M., Toni, I., Chieffi, S., & Pavesi, G. (1994). The role of proprioception in the control of prehension movements: A kinematic study in a peripherally deafferented patient and in normal subjects. *Exp Brain Res*, 99(3), 483-500. doi: 10.1007/BF00228985
- Gesell, A., & Ames, L. B. (1947). The development of handedness. *The Pedagogical Seminary and Journal of Genetic Psychology*, 70(2), 155-175. doi: 10.1080/08856559.1947.10533403
- Gilmore, J. H., Lin, W., Prastawa, M. W., Looney, C. B., Vetsa, Y. S., Knickmeyer, R. C., . . . Gerig, G. (2007). Regional gray matter growth, sexual dimorphism, and cerebral asymmetry in the neonatal brain. *The Journal of Neuroscience*, 27(6), 1255-1260. doi: 10.1523/jneurosci.3339-06.2007
- Goble, D. J., Lewis, C. A., Hurvitz, E. A., & Brown, S. H. (2005). Development of upper limb proprioceptive accuracy in children and adolescents. *Human Movement Science*, 24(2), 155-170. doi: 10.1016/j.humov.2005.05.004
- Gonzalez, C. L., Flindall, J. W., & Stone, K. D. (2015). Hand preference across the lifespan: Effects of end-goal, task nature, and object location. *Frontiers in Psychology*, 5, 1579. doi: 10.3389/fpsyg.2014.01579
- Gonzalez, C. L., Ganel, T., & Goodale, M. A. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of Neurophysiology*, 95(6), 3496-3501. doi: 10.1152/jn.01187.2005
- Gonzalez, C. L., & Goodale, M. A. (2009). Hand preference for precision grasping predicts language lateralization. *Neuropsychologia*, 47(14), 3182-3189. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2009.07.019>
- Gonzalez, C. L., Mills, K. J., Genee, I., Li, F., Piquette, N., Rosen, N., & Gibb, R. (2014). Getting the right grasp on executive function. *Frontiers in Psychology*, 5, 285. doi: 10.3389/fpsyg.2014.00285
- Gonzalez, C. L., Whitwell, R. L., Morrissey, B., Ganel, T., & Goodale, M. A. (2007). Left handedness does not extend to visually guided precision grasping. *Exp Brain Res*, 182(2), 275-279. doi: 10.1007/s00221-007-1090-1
- Goodale, M. A. (1988). Hemispheric differences in motor control. *Behavioural Brain Research*, 30(2), 203-214. doi: 10.1016/0166-4328(88)90149-0

- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends Neurosci*, *15*(1), 20-25. doi: 10.1016/0166-2236(92)90344-8
- Gooderham, S. E., & Bryden, P. J. (2014). Does your dominant hand become less dominant with time? The effects of aging and task complexity on hand selection. *Developmental Psychobiology*, *56*(3), 537-546. doi: 10.1002/dev.21123
- Gosselin-Kessiby, N., Kalaska, J. F., & Messier, J. (2009). Evidence for a proprioception-based rapid on-line error correction mechanism for hand orientation during reaching movements in blind subjects. *The Journal of Neuroscience*, *29*(11), 3485-3496. doi: 10.1523/jneurosci.2374-08.2009
- Graham, F. K., & Kendall, B. S. (1960). Memory-for-designs test: Revised general manual. *Perceptual and Motor Skills*, *11*(2), 147-188. doi: 10.2466/pms.1960.11.2.147
- Grefkes, C., Weiss, P. H., Zilles, K., & Fink, G. R. (2002). Crossmodal processing of object features in human anterior intraparietal cortex: An fMRI study implies equivalencies between humans and monkeys. *Neuron*, *35*(1), 173-184. doi: 10.1016/S0896-6273(02)00741-9
- Grezes, J., Tucker, M., Armony, J., Ellis, R., & Passingham, R. E. (2003). Objects automatically potentiate action: An fMRI study of implicit processing. *Eur J Neurosci*, *17*(12), 2735-2740. doi: 10.1046/j.1460-9568.2003.02695.x
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*(10-11), 1409-1422. doi: [http://dx.doi.org/10.1016/S0042-6989\(01\)00073-6](http://dx.doi.org/10.1016/S0042-6989(01)00073-6)
- Grosskopf, A., & Kutzt-Buschbeck, J. P. (2006). Grasping with the left and right hand: A kinematic study. *Exp Brain Res*, *168*(1-2), 230-240. doi: 10.1007/s00221-005-0083-1
- Grunwald, M. (2008). *Human haptic perception: Basics and applications*. Basel, Boston, Berlin: Birkhäuser.
- Haaland, K. Y., Elsinger, C. L., Mayer, A. R., Durgerian, S., & Rao, S. M. (2004). Motor sequence complexity and performing hand produce differential patterns of hemispheric lateralization. *Journal of Cognitive Neuroscience*, *16*(4), 621-636. doi: 10.1162/089892904323057344

- Haaland, K. Y., & Harrington, D. L. (1994). Limb-sequencing deficits after left but not right hemisphere damage. *Brain and Cognition*, 24(1), 104-122. doi: 10.1006/brcg.1994.1006
- Handy, T. C., Grafton, S. T., Shroff, N. M., Ketay, S., & Gazzaniga, M. S. (2003). Graspable objects grab attention when the potential for action is recognized. *Nature Neuroscience*, 6(4), 421-427. doi: 10.1038/nn1031
- Harada, T., Saito, D. N., Kashikura, K., Sato, T., Yonekura, Y., Honda, M., & Sadato, N. (2004). Asymmetrical neural substrates of tactile discrimination in humans: A functional magnetic resonance imaging study. *The Journal of Neuroscience*, 24(34), 7524-7530. doi: 10.1523/jneurosci.1395-04.2004
- Heilman, K. M., Meador, K. J., & Loring, D. W. (2000). Hemispheric asymmetries of limb-kinetic apraxia: A loss of deftness. *Neurology*, 55(4), 523-526. doi: 10.1212/WNL.55.4.523
- Helbig, H. B., & Ernst, M. O. (2007). Optimal integration of shape information from vision and touch. *Exp Brain Res*, 179(4), 595-606. doi: 10.1007/s00221-006-0814-y
- Held, R. (2009). Visual-haptic mapping and the origin of cross-modal identity. *Optometry and Vision Science*, 86(6), 595-598. doi: 10.1097/OPX.0b013e3181a72999
- Heller, M. A., Calcaterra, J. A., Burson, L. L., & Tyler, L. A. (1996). Tactual picture identification by blind and sighted people: Effects of providing categorical information. *Perception & Psychophysics*, 58(2), 310-323. doi: 10.3758/BF03211884
- Heller, M. A., Rogers, G. J., & Perry, C. L. (1990). Tactile pattern recognition with the Optacon: Superior performance with active touch and the left hand. *Neuropsychologia*, 28(9), 1003-1006. doi: 10.1016/0028-3932(90)90114-4
- Hepper, P. G., McCartney, G. R., & Shannon, E. A. (1998). Lateralised behaviour in first trimester human foetuses. *Neuropsychologia*, 36(6), 531-534. doi: 10.1016/S0028-3932(97)00156-5

- Hepper, P. G., Wells, D. L., & Lynch, C. (2005). Prenatal thumb sucking is related to postnatal handedness. *Neuropsychologia*, *43*(3), 313-315. doi: 10.1016/j.neuropsychologia.2004.08.009
- Hering-Hanit, R., Achiron, R., Lipitz, S., & Achiron, A. (2001). Asymmetry of fetal cerebral hemispheres: In utero ultrasound study. *Archives of Disease in Childhood. Fetal and Neonatal Edition*, *85*(3), F194-196. doi: 10.1136/fn.85.3.F194
- Hermelin, B., & O'Connor, N. (1971). Functional asymmetry in the reading of Braille. *Neuropsychologia*, *9*(4), 431-435. doi: 10.1016/0028-3932(71)90007-8
- Hermisdorfer, J., Elias, Z., Cole, J. D., Quaney, B. M., & Nowak, D. A. (2008). Preserved and impaired aspects of feed-forward grip force control after chronic somatosensory deafferentation. *Neurorehabilitation and Neural Repair*, *22*(4), 374-384. doi: 10.1177/1545968307311103
- Hill, E. L., & Khanem, F. (2009). The development of hand preference in children: The effect of task demands and links with manual dexterity. *Brain and Cognition*, *71*(2), 99-107. doi: 10.1016/j.bandc.2009.04.006
- Hinojosa, T., Sheu, C.-F., & Michel, G. F. (2003). Infant hand-use preferences for grasping objects contributes to the development of a hand-use preference for manipulating objects. *Developmental Psychobiology*, *43*(4), 328-334. doi: 10.1002/dev.10142
- Hopkins, W. D. (1995). Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): Cross-sectional analysis. *Journal of Comparative Psychology*, *109*(3), 291-297. doi: 10.1037/0735-7036.109.3.291
- Hopkins, W. D., Bennett, A. J., Bales, S. L., Lee, J., & Ward, J. P. (1993). Behavioral laterality in captive bonobos (*Pan paniscus*). *Journal of Comparative Psychology*, *107*(4), 403-410. doi: 10.1037/0735-7036.107.4.403
- Hopkins, W. D., & Fernández-Carriba, S. (2000). The effect of situational factors on hand preferences for feeding in 177 captive chimpanzees (*Pan troglodytes*). *Neuropsychologia*, *38*(4), 403-409. doi: [http://dx.doi.org/10.1016/S0028-3932\(99\)00092-5](http://dx.doi.org/10.1016/S0028-3932(99)00092-5)

- Hopkins, W. D., Gardner, M., Mingle, M., Reamer, L., & Schapiro, S. J. (2013). Within- and between-task consistency in hand use as a means of characterizing hand preferences in captive chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *127*(4), 380-391. doi: 10.1037/a0031071
- Hopkins, W. D., Hook, M., Braccini, S., & Schapiro, S. J. (2003). Population-level right handedness for a coordinated bimanual task in chimpanzees: Replication and extension in a second colony of apes. *International Journal of Primatology*, *24*(3), 677-689. doi: 10.1023/a:1023752816951
- Humphrey, T. (1978). Function of the nervous system during prenatal life. In U. Stave (Ed.), *Perinatal physiology* (pp. 651-683): Springer.
- Hupp, J. M., & Sloutsky, V. M. (2011). Learning to learn: From within-modality to cross-modality transfer during infancy. *Journal of Experimental Child Psychology*, *110*(3), 408-421. doi: 10.1016/j.jecp.2011.05.002
- Ittyerah, M. (2000). Hand skill and hand preference in blind and sighted children. *Laterality*, *5*(3), 221-235. doi: 10.1080/713754379
- Ittyerah, M. (2009). Hand ability and practice in congenitally blind children. *Journal of Developmental and Physical Disabilities*, *21*(5), 329-344. doi: 10.1007/s10882-009-9146-8
- Ittyerah, M., & Marks, L. E. (2007). Memory for curvature of objects: Haptic touch vs. vision. *British Journal of Psychology*, *98*(Pt 4), 589-610. doi: 10.1348/000712606x171531
- Jackson, G. M., Jackson, S. R., Husain, M., Harvey, M., Kramer, T., & Dow, L. (2000). The coordination of bimanual prehension movements in a centrally deafferented patient. *Brain*, *123* (Pt 2), 380-393. doi: <http://dx.doi.org/10.1093/brain/123.2.380>
- Jackson, G. M., Jackson, S. R., Newport, R., & Harvey, M. (2002). Coordination of bimanual movements in a centrally deafferented patient executing open loop reach-to-grasp movements. *Acta Psychologica*, *110*(2-3), 231-246.
- Jackson, S. R., Jackson, G. M., & Rosicky, J. (1995). Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. *Exp Brain Res*, *102*(3), 519-530. doi: 10.1007/BF00230656

- Jacobsohn, L., Rodrigues, P., Vasconcelos, O., Corbetta, D., & Barreiros, J. (2014). Lateral manual asymmetries: A longitudinal study from birth to 24 months. *Developmental Psychobiology*, *56*(1), 58-72. doi: 10.1002/dev.21091
- Jacquet, A. Y., Esseily, R., Rider, D., & Fagard, J. (2012). Handedness for grasping objects and declarative pointing: A longitudinal study. *Developmental Psychobiology*, *54*(1), 36-46. doi: 10.1002/dev.20572
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Exp Brain Res*, *86*(1), 199-208. doi: 10.1007/BF00231054
- James, T. W., Humphrey, G. K., Gati, J. S., Servos, P., Menon, R. S., & Goodale, M. A. (2002). Haptic study of three-dimensional objects activates extrastriate visual areas. *Neuropsychologia*, *40*(10), 1706-1714. doi: 10.1016/S0028-3932(02)00017-9
- James, T. W., James, K. H., Humphrey, G. K., & Goodale, M. A. (2006). *Do visual and tactile object representations share the same neural substrate?*
- James, T. W., Kim, S., & Fisher, J. S. (2007). The neural basis of haptic object processing. *Canadian Journal of Experimental Psychology*, *61*(3), 219-229. doi: 10.1037/cjep2007023
- Janssen, L., Meulenbroek, R. G., & Steenbergen, B. (2011). Behavioral evidence for left-hemisphere specialization of motor planning. *Exp Brain Res*, *209*(1), 65-72. doi: 10.1007/s00221-010-2519-5
- Johnson-Frey, S. H., Newman-Norlund, R., & Grafton, S. T. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral Cortex*, *15*(6), 681-695. doi: 10.1093/cercor/bhh169
- Kalenine, S., Pinet, L., & Gentaz, E. (2011). The visual and visuo-haptic exploration of geometrical shapes increases their recognition in preschoolers. *International Journal of Behavioral Development*, *35*(1), 18-26. doi: 10.1177/0165025410367443
- Kandula, M., Hofman, D., & Dijkerman, H. C. (2015). Visuo-tactile interactions are dependent on the predictive value of the visual stimulus. *Neuropsychologia*, *70*, 358-366. doi: 10.1016/j.neuropsychologia.2014.12.008

- Karl, J. M., Sacrey, L. A., Doan, J. B., & Whishaw, I. Q. (2012). Hand shaping using hapsis resembles visually guided hand shaping. *Exp Brain Res*, *219*(1), 59-74. doi: 10.1007/s00221-012-3067-y
- Karl, J. M., & Whishaw, I. Q. (2013). Different evolutionary origins for the reach and the grasp: An explanation for dual visuomotor channels in primate parietofrontal cortex. *Frontiers in Neurology*, *4*, 208. doi: 10.3389/fneur.2013.00208
- Kasprian, G., Langs, G., Brugger, P. C., Bittner, M., Weber, M., Arantes, M., & Prayer, D. (2011). The prenatal origin of hemispheric asymmetry: An in utero neuroimaging study. *Cerebral Cortex*, *21*(5), 1076-1083. doi: 10.1093/cercor/bhq179
- Kastner-Koller, U., Diemann, P., & Bruckner, J. (2007). Assessing handedness in pre-schoolers: Construction and initial validation of a hand preference test for 4-6-year-olds. *Psychology Science*, *49*(3), 239-254.
- Keefe, B. D., & Watt, S. J. (2009). The role of binocular vision in grasping: A small stimulus-set distorts results. *Exp Brain Res*, *194*(3), 435-444. doi: 10.1007/s00221-009-1718-4
- Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, *11*(6), 417-428. doi: 10.1038/nrn2919
- Keysers, C., Wicker, B., Gazzola, V., Anton, J. L., Fogassi, L., & Gallese, V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*, *42*(2), 335-346. doi: 10.1016/S0896-6273(04)00156-4
- Kim, S. G., Ashe, J., Hendrich, K., Ellermann, J. M., Merkle, H., Ugurbil, K., & Georgopoulos, A. P. (1993). Functional magnetic resonance imaging of motor cortex: Hemispheric asymmetry and handedness. *Science*, *261*(5121), 615-617. doi: 10.1126/science.8342027
- Kimura, D. (1977). Acquisition of a motor skill after left-hemisphere damage. *Brain*, *100*(3), 527-542. doi: <http://dx.doi.org/10.1093/brain/100.3.527>
- Kotwica, K. A., Ferre, C. L., & Michel, G. F. (2008). Relation of stable hand-use preferences to the development of skill for managing multiple objects from 7 to 13 months of age. *Developmental Psychobiology*, *50*(5), 519-529. doi: 10.1002/dev.20311

- Kritikos, A., & Beresford, M. (2002). Tactile interference in visually guided reach-to-grasp movements. *Exp Brain Res*, *144*(1), 1-7. doi: 10.1007/s00221-002-1004-1
- Kroliczak, G., & Frey, S. H. (2009). A common network in the left cerebral hemisphere represents planning of tool use pantomimes and familiar intransitive gestures at the hand-independent level. *Cerebral Cortex*, *19*(10), 2396-2410. doi: 10.1093/cercor/bhn261
- Kuhtz-Buschbeck, J. P., Ehrsson, H. H., & Forssberg, H. (2001). Human brain activity in the control of fine static precision grip forces: An fMRI study. *Eur J Neurosci*, *14*(2), 382-390. doi: 10.1046/j.0953-816x.2001.01639.x
- Kumar, S. (1977). Short term memory for a nonverbal tactual task after cerebral commissurotomy. *Cortex*, *13*(1), 55-61. doi: 10.1016/S0010-9452(77)80053-1
- Lacey, S., & Sathian, K. (2011). Multisensory object representation: Insights from studies of vision and touch. *Progress in Brain Research*, *191*, 165-176. doi: 10.1016/b978-0-444-53752-2.00006-0
- Lacey, S., & Sathian, K. (2014). Visuo-haptic multisensory object recognition, categorization, and representation. *Frontiers in Psychology*, *5*, 730. doi: 10.3389/fpsyg.2014.00730
- Lacey, S., Tal, N., Amedi, A., & Sathian, K. (2009). A putative model of multisensory object representation. *Brain Topography*, *21*(3-4), 269-274. doi: 10.1007/s10548-009-0087-4
- Lacreuse, A., Fagot, J., & Vauclair, J. (1996). Lateralisation hémisphérique et stratégies d'exploration dans des tâches de perception tactilo-kinesthésique. *L'Année psychologique*, *96*(1), 131-145.
- Lacreuse, A., & Fragaszy, D. (1996). Hand preferences for a haptic searching task by tufted capuchins (*Cebus apella*). *International Journal of Primatology*, *17*(4), 613-632. doi: 10.1007/BF02735194
- Lacreuse, A., & Fragaszy, D. M. (1997). Manual exploratory procedures and asymmetries for a haptic search task: A comparison between capuchins (*Cebus apella*) and humans. *Laterality*, *2*(3-4), 247-266. doi: 10.1080/713754275

- Lacreuse, A., & Fragaszy, D. M. (1999). Left hand preferences in capuchins (*Cebus apella*): Role of spatial demands in manual activity. *Laterality*, 4(1), 65-78. doi: 10.1080/713754321
- Laska, M. (1996). Manual laterality in spider monkeys (*Ateles geoffroyi*) solving visually and tactually guided food-reaching tasks. *Cortex*, 32(4), 717-726. doi: 10.1016/S0010-9452(96)80041-4
- Lawson, R., Boylan, A., & Edwards, L. (2013). Where you look can influence haptic object recognition. *Attention, Perception & Psychophysics*. doi: 10.3758/s13414-013-0579-x
- Leconte, P., & Fagard, J. (2004). Influence of object spatial location and task complexity on children's use of their preferred hand depending on their handedness consistency. *Developmental Psychobiology*, 45(2), 51-58. doi: 10.1002/dev.20019
- Lederman, S. J., & Klatzky, R. L. (1987). Hand movements: A window into haptic object recognition. *Cognitive Psychology*, 19(3), 342-368. doi: 10.1016/0010-0285(87)90008-9
- Lederman, S. J., & Klatzky, R. L. (1990). Haptic classification of common objects: Knowledge-driven exploration. *Cognitive Psychology*, 22(4), 421-459. doi: 10.1016/0010-0285(90)90009-S
- Lederman, S. J., & Klatzky, R. L. (2009). Haptic perception: A tutorial. *Attention, Perception & Psychophysics*, 71(7), 1439-1459. doi: 10.3758/app.71.7.1439
- Lhote, M., & Streri, A. (1998). Haptic memory and handedness in 2-month-old infants. *Laterality*, 3(2), 173-192. doi: 10.1080/713754298
- Liu, Y., Baleriaux, D., Kavec, M., Metens, T., Absil, J., Denolin, V., . . . Aeby, A. (2010). Structural asymmetries in motor and language networks in a population of healthy preterm neonates at term equivalent age: A diffusion tensor imaging and probabilistic tractography study. *Neuroimage*, 51(2), 783-788. doi: 10.1016/j.neuroimage.2010.02.066
- Loayza, F. R., Fernandez-Seara, M. A., Aznarez-Sanado, M., & Pastor, M. A. (2011). Right parietal dominance in spatial egocentric discrimination. *Neuroimage*, 55(2), 635-643. doi: 10.1016/j.neuroimage.2010.12.011

- MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Origins of the left & right brain. *Scientific American* 301(1), 60-67.
- MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences*, 10(02), 247-263. doi: 10.1017/S0140525X00047695
- Mahon, B. Z., Anzellotti, S., Schwarzbach, J., Zampini, M., & Caramazza, A. (2009). Category-specific organization in the human brain does not require visual experience. *Neuron*, 63(3), 397-405. doi: 10.1016/j.neuron.2009.07.012
- Main, J. C., & Carey, D. P. (2014). One hand or the other? Effector selection biases in right and left handers. *Neuropsychologia*, 64C, 300-309. doi: 10.1016/j.neuropsychologia.2014.09.035
- Mamolo, C. M., Roy, E. A., Bryden, P. J., & Rohr, L. E. (2004). The effects of skill demands and object position on the distribution of preferred hand reaches. *Brain and Cognition*, 55(2), 349-351. doi: 10.1016/j.bandc.2004.02.041
- Mamolo, C. M., Roy, E. A., Bryden, P. J., & Rohr, L. E. (2005). The performance of left-handed participants on a preferential reaching test. *Brain and Cognition*, 57(2), 143-145. doi: 10.1016/j.bandc.2004.08.033
- Mamolo, C. M., Roy, E. A., Rohr, L. E., & Bryden, P. J. (2006). Reaching patterns across working space: The effects of handedness, task demands, and comfort levels. *Laterality*, 11(5), 465-492. doi: 10.1080/13576500600775692
- Mani, S., Mutha, P. K., Przybyla, A., Haaland, K. Y., Good, D. C., & Sainburg, R. L. (2013). Contralateral motor deficits after unilateral stroke reflect hemisphere-specific control mechanisms. *Brain*, 136(Pt 4), 1288-1303. doi: 10.1093/brain/aws283
- Marcus, L., Lejeune, F., Berne-Audeoud, F., Gentaz, E., & Debillon, T. (2012). Tactile sensory capacity of the preterm infant: Manual perception of shape from 28 gestational weeks. *Pediatrics*, 130(1), e88-94. doi: 10.1542/peds.2011-3357
- Marschik, P. B., Einspieler, C., Strohmeier, A., Plienegger, J., Garzarolli, B., & Prechtel, H. F. (2008). From the reaching behavior at 5 months of age to hand preference at preschool age. *Developmental Psychobiology*, 50(5), 511-518. doi: 10.1002/dev.20307

- Martin, K., Jacobs, S., & Frey, S. H. (2011). Handedness-dependent and -independent cerebral asymmetries in the anterior intraparietal sulcus and ventral premotor cortex during grasp planning. *Neuroimage*, *57*(2), 502-512. doi: 10.1016/j.neuroimage.2011.04.036
- McColm, J. R., & Fleck, B. W. (2001). Retinopathy of prematurity: Causation. *Seminars in Neonatology*, *6*(6), 453-460. doi: 10.1053/siny.2001.0079
- McCormick, C. M., & Maurer, D. M. (1988). Unimanual hand preferences in 6-month-olds: Consistency and relation to familial-handedness. *Infant Behavior & Development*, *11*(1), 21-29. doi: 10.1016/S0163-6383(88)80013-4
- McManus, I. C., Sik, G., Cole, D. R., Mellon, A. F., Wong, J., & Kloss, J. (1988). The development of handedness in children. *British Journal of Developmental Psychology*, *6*(3), 257-273. doi: 10.1111/j.2044-835X.1988.tb01099.x
- Michel, G. F. (1981). Right-handedness: A consequence of infant supine head-orientation preference? *Science*, *212*(4495), 685-687. doi: 10.1126/science.7221558
- Michel, G. F., Ovrut, M. R., & Harkins, D. A. (1985). Hand-use preference for reaching and object manipulation in 6- through 13-month-old infants. *Genetic, Social, and General Psychology Monographs*, *111*(4), 407-427.
- Michel, G. F., Tyler, A. N., Ferre, C., & Sheu, C. F. (2006). The manifestation of infant hand-use preferences when reaching for objects during the seven-to thirteen-month age period. *Developmental Psychobiology*, *48*(6), 436-443. doi: 10.1002/dev.20161
- Millar, S. (1974). Tactile short-term memory by blind and sighted children. *British Journal of Psychology*, *65*(2), 253-263. doi: 10.1111/j.2044-8295.1974.tb01399.x
- Millar, S., & Al-Attar, Z. (2005). What aspects of vision facilitate haptic processing? *Brain and Cognition*, *59*(3), 258-268. doi: 10.1016/j.bandc.2005.07.005
- Milner, B., & Taylor, L. (1972). Right-hemisphere superiority in tactile pattern-recognition after cerebral commissurotomy: Evidence for nonverbal memory. *Neuropsychologia*, *10*(1), 1-15. doi: 10.1016/0028-3932(72)90038-3

- Morange-Majoux, F. (2011). Manual exploration of consistency (soft vs hard) and handedness in infants from 4 to 6 months old. *Laterality*, *16*(3), 292-312. doi: 10.1080/13576500903553689
- Morange-Majoux, F., Peze, A., & Bloch, H. (2000). Organisation of left and right hand movement in a prehension task: A longitudinal study from 20 to 32 weeks. *Laterality*, *5*(4), 351-362. doi: 10.1080/713754386
- Morange-Majoux, F., Cugnot, P., & Bloch, H. (1997). Hand tactual exploration of textures in infants from 4 to 6 months. *Early Development and Parenting*, *6*(3-4), 127-136. doi: 10.1002/(SICI)1099-0917(199709/12)6:3/43.0.CO;2-G
- Nava, E., Gunturkun, O., & Roder, B. (2013). Experience-dependent emergence of functional asymmetries. *Laterality*, *18*(4), 407-415. doi: 10.1080/1357650x.2012.697170
- Nelson, E. L., Campbell, J. M., & Michel, G. F. (2013). Unimanual to bimanual: Tracking the development of handedness from 6 to 24 months. *Infant Behavior & Development*, *36*(2), 181-188. doi: 10.1016/j.infbeh.2013.01.009
- Netelenbos, N., & Gonzalez, C. L. (2015). Is that graspable? Let your right hand be the judge. *Brain and Cognition*, *93*, 18-25. doi: 10.1016/j.bandc.2014.11.003
- Norman, J. F., Clayton, A. M., Norman, H. F., & Crabtree, C. E. (2008). Learning to perceive differences in solid shape through vision and touch. *Perception*, *37*(2), 185-196. doi: 10.1068/p5679
- Norman, J. F., Norman, H. F., Clayton, A. M., Lianekhammy, J., & Zielke, G. (2004). The visual and haptic perception of natural object shape. *Perception & Psychophysics*, *66*(2), 342-351. doi: 10.3758/BF03194883
- Nowak, D. A., Glasauer, S., & Hermsdorfer, J. (2004). How predictive is grip force control in the complete absence of somatosensory feedback? *Brain*, *127*(Pt 1), 182-192. doi: 10.1093/brain/awh016
- O'Boyle, M. W., Van Wyhe-Lawler, F., & Miller, D. A. (1987). Recognition of letters traced in the right and left palms: Evidence for a process-oriented tactile asymmetry. *Brain and Cognition*, *6*(4), 474-494. doi: 10.1016/0278-2626(87)90141-2

- Opsommer, E., Zwissig, C., & Weiss, T. (2013). Effectiveness of temporary deafferentation of the arm on somatosensory and motor functions following stroke: A systematic review protocol. *The JBI Database of Systematic Reviews and Implementation Reports*, *11*(11), 112-124. doi: 10.11124/jbisrir-2013-1008
- Parr, L. A., Hopkins, W. D., & de Waal, F. B. (1997). Haptic discrimination in capuchin monkeys (*Cebus apella*): Evidence of manual specialization. *Neuropsychologia*, *35*(2), 143-152. doi: 10.1016/S0028-3932(96)00056-5
- Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain*, *111*((Pt 3)), 643-674. doi: <http://dx.doi.org/10.1093/brain/111.3.643>
- Petoe, M. A., Jaque, F. A., Byblow, W. D., & Stinear, C. M. (2013). Cutaneous anesthesia of the forearm enhances sensorimotor function of the hand. *Journal of Neurophysiology*, *109*(4), 1091-1096. doi: 10.1152/jn.00813.2012
- Pettypiece, C. E., Goodale, M. A., & Culham, J. C. (2010). Integration of haptic and visual size cues in perception and action revealed through cross-modal conflict. *Exp Brain Res*, *201*(4), 863-873. doi: 10.1007/s00221-009-2101-1
- Pietrini, P., Furey, M. L., Ricciardi, E., Gobbini, M. I., Wu, W. H., Cohen, L., . . . Haxby, J. V. (2004). Beyond sensory images: Object-based representation in the human ventral pathway. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(15), 5658-5663. doi: 10.1073/pnas.0400707101
- Poirier, C., Collignon, O., Scheiber, C., Renier, L., Vanlierde, A., Tranduy, D., . . . De Volder, A. G. (2006). Auditory motion perception activates visual motion areas in early blind subjects. *Neuroimage*, *31*(1), 279-285. doi: 10.1016/j.neuroimage.2005.11.036
- Pool, E. M., Rehme, A. K., Eickhoff, S. B., Fink, G. R., & Grefkes, C. (2015). Functional resting-state connectivity of the human motor network: Differences between right- and left-handers. *Neuroimage*, *109*, 298-306. doi: 10.1016/j.neuroimage.2015.01.034
- Postma, A., Zuidhoek, S., Noordzij, M. L., & Kappers, A. M. (2007). Differences between early-blind, late-blind, and blindfolded-sighted people in haptic spatial-configuration learning and resulting memory traces. *Perception*, *36*(8), 1253-1265. doi: 10.1068/p5441

- Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, *92*(4), 1651-1697. doi: 10.1152/physrev.00048.2011
- Proverbio, A. M., Azzari, R., & Adorni, R. (2013). Is there a left hemispheric asymmetry for tool affordance processing? *Neuropsychologia*, *51*(13), 2690-2701. doi: 10.1016/j.neuropsychologia.2013.09.023
- Radoeva, P. D., Cohen, J. D., Corballis, P. M., Lukovits, T. G., & Koleva, S. G. (2005). Hemispheric asymmetry in a dissociation between the visuomotor and visuoperceptual streams. *Neuropsychologia*, *43*(12), 1763-1773. doi: 10.1016/j.neuropsychologia.2005.02.005
- Ramsay, D. S. (1980). Onset of unimanual handedness in infants. *Infant Behavior & Development*, *3*, 377-385. doi: [http://dx.doi.org/10.1016/S0163-6383\(80\)80045-2](http://dx.doi.org/10.1016/S0163-6383(80)80045-2)
- Rand, M. K., Lemay, M., Squire, L. M., Shimansky, Y. P., & Stelmach, G. E. (2007). Role of vision in aperture closure control during reach-to-grasp movements. *Exp Brain Res*, *181*(3), 447-460. doi: 10.1007/s00221-007-0945-9
- Reales, J. M., & Ballesteros, S. (1999). Implicit and explicit memory for visual and haptic objects: Cross-modal priming depends on structural descriptions. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*(3), 644-663. doi: 10.1037/0278-7393.25.3.644
- Reich, L., Szwed, M., Cohen, L., & Amedi, A. (2011). A ventral visual stream reading center independent of visual experience. *Current Biology*, *21*(5), 363-368. doi: 10.1016/j.cub.2011.01.040
- Renier, L. A., Anurova, I., De Volder, A. G., Carlson, S., VanMeter, J., & Rauschecker, J. P. (2010). Preserved functional specialization for spatial processing in the middle occipital gyrus of the early blind. *Neuron*, *68*(1), 138-148. doi: 10.1016/j.neuron.2010.09.021
- Rhodes, D. L., & Schwartz, G. E. (1981). Lateralized sensitivity to vibrotactile stimulation: Individual differences revealed by interaction of threshold and signal detection tasks. *Neuropsychologia*, *19*(6), 831-835. doi: 10.1016/0028-3932(81)90097-X

- Ricciardi, E., Bonino, D., Sani, L., Vecchi, T., Guazzelli, M., Haxby, J. V., . . . Pietrini, P. (2009). Do we really need vision? How blind people "see" the actions of others. *The Journal of Neuroscience*, *29*(31), 9719-9724. doi: 10.1523/jneurosci.0274-09.2009
- Ricciardi, E., Vanello, N., Sani, L., Gentili, C., Scilingo, E. P., Landini, L., . . . Pietrini, P. (2007). The effect of visual experience on the development of functional architecture in hMT+. *Cerebral Cortex*, *17*(12), 2933-2939. doi: 10.1093/cercor/bhm018
- Riege, W. H., Metter, E. J., & Williams, M. V. (1980). Age and hemispheric asymmetry in nonverbal tactual memory. *Neuropsychologia*, *18*(6), 707-710. doi: 10.1016/0028-3932(80)90112-8
- Riolo-Quinn, L. (1991). Relationship of hand preference to accuracy on a thumb-positioning task. *Perceptual and Motor Skills*, *73*(1), 267-273.
- Rognini, G., Sengul, A., Aspell, J. E., Salomon, R., Bleuler, H., & Blanke, O. (2013). Visuo-tactile integration and body ownership during self-generated action. *Eur J Neurosci*, *37*(7), 1120-1129. doi: 10.1111/ejn.12128
- Ronnqvist, L., & Domellof, E. (2006). Quantitative assessment of right and left reaching movements in infants: A longitudinal study from 6 to 36 months. *Developmental Psychobiology*, *48*(6), 444-459. doi: 10.1002/dev.20160
- Rose, S. A. (1984). Developmental changes in hemispheric specialization for tactual processing in very young children: Evidence from cross-modal transfer. *Developmental Psychology*, *20*(4), 568. doi: 10.1037/0012-1649.20.4.568
- Rothwell, J. C., Traub, M. M., Day, B. L., Obeso, J. A., Thomas, P. K., & Marsden, C. D. (1982). Manual motor performance in a deafferented man. *Brain*, *105* (Pt 3), 515-542. doi: 10.1093/brain/105.3.515
- Roy, E. A., & Elliott, D. (1986). Manual asymmetries in visually directed aiming. *Canadian Journal of Psychology*, *40*(2), 109-121. doi: <http://dx.doi.org/10.1037/h0080087>
- Roy, E. A., & Elliott, D. (1989). Manual asymmetries in aimed movements. *The Quarterly Journal of Experimental Psychology*, *41*(3), 501-516. doi: 10.1080/14640748908402379

- Roy, E. A., Kalbfleisch, L., & Elliott, D. (1994). Kinematic analyses of manual asymmetries in visual aiming movements. *Brain and Cognition*, *24*(2), 289-295. doi: <http://dx.doi.org/10.1006/brcg.1994.1017>
- Sacrey, L. A., Arnold, B., Whishaw, I. Q., & Gonzalez, C. L. (2013). Precocious hand use preference in reach-to-eat behavior versus manual construction in 1- to 5-year-old children. *Developmental Psychobiology*, *55*(8), 902-911. doi: [10.1002/dev.21083](http://dx.doi.org/10.1002/dev.21083)
- Sadato, N., Okada, T., Honda, M., & Yonekura, Y. (2002). Critical period for cross-modal plasticity in blind humans: A functional MRI study. *Neuroimage*, *16*(2), 389-400. doi: <http://dx.doi.org/10.1006/nimg.2002.1111>
- Sainburg, R. L. (2014). Convergent models of handedness and brain lateralization. *Frontiers in Psychology*, *5*, 1092. doi: [10.3389/fpsyg.2014.01092](http://dx.doi.org/10.3389/fpsyg.2014.01092)
- Sambo, C. F., Vallar, G., Fortis, P., Ronchi, R., Posteraro, L., Forster, B., & Maravita, A. (2012). Visual and spatial modulation of tactile extinction: Behavioural and electrophysiological evidence. *Frontiers in Human Neuroscience*, *6*, 217. doi: [10.3389/fnhum.2012.00217](http://dx.doi.org/10.3389/fnhum.2012.00217)
- Saunders, J. A., & Knill, D. C. (2003). Humans use continuous visual feedback from the hand to control fast reaching movements. *Exp Brain Res*, *152*(3), 341-352. doi: [10.1007/s00221-003-1525-2](http://dx.doi.org/10.1007/s00221-003-1525-2)
- Schettino, L. F., Adamovich, S. V., & Poizner, H. (2003). Effects of object shape and visual feedback on hand configuration during grasping. *Exp Brain Res*, *151*(2), 158-166. doi: [10.1007/s00221-003-1435-3](http://dx.doi.org/10.1007/s00221-003-1435-3)
- Schiavetto, A., Lepore, F., & Lassoche, M. (1993). Somesthetic discrimination thresholds in the absence of the corpus callosum. *Neuropsychologia*, *31*(7), 695-707. doi: [10.1016/0028-3932\(93\)90141-L](http://dx.doi.org/10.1016/0028-3932(93)90141-L)
- Sens, E., Knorr, C., Preul, C., Meissner, W., Witte, O. W., Miltner, W. H., & Weiss, T. (2013). Differences in somatosensory and motor improvement during temporary functional deafferentation in stroke patients and healthy subjects. *Behavioural Brain Research*, *252*, 110-116. doi: [10.1016/j.bbr.2013.05.048](http://dx.doi.org/10.1016/j.bbr.2013.05.048)
- Sens, E., Teschner, U., Meissner, W., Preul, C., Huonker, R., Witte, O. W., . . . Weiss, T. (2012). Effects of temporary functional deafferentation on the brain, sensation,

and behavior of stroke patients. *The Journal of Neuroscience*, 32(34), 11773-11779. doi: 10.1523/jneurosci.5912-11.2012

Serrien, D. J., Ivry, R. B., & Swinnen, S. P. (2006). Dynamics of hemispheric specialization and integration in the context of motor control. *Nature Reviews Neuroscience*, 7(2), 160-166. doi: 10.1038/nrn1849

Serrien, D. J., & Sovijarvi-Spape, M. M. (2015). Hemispheric asymmetries and the control of motor sequences. *Behavioural Brain Research*, 283c, 30-36. doi: 10.1016/j.bbr.2015.01.021

Sober, S. J., & Sabes, P. N. (2003). Multisensory integration during motor planning. *The Journal of Neuroscience*, 23(18), 6982-6992. doi: 10.1080/00222895.2015.1015674

Spence, C., & Walton, M. (2005). On the inability to ignore touch when responding to vision in the crossmodal congruency task. *Acta Psychologica*, 118(1-2), 47-70. doi: 10.1016/j.actpsy.2004.10.003

Spinozzi, G., & Cacchiarelli, B. (2000). Manual laterality in haptic and visual reaching tasks by tufted capuchin monkeys (*Cebus apella*). An association between hand preference and hand accuracy for food discrimination. *Neuropsychologia*, 38(13), 1685-1692. doi: 10.1016/S0028-3932(00)00080-4

Spinozzi, G., Castorina, M. G., & Truppa, V. (1998). Hand preferences in unimanual and coordinated-bimanual tasks by tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 112(2), 183. doi: 10.1037/0735-7036.112.2.183

Squeri, V., Sciutti, A., Gori, M., Masia, L., Sandini, G., & Konczak, J. (2012). Two hands, one perception: How bimanual haptic information is combined by the brain. *Journal of Neurophysiology*, 107(2), 544-550. doi: 10.1152/jn.00756.2010

Stilla, R., & Sathian, K. (2008). Selective visuo-haptic processing of shape and texture. *Human Brain Mapping*, 29(10), 1123-1138. doi: 10.1002/hbm.20456

Stone, K. D., Bryant, D. C., & Gonzalez, C. L. (2013). Hand use for grasping in a bimanual task: Evidence for different roles? *Exp Brain Res*, 224(3), 455-467. doi: 10.1007/s00221-012-3325-z

- Stone, K. D., & Gonzalez, C. L. (2014a). Grasping with the eyes of your hands: Haptics and vision modulate hand preference. *Exp Brain Res*, 232(2), 385-393. doi: 10.1007/s00221-013-3746-3
- Stone, K. D., & Gonzalez, C. L. (2014b). Grasping without sight: Insights from the congenitally blind. *PLoS ONE*, 9(10), e110175. doi: 10.1371/journal.pone.0110175
- Stone, K. D., & Gonzalez, C. L. (2015a). Manual preferences for visually- and haptically-guided grasping. *Acta Psychologica* 160, 1-10. doi: 10.1016/j.actpsy.2015.06.004
- Stone, K. D., & Gonzalez, C. L. (2015b). Visual and haptic contributions to the development of hand preference for grasping. *Journal of Cognitive Neuroscience*, 57-57.
- Striem-Amit, E., Dakwar, O., Reich, L., & Amedi, A. (2012). The large-scale organization of "visual" streams emerges without visual experience. *Cerebral Cortex*, 22(7), 1698-1709. doi: 10.1093/cercor/bhr253
- Tal, N., & Amedi, A. (2009). Multisensory visual-tactile object related network in humans: Insights gained using a novel crossmodal adaptation approach. *Exp Brain Res*, 198(2-3), 165-182. doi: 10.1007/s00221-009-1949-4
- Theurel, A., Frileux, S., Hatwell, Y., & Gentaz, E. (2012). The haptic recognition of geometrical shapes in congenitally blind and blindfolded adolescents: Is there a haptic prototype effect? *PLoS ONE*, 7(6), e40251. doi: 10.1371/journal.pone.0040251
- Theurel, A., Witt, A., Claudet, P., Hatwell, Y., & Gentaz, E. (2013). Tactile picture recognition by early blind children: The effect of illustration technique. *Journal of Experimental Psychology. Applied*, 19(3), 233-240. doi: 10.1037/a0034255
- Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin*, 121(1), 20-42. doi: 10.1037/0033-2909.121.1.20
- Tipper, S. P., Lloyd, D., Shorland, B., Dancer, C., Howard, L. A., & McGlone, F. (1998). Vision influences tactile perception without proprioceptive orienting. *Neuroreport*, 9(8), 1741-1744. doi: 10.1097/00001756-199806010-00013

- Tomlinson, S. P., Davis, N. J., Morgan, H. M., & Bracewell, R. M. (2011). Hemispheric specialisation in haptic processing. *Neuropsychologia*, *49*(9), 2703-2710. doi: 10.1016/j.neuropsychologia.2011.05.018
- Travieso, D., & Lederman, S. J. (2007). Assessing subclinical tactual deficits in the hand function of diabetic blind persons at risk for peripheral neuropathy. *Archives of Physical Medicine and Rehabilitation*, *88*(12), 1662-1672. doi: 10.1016/j.apmr.2007.09.007
- Tremblay, L., Hansen, S., Kennedy, A., & Cheng, D. T. (2013). The utility of vision during action: Multiple visuomotor processes? *Journal of Motor Behavior* *45*(2), 91-99. doi: 10.1080/00222895.2012.747483
- van Doorn, R. R. A. (2008). Manual asymmetries in the temporal and spatial control of aimed movements. *Human Movement Science*, *27*(4), 551-576. doi: <http://dx.doi.org/10.1016/j.humov.2007.11.006>
- Varney, N. R., & Benton, A. L. (1975). Tactile perception of direction in relation to handedness and familial handedness. *Neuropsychologia*, *13*(4), 449-454. doi: [http://dx.doi.org/10.1016/0028-3932\(75\)90068-8](http://dx.doi.org/10.1016/0028-3932(75)90068-8)
- Ververs, I. A., de Vries, J. I., van Geijn, H. P., & Hopkins, B. (1994). Prenatal head position from 12-38 weeks. I. Developmental aspects. *Early Human Development*, *39*(2), 83-91. doi: 10.1016/0378-3782(94)90157-0
- Volcic, R., Wijntjes, M. A., Kool, E., & Kappers, A. L. (2010). Cross-modal visuo-haptic mental rotation: Comparing objects between senses. *Exp Brain Res*, *203*(3), 621-627. doi: 10.1007/s00221-010-2262-y
- Wallraven, C., Bulthoff, H. H., Waterkamp, S., van Dam, L., & Gaissert, N. (2013). The eyes grasp, the hands see: Metric category knowledge transfers between vision and touch. *Psychonomic Bulletin & Review*. doi: 10.3758/s13423-013-0563-4
- Wang, J., & Sainburg, R. L. (2007). The dominant and nondominant arms are specialized for stabilizing different features of task performance. *Exp Brain Res*, *178*(4), 565-570. doi: 10.1007/s00221-007-0936-x
- Weinstein, S. (1978). Functional cerebral hemispheric asymmetry. *Asymmetrical Function of the Brain*, 17-48.

- Weiss, T., Sens, E., Teschner, U., Meissner, W., Preul, C., Witte, O. W., & Miltner, W. H. (2011). Deafferentation of the affected arm: A method to improve rehabilitation? *Stroke*, *42*(5), 1363-1370. doi: 10.1161/strokeaha.110.601138
- Werhahn, K. J., Mortensen, J., Kaelin-Lang, A., Boroojerdi, B., & Cohen, L. G. (2002). Cortical excitability changes induced by deafferentation of the contralateral hemisphere. *Brain*, *125*(Pt 6), 1402-1413. doi: <http://dx.doi.org/10.1093/brain/awf140>
- Wesslein, A. K., Spence, C., & Frings, C. (2014). Vision affects tactile target and distractor processing even when space is task-irrelevant. *Frontiers in Psychology*, *5*. doi: 10.3389/fpsyg.2014.00084
- Westwood, D. A., Heath, M., & Roy, E. A. (2003). No evidence for accurate visuomotor memory: Systematic and variable error in memory-guided reaching. *Journal of Motor Behavior*, *35*(2), 127-133. doi: 10.1080/00222890309602128
- Wiles, P. G., Pearce, S. M., Rice, P. J., & Mitchell, J. M. (1990). Reduced vibration perception in right hands of normal subjects: An acquired abnormality? *British Journal of Industrial Medicine*, *47*(10), 715-716. doi: 10.1136/oem.47.10.715
- Wilkinson, J. M., & Carr, T. H. (1987). Strategic hand use preferences and hemispheric specialization in tactual reading: Impact of the demands of perceptual encoding. *Brain and Language*, *32*(1), 97-123. doi: 10.1016/0093-934X(87)90119-2
- Wing, A. M., Turton, A., & Fraser, C. (1986). Grasp size and accuracy of approach in reaching. *Journal of Motor Behavior*, *18*(3), 245-260. doi: 10.1080/00222895.1986.10735380
- Winges, S. A., Weber, D. J., & Santello, M. (2003). The role of vision on hand preshaping during reach to grasp. *Exp Brain Res*, *152*(4), 489-498. doi: 10.1007/s00221-003-1571-9
- Witelson, D. F. (1976). Sex and the single hemisphere: Specialization of the right hemisphere for spatial processing. *Science*, *193*(4251), 425-427. doi: 10.1007/BF02653735
- Witelson, S. F. (1974). Hemispheric specialization for linguistic and nonlinguistic tactual perception using a dichotomous stimulation technique. *Cortex*, *10*(1), 3-17.

- Woods, A. T., & Newell, F. N. (2004). Visual, haptic and cross-modal recognition of objects and scenes. *Journal of Physiology Paris*, 98(1-3), 147-159. doi: 10.1016/j.jphysparis.2004.03.006
- Woodworth, R. S. (1899). Accuracy of voluntary movement. *The Psychological Review: Monograph Supplements*, 3(3), i. doi: <http://dx.doi.org/10.1037/h0092992>
- Xu, Y., O'Keefe, S., Suzuki, S., & Franconeri, S. L. (2012). Visual influence on haptic torque perception. *Perception*, 41(7), 862-870. doi: 10.1068/p7090
- Yalachkov, Y., Kaiser, J., Doehrmann, O., & Naumer, M. J. (2015). Enhanced visuo-haptic integration for the non-dominant hand. *Brain Research*. doi: 10.1016/j.brainres.2015.04.020
- Zangaladze, A., Epstein, C. M., Grafton, S. T., & Sathian, K. (1999). Involvement of visual cortex in tactile discrimination of orientation. *Nature*, 401(6753), 587-590. doi: 10.1038/44139
- Zhang, M., Weisser, V. D., Stilla, R., Prather, S. C., & Sathian, K. (2004). Multisensory cortical processing of object shape and its relation to mental imagery. *Cognitive, Affective & Behavioral Neuroscience*, 4(2), 251-259. doi: 10.3758/CABN.4.2.251

CHAPTER 3

Limitations, future directions, and implications

Limitations and Future Directions

Discussed next are three major limitations of the work presented in this thesis and plausible approaches to resolve them. First, hand preference was the major dependent variable investigated in all studies. Perhaps other dependent variables that could provide insight into sensory asymmetries during grasping would be task accuracy and performance. For example, this might include having more challenging models that would prompt participants to make mistakes, measuring the time spent by each hand manipulating the model and targets, and/or recording changes in hand selection over time. Interestingly too would be to see if a correlation exists between task accuracy and hand use, particularly when using challenging models. Perhaps the models built without mistakes during the vision condition correlated with greater right-hand use, and vice-versa for models built using haptics (i.e. fewer mistakes if the left hand was used more often). Alternatively, accuracy could be measured using kinematic analysis. It remains unknown if there are kinematic differences between the left and right hands when grasping an object without vision. It is conceivable that the left hand is more proficient than the right hand (via smaller grip apertures, smoother movement trajectories, faster movement times, etc.) at haptically-guided grasping.

Second, all of the models used were arranged in a “2D configuration”; that is, all blocks that made up each model were visible from the front view, and therefore mental or physical rotation of the model was not required in order to complete the task. Another well-known specialization of the right hemisphere is spatial processing (M. C. Corballis, 1997; P. M. Corballis, 2003; Ernest, 1998; Vogel, Bowers, & Vogel, 2003), thus it is possible that the inclusion of 3D model configurations (i.e. that require physical and

mental rotation) would increase left-hand use (perhaps beyond 50%), particularly during haptically-guided grasps. In the same vein, analyzing hand use in peri-personal space (right-near, right-far, left-near and left-far) would also be of value. It has been shown that during visually-guided grasping, healthy individuals attend to the right-near space and neglect the left-far space (de Bruin, Bryant, & Gonzalez, 2014). It remains unknown if these spatial preferences are present during haptically-guided grasping. When vision is occluded, is there a tendency to neglect specific portions of space? Addressing this question might provide insight into neurological disorders such as hemispatial neglect.

A third limitation of the current thesis is the inclusion of only congenitally blind (CB) as a special population. Testing other sensory-deprived or -impaired, and very young (under 5 years of age) populations would be beneficial. The CB in the current thesis offered interesting results: a right-hand preference for grasping, even under the guidance of haptics. This was in contrast to the blindfolded visually-unimpaired groups who showed an equal preference to use either hand (demonstrating an increased reliance on the right hemisphere in the absence of vision). CB individuals show extensive brain reorganization early in development with similarity in functional networks that support sensory-guided actions. Perhaps recording hand use in a late-blind population would be a better comparison to the behavior observed in the blindfolded visually-unimpaired individuals. If late-blind individuals show similar preferences to the blindfolded group, then this would provide further support for the theory of hemispheric asymmetries in sensory processing for grasping.

Because the results of this thesis showed that *both* vision and haptics contribute to hand preference for grasping, another interesting population to test would be the

haptically-deprived, also known as deafferented individuals. These individuals lack sense of touch, proprioception, or sometimes both. Since deafferentation affects people later in life, it is plausible to predict a right-hand preference similar to the one observed when participants had vision but also wore a pair of gloves (see Appendix 3), as this manipulation was intended to partly mimic deafferentation. Moreover, testing individuals with other touch disorders such as tactile apraxia (the inability to use proper exploratory procedures to extract object properties), tactile aphasia (the inability to name objects perceived by touch) or tactile agnosia (the inability to create a neural representation of touched objects) would extend the findings of the current thesis. Together these special populations could provide insight beyond hand preference, possibly into other factors influencing hand movement.

The results of this thesis lend to a number of additional future experiments. A question that arises from the result that vision plays a significant role in hand preference is whether or not this preference is influenced by eye movements. Studies have reported that during visually-guided grasping, the hands follow the eyes (Ambrosini et al., 2013; Crawford, Henriques, Medendorp, & Khan, 2003; Flanagan & Johansson, 2003), but recently de Bruin et al. (2014) found a dissociation between hand use and gaze patterns. Participants delayed grasping in left-far space even though their eyes made numerous saccades to that space. Is this “neglect” to grasp in left space because it makes more sense (i.e. biomechanically) to use the non-dominant left hand? It would be interesting to document gaze patterns and hand selection in space. Furthermore, gaze patterns during haptically-guided grasping remain unknown. During the haptically-guided tasks in this thesis, the participants’ eyes were presumably closed under the blindfold so it was not

possible to answer this question. Having participants complete the task with a curtain occluding the working space and using eye-tracking technology would help address this query.

Another question that arises from the results of this thesis is: What aspects of vision modulate hand preference for grasping? In the current studies vision was either completely blocked or available to the participant. In our everyday actions however, we often have peripheral or only partial vision of the objects we reach-to-grasp. Thus, is there a hand preference when grasping in the periphery? Furthermore, is the sensory modulation of hand preference on a continuum? If visual availability slowly degrades over time in a way that haptics becomes a more reliable source of information, would this produce a change from initial hand preference?

Similarly, the present thesis also raises the question of what aspects of *haptics* modulate hand preference for grasping? Haptics is the perception of combined cutaneous and kinesthetic inputs, so the contribution of each component of haptics to grasping could be assessed separately. One way to block cutaneous inputs would be to apply a local anesthetic cream to the hands prior to completing a natural grasping task (such as EMLA© cream, often used for rehabilitation of the affected arm in stroke patients; Sens et al. 2013). An anesthetic cream would be a non-invasive, viable alternative to the fitted gloves. If hand use does not change under these conditions, then it is possible that kinesthesia plays a larger role in mediating hand preference for grasping. In contrast, if hand use changes under these conditions, then it is possible that touch (i.e. cutaneous information) plays a larger role in hand selection.

Another logical extension of this thesis' findings would be to look at the neural correlates of hemispheric specialization for sensory-guided grasping leading to hand preference. To understand the contributions of haptics to manual action at the neural level, one could apply transcranial magnetic stimulation (TMS) to the surface brain areas associated with haptics. In the primary somatosensory cortex, Brodmann's areas (BA) 1, 2, and 3 are implicated in haptics. Whereas BA3a receives proprioceptive input and BA3b receives tactile (touch) input, BA2 combines these inputs to create haptics (Keyzers, Kaas, & Gazzola, 2010). Applying TMS to these specific areas and documenting hand use would confirm (or not) the behavioural findings of this thesis. Certainly, due to the close proximity of these areas in the brain, an experiment like this would have to be carefully crafted. Perhaps fMRI studies designed to look at hemispheric differences during processing of object properties either with vision or with haptics in both hands could be conducted more easily. This information would indirectly support the hand preference biases observed in the thesis.

Finally, it would be interesting to explore the contributions of other sensory systems to hand preference during grasping. Human behaviour is dynamic and complex, so it is quite possible that hand preference for grasping is influenced by other sensory modalities beyond vision and haptics. Audition, for example, plays a critical role in perceiving the world and guiding one's movement. One way to test the influence of audition on hand preference for grasping might be by having an auditory stimuli (such as a beep) occur on the left or right sides of the table while the participant grasps for objects. It is possible that the side of auditory stimulation would correspond with hand selection. This could be tested during visually- and haptically-guided grasping.

An alternative explanation for the results of this thesis is that visually-guided and haptically-guided grasping are mediated by two different systems; the dorsal and the ventral streams. The dorsal (or vision-for-action) system provides information on *how* to manipulate an object (e.g. grasping using a pincer grasp). The ventral (or vision-for-perception) system provides information about *what* the object is (e.g. a LEGO block). It has been proposed that the dorsal system utilizes real-time online feedback to transform visual information into a motor action. The ventral system, instead, creates a perceptual image of the target that may be stored in memory for later use (Goodale & Milner, 1992; Milner & Goodale, 2008). Thus it is possible that the visually-guided grasping task used in this thesis depended more on dorsal (online action) processes, whereas haptically-guided grasping relied more on ventral (memory-guided perceptual) processes. Studies have suggested that the dorsal stream enjoys a left-hemisphere advantage, whereas ventral stream processes may be more specialized to the right-hemisphere (Chen, Sperandio, & Goodale, 2015; Gonzalez, Ganel, & Goodale, 2006; Gonzalez, Ganel, Whitwell, Morrissey, & Goodale, 2008; Hickok & Poeppel, 2007; Radoeva, Cohen, Corballis, Lukovits, & Koleva, 2005). For instance, Gonzalez and colleagues reported that the kinematics of the left, but not the right, hand are affected when grasping an object that is embedded in a visual illusion (Gonzalez et al., 2006; Gonzalez et al., 2008). This effect persists when the target object is ‘crowded’ by other irrelevant objects. Recently, Chen et al. (2015) asked participants to reach-to-grasp or simply estimate the size of a block that was crowded by other blocks. Results showed that the kinematics of the left hand were influenced by the crowded environment during *both* grasping and estimating (size of) the object. The estimates, but not the grasps, made with the right hand were

affected by the environment. Because the perceptual scene influenced movement of the left but not the right hand for these tasks, the results highlight hemispheric differences for dorsal (left-hemisphere for action) and ventral (right-hemisphere for perception) processing.

Although this alternative explanation remains a possibility, it is unlikely. If the results of the visually-guided grasping tasks were based solely on dorsal stream processes, then right-hand use should not be susceptible to changes in haptic feedback. This was not the case. When haptics was constrained (Vision/Constrained-Haptics; see Appendix 3) right hand use increased significantly. Moreover, when vision was occluded *and* haptics was constrained (No Vision/Constrained-Haptics; Appendix 3), the right hand was preferred. Finally, when participants completed the haptically-guided portion of the task prior to the visually-guided portion (see Appendix 1), right-hand use did not differ. If the two parts of the task were mediated by different motor and perceptual systems, then there should have been a significant increase in right-hand use during the visually-guided condition when compared to the haptically-guided condition. Future experiments should design experiments to specifically investigate the contributions of the dorsal and ventral streams to visually- and haptically-guided grasping.

In sum, many outlets for understanding the sensory contributions to grasping exist. Together, exploring the contributions of the sensory systems to grasping allows for a more comprehensive model of human hand use.

Implications

Taken together, the results of the thesis further our knowledge about the sensory factors that influence hand selection for grasping and make at least one main contribution to the literature. That is, they suggest that hemispheric specializations for sensory (visual and haptic) processing modulate and shape hand preference for grasping. As hand preference is closely linked to handedness, this thesis could provide insight into the evolutionary origins of handedness. It still remains unknown *why* the majority of the population is right-handed; many theories have been proposed involving genetic and environmental factors. This thesis suggests that sensory (visual and haptic) information also contributes to handedness. Particularly, it seems that vision plays a greater role than haptics in the development and maintenance of hand preference for grasping. Studies have suggested a left-hemisphere advantage for visual object recognition (Helmich & Lausberg, 2014; Johnson-Frey, 2004; Lewis, 2006; Schintu et al., 2014), which might prime the right hand to reach out and grasp a visually-identified object. However in the absence of vision, the right hand cannot be prompted by visual cues, leading to no hand preference. Perhaps the unequal contribution of vision and haptics to hand preference plays a major role in determining handedness at an early age.

Another contribution (albeit small) of this thesis to the literature is the implementation of grasping as a viable model to investigate the haptic system. Traditionally studies have used passive and/or exploratory procedures to study haptics, but as brought up by Lederman and Klatzky (2009), grasping is the best (most effective) method to haptically identify an object. Because grasping is an action we make hundreds of times per day, it is a practical model to use when examining hemispheric asymmetries

for sensory processing. Future studies could use grasping as a tool to assess manual lateralization for haptics.

The foundation of the thesis was based on basic research questions, but it has the potential to assist in the development of possible interventions for individuals with sensorimotor deficits. For instance, if there is a left-hand advantage for haptic processing, maybe training the left hand on manual actions as vision impairments progress (e.g. macular degeneration) could ease the transition from a primary visual being to a more haptic one. Likewise, the knowledge learned could be helpful in the development of therapeutic devices for stroke rehabilitation. Knowing how each hemisphere utilizes sensory information during grasping could assist in creating more proficient prosthetics. Additionally, there are many developmental disorders (such as autism, sensory processing disorder, cerebral palsy) that are associated with deficits in visual and/or haptic perception (Gori et al., 2012; Mari, Castiello, Marks, Marraffa, & Prior, 2003; Teitelbaum, Teitelbaum, Nye, Fryman, & Maurer, 1998). Again, therapeutic options associated with training each hand on sensory-specific tasks may help with these deficits.

References

- Ambrosini, E., Reddy, V., de Looper, A., Costantini, M., Lopez, B., Sinigaglia, C., & Lappe, M. (2013). Looking Ahead: Anticipatory gaze and motor ability in infancy. *PLoS ONE*, *8*(7), e67916. doi: 10.1371/journal.pone.0067916
- Chen, J., Sperandio, I., & Goodale, M. A. (2015). Differences in the effects of crowding on size perception and grip scaling in densely cluttered 3-d scenes. *Psychological science*, *26*(1), 58-69. doi: 10.1177/0956797614556776
- Corballis, M. C. (1997). The genetics and evolution of handedness. *Psychological Review*, *104*(4), 714-727. doi: 10.1037/0033-295X.104.4.714
- Corballis, P. M. (2003). Visuospatial processing and the right-hemisphere interpreter. *Brain and Cognition*, *53*(2), 171-176. doi: 10.1016/S0278-2626(03)00103-9
- Crawford, J. D., Henriques, D. Y., Medendorp, W. P., & Khan, A. Z. (2003). Ocular kinematics and eye-hand coordination. *Strabismus*, *11*(1), 33-47.
- de Bruin, N., Bryant, D. C., & Gonzalez, C. L. (2014). "Left neglected," but only in far space: Spatial biases in healthy participants revealed in a visually guided grasping task. *Frontiers in Neurology*, *5*, 4. doi: 10.3389/fneur.2014.00004
- Ernest, C. H. (1998). Spatial ability and lateralization in the haptic modality. *Brain and Cognition*, *36*(1), 1-20. doi: <http://dx.doi.org/10.1006/brcg.1997.0959>
- Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, *424*(6950), 769-771. doi: 10.1038/nature01861
- Gonzalez, C. L., Ganel, T., & Goodale, M. A. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of Neurophysiology*, *95*(6), 3496-3501. doi: 10.1152/jn.01187.2005
- Gonzalez, C. L., Ganel, T., Whitwell, R. L., Morrissey, B., & Goodale, M. A. (2008). Practice makes perfect, but only with the right hand: Sensitivity to perceptual illusions with awkward grasps decreases with practice in the right but not the left hand. *Neuropsychologia*, *46*(2), 624-631. doi: 10.1016/j.neuropsychologia.2007.09.006

- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends Neurosci*, *15*(1), 20-25. doi: 10.1016/0166-2236(92)90344-8
- Gori, M., Squeri, V., Sciutti, A., Masia, L., Sandini, G., & Konczak, J. (2012). Motor commands in children interfere with their haptic perception of objects. *Exp Brain Res*, *223*(1), 149-157. doi: 10.1007/s00221-012-3248-8
- Helmich, I., & Lausberg, H. (2014). Hand movements with a phase structure and gestures that depict action stem from a left hemispheric system of conceptualization. *Exp Brain Res*, *232*(10), 3159-3173. doi: 10.1007/s00221-014-4006-x
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*(5), 393-402. doi: 10.1038/nrn2113
- Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends Cogn Sci*, *8*(2), 71-78. doi: 10.1016/j.tics.2003.12.002
- Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, *11*(6), 417-428. doi: 10.1038/nrn2919
- Lederman, S. J., & Klatzky, R. L. (2009). Haptic perception: A tutorial. *Attention, Perception & Psychophysics*, *71*(7), 1439-1459. doi: 10.3758/app.71.7.1439
- Lewis, J. W. (2006). Cortical networks related to human use of tools. *Neuroscientist*, *12*(3), 211-231. doi: 10.1177/1073858406288327
- Mari, M., Castiello, U., Marks, D., Marraffa, C., & Prior, M. (2003). The reach-to-grasp movement in children with autism spectrum disorder. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *358*(1430), 393-403. doi: 10.1098/rstb.2002.1205
- Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*(3), 774-785. doi: 10.1016/j.neuropsychologia.2007.10.005
- Radoeva, P. D., Cohen, J. D., Corballis, P. M., Lukovits, T. G., & Koleva, S. G. (2005). Hemispheric asymmetry in a dissociation between the visuomotor and visuoperceptual streams. *Neuropsychologia*, *43*(12), 1763-1773. doi: 10.1016/j.neuropsychologia.2005.02.005

- Schintu, S., Hadj-Bouziane, F., Dal Monte, O., Knutson, K. M., Pardini, M., Wassermann, E. M., . . . Krueger, F. (2014). Object and space perception - is it a matter of hemisphere? *Cortex*, *57*, 244-253. doi: 10.1016/j.cortex.2014.04.009
- Sens, E., Knorr, C., Preul, C., Meissner, W., Witte, O. W., Miltner, W. H., & Weiss, T. (2013). Differences in somatosensory and motor improvement during temporary functional deafferentation in stroke patients and healthy subjects. *Behavioural Brain Research*, *252*, 110-116. doi: 10.1016/j.bbr.2013.05.048
- Teitelbaum, P., Teitelbaum, O., Nye, J., Fryman, J., & Maurer, R. G. (1998). Movement analysis in infancy may be useful for early diagnosis of autism. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(23), 13982-13987. doi: 10.1073/pnas.95.23.13982
- Vogel, J. J., Bowers, C. A., & Vogel, D. S. (2003). Cerebral lateralization of spatial abilities: A meta-analysis. *Brain and Cognition*, *52*(2), 197-204. doi: [http://dx.doi.org/10.1016/S0278-2626\(03\)00056-3](http://dx.doi.org/10.1016/S0278-2626(03)00056-3)

APPENDIX 1

Grasping with the Eyes of your Hands: Vision and Hapsis Modulate Hand Preference for Grasping*

* **Stone, K. D.**, & Gonzalez, C. L. (2014a). Grasping with the eyes of your hands: Hapsis and vision modulate hand preference. *Experimental Brain Research*, 232(2), 385-393. doi: 10.1007/s00221-013-3746-3

Abstract

Right-hand preference has been demonstrated for visually-guided reaching and grasping. Grasping however, requires the integration of both visual and haptic cues. To what extent does vision influence hand preference for grasping? Is there a hand preference for haptically-guided grasping? Two experiments were designed to address these questions. In Experiment One, individuals were tested in a reaching-to-grasp task with vision (sighted condition) and with haptics (blindfolded condition). Participants were asked to put together 3D models using building blocks scattered on a tabletop. The models were simple, composed of 10 blocks of 3 different shapes. Starting condition (Vision-First or Haptics-First) was counterbalanced among participants. Right-hand preference was greater in visually-guided grasping but only in the Vision-First group. Participants who initially built the models while blindfolded (Haptics-First group) used their right hand significantly less for the visually-guided portion of the task. To investigate if grasping using haptics modifies subsequent hand preference, participants received an additional haptic experience in a follow-up experiment. While blindfolded, participants manipulated the blocks in a container for five minutes prior to the task. This additional experience did not affect right hand use on visually-guided grasping but had a robust effect on haptically-guided grasping. Together, the results demonstrate first, that hand preference for grasping is influenced by both vision and haptics, and second, they highlight how flexible this preference could be when modulated by haptics.

Introduction

Many studies have investigated hand preference during visually-guided grasping. Tasks that require the use of one hand to pick up an object (i.e. unimanual) have shown that participants will reach and grasp with the hand closest to the object (i.e. ipsilateral; e.g. (Annett, Annett, Hudson, & Turner, 1979; M. P. Bryden, Singh, Steenhuis, & Clarkson, 1994). When the target is located at the midline however, participants prefer their right hand to pick it up (P. J. Bryden, Pryde, & Roy, 2000; Gabbard & Rabb, 2000). This right hand preference for grasping has been observed when picking up different objects: geometric 3D shapes (Gabbard, Tapia, & Helbig, 2003), cards (D. Bishop, V. Ross, M. Daniels, & P. Bright, 1996; G. Calvert, 1998; M. Carlier, A.L. Doyen, & C. Lamard, 2006), toys (P. J. Bryden & E. Roy, 2006; L. A. R. Sacrey, J. M. Karl, & I. Q. Whishaw, 2012), tools (C.M. Mamolo, E.A. Roy, P.J. Bryden, & L.E. Rohr, 2004; Mamolo, Roy, Bryden, & Rohr, 2005; C.M. Mamolo, E.A. Roy, L.E. Rohr, & P.J. Bryden, 2006), or blocks (Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Stone, Bryant, & Gonzalez, 2013), and it has also been shown in studies that employ bimanual tasks (Fagard & Marks, 2000; Stone et al., 2013). An example of a bimanual task is the block building task, where participants are asked to reproduce an exact copy of a given model using the numerous blocks available from a tabletop. The interaction of the two hands is essential in order to complete the task. Using this task, a marked right hand preference has been shown, even for contralateral grasps (Gonzalez et al., 2007; Stone et al., 2013). However, all these previous studies have documented hand preference for grasping when vision is available; this is, when the movement is guided by vision. To what extent does vision contribute to this right hand preference?

To our knowledge no study has investigated hand preference for grasping without vision. Kinematic studies have shown differences in hand use when vision is occluded: peak velocities are lower, maximum grip apertures are larger, overall movement time is longer (Connolly & Goodale, 1999; Kritikos & Beresford, 2002; Pettypiece, Culham, & Goodale, 2009; Schettino, Adamovich, & Poizner, 2003; Winges, Weber, & Santello, 2003). Even when vision of *one* eye is occluded, individuals reach slower and grasp with less accuracy (Melmoth, Finlay, Morgan, & Grant, 2009). These studies emphasize the critical role that vision plays during reaching and grasping movements. Perhaps it should not be surprising that in the absence of vision, hand preference would also be affected. Studies investigating object recognition without vision (i.e. with hapsis) have shown a left-hand advantage during haptic discrimination (Benton, Levin, & Varney, 1973; De Renzi, Faglioni, & Scotti, 1969; Fagot, Hopkins, & Vauclair, 1993; Milner & Taylor, 1972; Riege, Metter, & Williams, 1980; Tomlinson, Davis, Morgan, & Bracewell, 2011). For example Fagot et al. (1993) presented participants with a shape identification task and found that the left hand was better at identifying the correct shape. Similarly, Tomlinson et al. (2011) asked blindfolded participants to lift a dowel with a textured knob and to rate the 'coarseness' of the knob on a 3-point scale. After an equivalent number of lifts with each hand, they found that participants were significantly more accurate with their left hand. These studies demonstrate the left-hand advantage during haptic recognition. With this information in mind, one might ask what hand would be used when trying to pick up an object in the dark (e.g. in the middle of the night). Would it be the hand that is used more often for grasping (i.e. right hand) or the one that is more

proficient for haptic object recognition (i.e. left hand)? Two experiments were conducted to address these questions.

In both experiments participants were tested on the block building task (Gonzalez et al., 2007; Stone et al., 2013) and hand preference for grasping was documented. In Experiment One, participants built models sighted and blindfolded (counterbalanced). In Experiment Two, participants received an additional haptic experience (i.e. blindfolded) by manipulating the blocks in a container before completing the task as in Experiment One.

Methods and Procedures

1. Experiment One: Grasping with and without vision

1.1.1. Participants

Thirty-eight self-reported right-handed individuals from the University of Lethbridge, between the ages of 18 and 35, participated. Nineteen (eight males) and nineteen (four males) were assigned to the Vision-First and the Haptic-First groups respectively. 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.

1.1.2. 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 Stone et al. 2013 for a full version of the questionnaire) at the end of the block building task. This version of the questionnaire included questions on hand preference for 22 different tasks. Participants had to rate which hand they prefer on a scale of +2 (right always), +1 (right usually), 0 (equal), -1 (left usually), or -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 five models built with MEGA BLOKS® were used for the experiment. The blocks ranged in size from 3.1 L x 3.1 W x 2.0 cm H to 6.3 L x 3.1 W x 2.0 cm H. Each model contained 10 blocks of various colours and three types of shapes. The blocks that made up the models were scattered on a table with a working space of 122 L x 122 W x 74 cm H. A strip of clear tape was used to divide the workspace in half and an equal number of pieces were distributed onto the left and right sides.

1.1.3. Procedures

Participants were comfortably seated centrally in front of a table and were instructed to replicate five different models. Participants started the task either sighted (Vision-First group) or blindfolded (by using a blindfold;

Hapsis-First group). In the Vision-First group the 50 blocks that made all five models were available on the tabletop. One model at a time, participants replicated two 10-piece models sighted followed by three 10-piece models blindfolded. In the Hapsis-First group only 30 blocks were available on the tabletop. Participants were asked to replicate three models blindfolded. After the completion of the three models the investigator placed back all 50 blocks and allowed the participant to build two models while sighted. This procedure was done to maintain consistency in the number of blocks that participants would use to build each model between the Vision- and Hapsis-First groups. In both conditions the 10-piece model to be replicated was placed on a building plate directly in front of the participant within arms' reach. Participants were instructed to replicate the model as quickly and accurately as possible on a second building plate positioned in front of them (see figures 1 and 2). No other information was given to the participants. Following replication of the model, both models were removed and a different model to be replicated was provided. The same five models were used for all participants. Starting condition (Vision-First/Hapsis-First) was counterbalanced and model presentation order was randomised between participants. The task was recorded on a JVC HD Everio video recorder approximately 160cm away from the individual with a clear view of the tabletop, building blocks, and participants' hands.

1.1.3. 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 for right-hand use (number of right grasps/total number of grasps X 100). The time in which it took participants to construct each model was recorded on a stopwatch and reported in seconds. Data was assessed and no violations for homogeneity of variance and normalcy were found prior to analysis. Partial Eta Squared values were used to show effect size (ES).

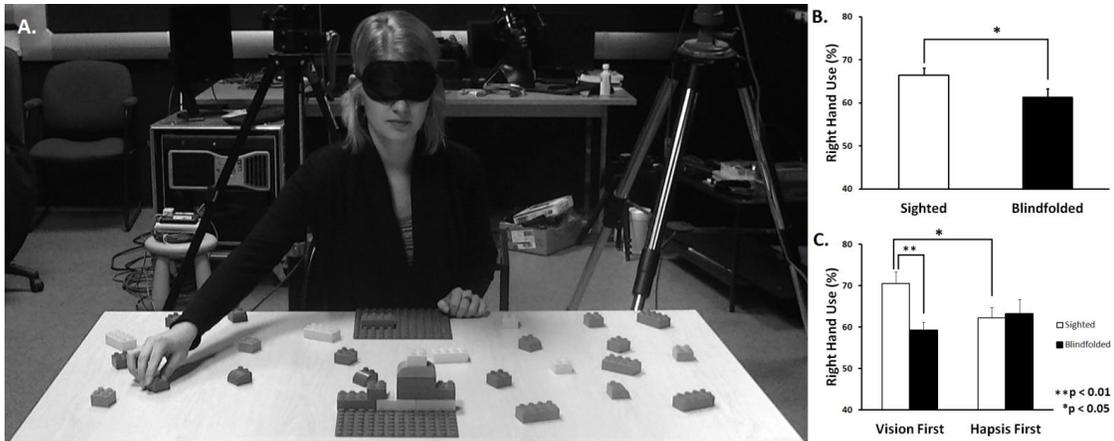


Fig. 1 (A) Photograph of a participant engaging in the building task in Experiment 1. Please note that the participant is blindfolded and cannot see her working space. (B) This graph demonstrates the average right-hand use in percentage for all participants in both the sighted and blindfolded conditions. Note the significant difference in right-hand use between these conditions. (C) This graph demonstrates right-hand use in percentage for starting condition: Vision-First and Haptic-First. Both groups are divided into sighted (white bars) and blindfolded (black bars) conditions. Note the significant differences within the Vision-First group and between the sighted conditions.



Fig. 2 (A) Photograph of a participant from Experiment 2 manipulating the blocks in a container prior to the building task. (B) This graph demonstrates the average right-hand use in percentage for all participants in both the sighted and blindfolded conditions. Note the significant difference in right-hand use between these conditions. (C) This graph demonstrates right-hand use in percentage for starting condition: Vision-First and Hapsis-First. Both groups are divided into sighted (white bars) and blindfolded (black bars) conditions. Note the significant differences within both starting conditions and between the sighted conditions.

1.2. Results

Means and standard error are reported in percentage and seconds.

1.2.1. Handedness questionnaire

All participants self-reported as right-handers and this was confirmed by the handedness questionnaire. Overall, the average score on the questionnaire was +30.5 (± 1.0 SE; range +15 to +40) out of the maximum possible score of +44/-44. The Vision-First group scored an average of +31.0 (± 1.6 SE; range +15 to +40), and the Hapsis-First group scored an average of +30.0 (± 1.1 SE; range +18 to +37). The difference between the two groups was not significant ($p = 0.6$).

1.2.2. Hand use for grasping

Analysis using a 2 (visual availability) X 2 (starting condition) repeated measures ANOVA was performed on the percentage of right-hand use for grasping during the task. Visual availability (sighted, blindfolded) was a within subject factor and starting condition (Vision-First, Hapsis-First) a between subject factor. Overall, we found a main effect of visual availability ($F(1, 36) = 6.4$; $p = 0.01$, $ES = 0.151$) as shown in figure 1B. Please note that during the blindfolded condition participants could only use their sense of touch (hapsis) to construct the models. Participants used their right hand significantly more to grasp the blocks when they were sighted ($66.3 \pm 1.8\%$) than when they were blindfolded ($61.2 \pm 2.1\%$). There was no main effect of starting condition ($F(1, 36) = 0.4$; $p > 0.1$, $ES = 0.01$). However, the interaction between visual availability and starting condition was significant ($F(1, 36) = 9.1$; $p = 0.005$, $ES = 0.203$; see figure 1C). Follow up analysis (pairwise *t-test*) revealed that in the Vision-First group right-hand use significantly decreased when participants were blindfolded ($t(18) = 4.6$; $p < 0.001$), yet this was not the case in the Hapsis-First group ($p > 0.1$). In addition, when comparing both sighted conditions, the right-hand was used significantly less in the Hapsis-First group ($t(36) = 2.3$; $p < 0.05$; independent samples *t-test*). Figure 1C shows that even though in both groups participants were sighted, right-hand use was $70.5 \pm 2.8\%$ in the Vision-First group but only $62.2 \pm 2.8\%$ in the Hapsis-First group. In none of the conditions did hand use decrease to chance level (revealed by performing a pairwise *t-test* on the values of right-hand use for grasping against 50; Vision-First; $t(18) = 3.82$; $p = 0.001$; Hapsis-First; $t(18) = 3.84$; $p = 0.001$). In other words, regardless of the sensory domain being utilized, a right-hand preference for grasping remained. Number of grasps: To investigate if the number of grasps executed between the sighted and blindfolded conditions differed, we conducted a repeated measures ANOVA with visual availability (sighted, blindfolded) as a within subjects factor and starting condition as between subject factor. Results showed a main effect of visual availability: participants executed more grasps per model while blindfolded (13.6) when compared to when they were sighted (10.4; $F(1,36) = 58.1$; $p < .0001$, $ES = 0.61$). There was no main effect of starting condition

($F(1,36) = 0.007$; $p = 0.93$) or significant interaction ($F(1,36) = 0.002$; $p = 0.96$).

1.2.3. Build times for models

Overall, participants were faster at building models while sighted than while blindfolded ($F(1, 36) = 44.8$; $p < 0.001$, $ES = 0.886$). During the sighted trials, it took participants in the Vision-First group on average 29.7 ± 2.0 s to complete one model, whereas it took participants in the Hapsis-First group on average 27.3 ± 1.4 s to complete one model. These values were not significantly different from one another ($p = 0.3$). During the blindfolded trials, participants in the Vision-First group completed one model on average 142.3 ± 9.5 s, whereas participants in the Hapsis-First group completed one model on average 114.1 ± 9.2 s. There was a significant difference between these two values ($t(36) = 2.1$; $p < 0.05$; independent samples *t-test*).

1.3. Discussion

The results showed a decrease in right-hand use for haptically-guided grasping. Participants used their right hand less often to grasp the blocks when blindfolded than when they were sighted. This change however, was modulated by starting condition. Participants in the Vision-First group used their right hand 70.5% of the time while sighted, but once they were blindfolded, right-hand use decreased significantly to 59.2%. On the other hand, participants in the Hapsis-First group demonstrated similar hand preference regardless of visual condition (62.2% while sighted; 63.2% while blindfolded). One puzzling finding of these results was the significant decrease (~8%) in right-hand use in the Hapsis-First group when participants were sighted. In other words, even though participants were locating the pieces and guiding their movements using vision, they used their right hand less often if they have completed the hapsis portion of the task first. Could a brief haptic experience modulate subsequent hand preference for grasping? We tested this suggestion in Experiment Two.

2. Experiment Two: Grasping with an added haptic experience

2.1.1. Participants

Thirty-eight self-reported right-handed individuals from the University of Lethbridge, between the ages of 18 and 35, participated. Nineteen (five males) and nineteen (six males) were assigned to the Vision-First and the Hapsis-First groups respectively. 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.

2.1.2. Apparatus and Stimuli

All the display material and equipment were the same as Experiment One, except that one model was added to the sighted condition. Thus participants built three models sighted and three models blindfolded.

2.1.3. Procedures

All procedures were the same as Experiment One except that participants were blindfolded and asked to manipulate the MEGA BLOKS® in a container (42 L x 30 W x 30 cm H; see figure 2A) for five minutes prior to starting the block building task.

2.1.4. Data Analysis

Data analysis was the same as Experiment One.

2.2. Results

Means and standard error are reported in percentage and seconds.

2.2.1. Handedness questionnaire

The average score on the Handedness Questionnaire was +33.5 (± 1.1 SE; range: +20 to +44) out of a total possible +44/-44. The Vision-First group scored an average of +32.5 (± 1.5 SE; range: +20 to +42), and the Hapsis-First group scored an average of +34.5 (± 1.7 SE; range: +23 to +44). The difference between the two groups was not significant ($p = 0.3$).

2.2.2. Hand use for grasping

Analysis using a 2 (visual availability) X 2 (starting condition) repeated measures ANOVA was performed on the percentage of right-hand use for grasping during the task. Visual availability (sighted, blindfolded) was a within subject factor and starting condition (Vision-First, Hapsis-First) a between subject factor. Overall, we found a main effect of visual availability, as shown in figure 2B. Participants used their right hand significantly more to grasp the blocks while sighted ($67.7 \pm 2.3\%$) than while blindfolded ($52.6 \pm 1.9\%$). There was no main effect of starting condition ($F(1, 36) = 1.4$; $p > 0.1$, $ES = 0.039$) but once again, the interaction between visual availability and starting condition was significant ($F(1, 36) = 7.3$; $p = 0.01$, $ES = 0.170$). Follow up analysis (independent samples *t-test*) showed that, as in Experiment One, when comparing both sighted conditions, the right hand was used significantly less in the Hapsis-First condition ($t(36) = 2.1$; $p < 0.05$). In contrast to Experiment One however, the reduction in right-hand use when blindfolded was significant regardless of starting condition ($t(18) = 5.7$, $p < 0.001$; $t(18) = 3.2$, $p < 0.01$; for the Vision-First and Hapsis-First groups respectively). The prior haptic experience of touching the blocks blindfolded thus affected hand preference within its own sensory domain. In contrast to Experiment One, in Experiment Two hand use did decrease to chance level, but only for the Vision-First group. Once again, we performed a pairwise *t-test* analysis on the values of right-hand use for grasping against 50. The results show that for the Vision-First group these values were not significantly different ($t(18) = 0.58$; $p = 0.56$). However, for the Hapsis-First group, the values were significantly different from 50% ($t(18) = 2.6$; $p = 0.015$). These results suggest that the brief haptic experience had a different effect on hand use

with hapsis depending on the starting condition. If they started with vision, right-hand use was reduced to chance. Number of grasps: Again, to investigate if the number of grasps executed between the sighted and blindfolded conditions differed, we conducted a repeated measures ANOVA with visual availability (sighted, blindfolded) as a within subjects factor and starting condition as between subject factor. Results showed a main effect of visual availability: participants executed more grasps per model while blindfolded (14.1) when compared to when they were sighted (10.3; $F(1, 36) = 87.1$; $p < 0.001$, $ES = 0.708$). There was no main effect of starting condition ($F(1,36) = 0.211$; $p = 0.64$) or significant interaction ($F(1,36) = 0.92$; $p = 0.34$).

2.2.3. Build times for models

Overall, participants were faster at building models while sighted than while blindfolded ($F(1, 36) = 68.0$; $p < 0.001$, $ES = 0.901$). During the sighted trials, it took participants in the Vision-First group approximately 27.6 ± 1.2 s to complete one model, whereas it took participants in the Hapsis-First group approximately 26.2 ± 1.3 s to complete one model. These values were not significantly different from one another ($p = 0.4$). During the blindfolded trials, participants in the Vision-First group completed one model on average 139.6 ± 10.0 s, whereas participants in the Hapsis-First group completed one model on average 141.4 ± 8.5 s. Again, these values were not significantly different ($p = 0.8$).

2.2.4. Comparison between Experiment One and Experiment Two

To gain a better understanding of how the added haptic experience affected hand use, we directly compared experiments One and Two. Visual availability (Sighted, Blindfolded) was a within subject factor, starting condition (Vision-First, Hapsis-First) and experience (Additional-Haptic Experience, No-additional Experience) were between subject factors. The repeated measures ANOVA showed a main effect of visual availability ($F(1,74) = 43.3$, $p < 0.001$). Participants used their right hand significantly more when they were sighted ($67.0 \pm 1.4\%$) than when they were blindfolded ($56.9 \pm 1.2\%$). There was no main effect of starting condition or experience but there was a significant interaction between visual availability and starting condition ($F(1,74) = 16.2$, $p < 0.001$). While sighted, the Hapsis-First group used their right hand significantly less ($62.5 \pm 2.0\%$) than the Vision-First group ($71.5 \pm 2.0\%$). This interaction is illustrated in figure 3A. There was also a significant interaction between visual availability and experience ($F(1,74) = 10.4$, $p = 0.002$). Follow up analysis (independent samples *t-test*) revealed that this interaction was due to the significant reduction in right-hand use during the blindfolded condition when participants had additional haptic experience with the blocks ($t(74) = -3.3$; $p < 0.05$). If participants manipulated the blocks in the container before starting the building task (Experiment Two), they used their right hand $52.6 \pm 1.7\%$ of the time (see

figure 3B). Without this experience (Experiment One), participants used their right hand $61.2 \pm 1.7\%$ of the time. This was regardless of starting condition as the three way interaction (visual availability, starting condition, and experience) was not significant ($F(1, 74) = 0.001, p = 0.9$).

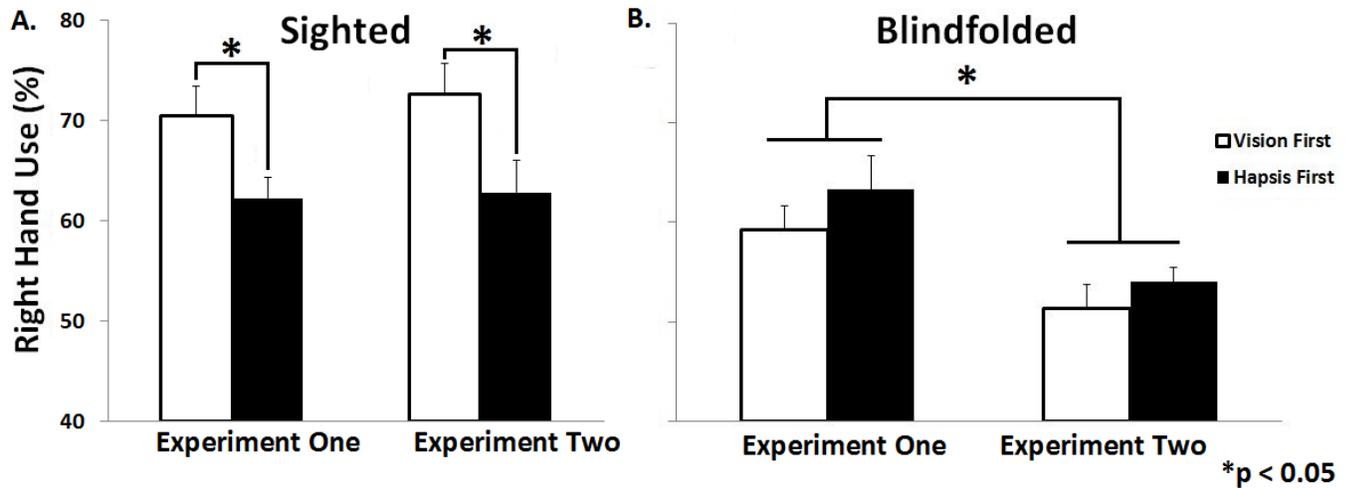


Fig 3. (A) This graph demonstrates right-hand use in percentage for Experiments 1 and 2 while sighted. White bars represent the Vision-First groups. Black bars represent the Hapsis-First groups. Note the significant reduction in right-hand use for the Hapsis-First group. **(B)** This graph demonstrates right-hand use in percentage for Experiments 1 and 2 while blindfolded. White bars represent the Vision-First groups. Black bars represent the Hapsis-First groups. Note the significant reduction in right-hand use in both groups during Experiment 2.

General Discussion

The series of experiments assessed hand use for grasping with and without vision. Many studies have investigated the kinematics of grasping when vision is occluded (e.g. (Connolly & Goodale, 1999; Kritikos & Beresford, 2002; Pettypiece et al., 2009; Schettino et al., 2003; Winges et al., 2003), but none, to our knowledge, have assessed if hand preference is affected when vision is prevented. Participants were asked to replicate 3D block models from a tabletop containing numerous blocks, while sighted and while blindfolded. Hand use for grasping the blocks was documented. The results of Experiment One showed that when blindfolded, participants used their right hand significantly less than when they were sighted. Interestingly, starting condition played a significant role in the modulation of hand use. Participants that started the task with vision demonstrated a significant decrease in right-hand use when blindfolded. When compared to participants that started the task with vision, participants that started the task blindfolded displayed a significant decrease in right-hand use while sighted. Experiment Two investigated the possibility that the haptic experience of touching the blocks without vision had influenced hand use during the sighted portion of the task. To this end, blindfolded participants manipulated the blocks in a container prior to the building task. This haptic experience did not affect right-hand use while sighted regardless of starting condition. The experience however, significantly affected hand use while blindfolded: when compared to Experiment One, participants used their right hand less often in both starting conditions. Together these results demonstrate first, that hand preference for grasping is influenced by vision, and second, they highlight how flexible this preference could be when modulated by haptics.

The results demonstrated a decrease in right-hand preference for haptically-guided grasping when compared to visually-guided grasping. Numerous studies have shown a right-hand preference for grasping during uni- and bi-manual tasks (D. V. Bishop, V. A. Ross, M. S. Daniels, & P. Bright, 1996; P. J. Bryden & E. A. Roy, 2006; G. A. Calvert & Bishop, 1998; M. Carlier, A. L. Doyen, & C. Lamard, 2006; C. M. Mamolo, E. A. Roy, P. J. Bryden, & L. E. Rohr, 2004; C. M. Mamolo, E. A. Roy, L. E. Rohr, & P. J. Bryden, 2006; L. A. Sacrey, J. M. Karl, & I. Q. Whishaw, 2012). In the course of our investigations using the block building task, we have shown the robustness of this preference in right-handers and even in some left-handers (Gonzalez et al. 2007, Gonzalez and Goodale 2009; Stone et al. 2013). The reduction in right-hand use when vision is unavailable shown in the current study is therefore noteworthy. We consider two possible explanations for this reduction. First, studies have shown a left-hand advantage for object discrimination when guided by haptics (Benton et al. 1978; De Renzi et al. 1969; Fagot et al. 1993; Milner and Taylor 1972; Riege et al 1980; Squeri et al. 2012; Tomlinson et al. 2011). Squeri et al. (2012) for example, found that during a passive discrimination haptic task, right-handers performed better when they used their left hand. In another haptic discrimination task, Tomlinson et al. (2011) found that the left hand was more specialized for identifying the haptic-related properties of the object (e.g. texture). Based on these studies, it is possible to speculate that when grasping for an object that you cannot see one would resort to the hand with greater discriminatory abilities (i.e. the left hand). In the current experiments, there was a significant decrease in right-hand use when participants were blindfolded (and an even greater decrease with prior haptic

manipulation). It is possible that left-hand use for grasping increased because it was being recruited for the discrimination of the blocks.

A second factor that could have contributed to the reduction in right-hand use for haptically-guided grasping is the difference in spatial demands between sighted and blindfolded conditions. Arguably, understanding the spatial characteristics of the environment would be more demanding without vision. In a review on spatial representations, Thinus-Blanc and Gaunet (1997) assert that perceiving the environment without vision takes significantly more cognitive resources than with vision. Millar and Al-Attar (2005) tested participants on a spatial task with and without vision. Participants were presented with a tactile map and asked to remember the location of six landmarks. They traced the map with their right index finger under both conditions. Participants were significantly more accurate when using vision. The authors suggested that spatial demands of the task had a greater effect on haptic condition. A fundamental aspect of the block building task used in the current experiments is to recognize the spatial arrangement of the blocks on the tabletop and to construct a spatial map in which to guide their movements. This would be particularly relevant when participants are blindfolded. With these increased spatial demands, it is possible that both hands would be recruited more in order to gain a better understanding of space. Furthermore, it has been suggested that the right hemisphere, which controls movement of the left hand, is responsible for encoding the spatial aspects of the environment (Bartolomeo, 2006; Serrien, Ivry, & Swinnen, 2006; Vallar, 1997; Vogel, Bowers, & Vogel, 2003). One could speculate that increased spatial demands would lead to an increase in left-hand use. Future experiments could investigate whether hand use changes as a function of spatial demands with and without vision.

The next finding, present in both experiments, was the interaction between starting condition and visual availability. That is, in the Vision-First group right-hand use decreased in the subsequent blindfolded part of the task. However, hand use in the Hapsis-First group was not significantly different between the vision and blindfolded condition. This was due to the 10% reduction in right-hand use during the sighted portion of the task. This is intriguing as in both groups (Vision-First, Hapsis-First) participants were building the same models, performing the task with full vision, and the only difference was that one group had completed the blindfolded condition first. This finding suggests that haptically-guided grasping has a powerful effect on subsequent hand use behaviour. Other studies have also found interactions between visual and haptic modalities. For example, Wismeijer, Gegenfurtner, and Drewing (2012) found that information in the haptic domain is transferred more readily to the visual domain than vice versa. The authors suggest that learning between the senses depends on its direction (Wismeijer et al., 2012). It is possible that in our experiment the increase in left-hand use during the haptic portion of the task influenced subsequent hand use in the visual domain. Our results align with Wismeijer and colleagues suggesting that learning can be unidirectional across sensory modalities. Other studies have also shown that information extracted in one sensory modality is later utilized by a different modality. Participants that had received experience identifying the properties of an object either by touch or vision, were better at identifying the same property but in the other sensory domain (Förster, 2011). This suggests that the initial focus of a task, whether it be in the visual or haptic domain, could be carried over into the next part of the task. Again, we could

speculate that increased left-hand use during the haptic portion of the task carried over into the visual condition. The initial focus of the task also seemed to affect build times in the blindfolded condition. In Experiment One, we found that participants were faster to complete the models if they had started the task with hapsis. That is, it took participants longer to build the models while blindfolded if they had built the models while sighted first. This suggests that perhaps the visual experience interfered with the subsequent performance of building the models with hapsis. Intriguingly, however, this was not found in the second experiment. Future studies investigating visual and haptic interactions that focus on performance time should examine the effects of starting condition on this variable.

Experiment Two was designed to assess the possibility that touching the blocks blindfolded prior to the building task could lead to the increase in left-hand use seen during the visual condition in the Hapsis-First group. Contrary to our prediction we did not find this to be the case. When comparing experiments One and Two, participants did not further reduce their right-hand use in the visual condition, and hand use between the two experiments was in fact, virtually identical (figure 3A). It is possible that right hand preference for grasping when vision is available could not reach lower levels (i.e. “floor effect”) and that is why the additional haptic experience did not further decrease its use. The results suggest that other factors, besides the haptic feedback, modulates hand preference across the two sensory modalities. In other words, simply ‘feeling’ the blocks while blindfolded was not sufficient to change hand use in a different sensory domain (vision). Transfer of information between sensory domains has been shown in some studies (Bratzke, Seifried, & Ulrich, 2012; Gottfried, Rose, & Bridger, 1977; Held, 2009; Norman, Clayton, Norman, & Crabtree, 2008; Volcic, Wijntjes, Kool, & Kappers, 2010), but not in others. For example, Newell, Ernst, Tjan, and Bulthoff (2001) showed that participants perform worse when transferring information from one sensory modality to the other (i.e. vision to haptics) than within sensory modalities. In their experiment participants had to visually or haptically assess a platform in which various wooden objects were placed. For the cross-modal condition participants studied the platform in one sensory modality and were tested in the other sensory modality. Errors were significantly higher in the cross-modal condition. In our experiment, we did not find that additional experience in the haptic domain (i.e. feeling the blocks in the container) influenced hand preference in the vision domain. However this additional experience did have a significant impact on hand preference within the haptic domain. That is, hand preference for participants in the Vision-First group was significantly reduced to the point that the right and the left hand were used equally (i.e. 51% right-hand preference) to grasp the blocks while blindfolded. These results suggest the possibility that there is a transfer of information within the haptic domain. Evidence for transfer within sensory modalities has been shown before (Butler & James, 2011; Easton, Greene, & Srinivas, 1997; Hupp & Sloutsky, 2011; Reales & Ballesteros, 1999) but none have documented a change in hand use or preference.

Regardless of starting condition and compared to Experiment One, participants in Experiment Two displayed an additional and substantial reduction in right-hand use when they were blindfolded. This is, 10% and 11% reduction in right-hand use in the Vision-First and the Hapsis-First groups respectively. We speculate that the additional ~10% decrease in the blindfolded conditions was due specifically to the haptic manipulation of

the blocks in the container. The results of some studies have shown that experience within sensory modalities significantly influence subsequent behaviour. Craddock and Lawson (2008), for example, conducted an identification task where participants either studied specific objects using vision or using haptics. During the test period, they were asked to identify these objects using haptics only. The group who had used haptics to study the objects were significantly faster at identifying them. These results suggest that experience within one modality affects later performance in the same modality. In our study, the haptic experience of touching the blocks in the container altered hand use while blindfolded. Because participants were blindfolded and used both hands to explore the blocks in the container, it is possible that they adopted the same strategy when presented with the blindfolded condition. It is also likely that if there is a left-hand advantage for haptic discrimination (Benton et al., 1973; De Renzi et al., 1969; Fagot et al., 1993; Milner & Taylor, 1972; Riege et al., 1980; Squeri et al., 2012; Tomlinson et al., 2011), a prior exposure to the details of the blocks (in the container) prompted its use.

In conclusion, hand preference for grasping is modulated by vision *and* by haptics. Haptically-guided grasping remains lateralized but to a lesser extent than visually-guided grasping, particularly if followed by a brief haptic experience. Future research in special populations such as congenitally blind individuals and deafferented patients would bring insight into the sensorimotor control of hand actions, and the preferences that follow.

References

- Annett, J., Annett, M., Hudson, P. T. W., & Turner, A. (1979). The control of movement in the preferred and non-preferred hands. *Quarterly Journal of Experimental Psychology*, *31*(4), 641-652. doi: 10.1080/14640747908400755
- Bartolomeo, P. (2006). A parietofrontal network for spatial awareness in the right hemisphere of the human brain. *Archives of Neurology*, *63*(9), 1238-1241.
- Benton, A. L., Levin, H. S., & Varney, N. R. (1973). Tactile perception of direction in normal subjects: Implications for hemispheric cerebral dominance. *Neurology*, *23*(11), 1248-1250. doi: 10.1212/WNL.23.11.1248
- Bishop, D., Ross, V., Daniels, M., & Bright, P. (1996). The measurement of hand preference: A validation study comparing three groups of right-handers. *British Journal of Psychology*, *87*(2), 269-285.
- Bishop, D. V., Ross, V. A., Daniels, M. S., & Bright, P. (1996). The measurement of hand preference: A validation study comparing three groups of right-handers. *British Journal of Psychology*, *87* (Pt 2), 269-285. doi: 10.1111/j.2044-8295.1996.tb02590.x
- Bratzke, D., Seifried, T., & Ulrich, R. (2012). Perceptual learning in temporal discrimination: Asymmetric cross-modal transfer from audition to vision. *Experimental Brain Research*, *221*(2), 205-210. doi: 10.1007/s00221-012-3162-0
- Bryden, M. P., Singh, M., Steenhuis, R. E., & Clarkson, K. L. (1994). A behavioral measure of hand preference as opposed to hand skill. *Neuropsychologia*, *32*(8), 991-999. doi: [http://dx.doi.org/10.1016/0028-3932\(94\)90048-5](http://dx.doi.org/10.1016/0028-3932(94)90048-5)
- Bryden, P. J., Pryde, K. M., & Roy, E. A. (2000). A performance measure of the degree of hand preference. *Brain and Cognition*, *44*(3), 402-414. doi: 10.1006/brcg.1999.1201
- Bryden, P. J., & Roy, E. (2006). Preferential reaching across regions of hemispace in adults and children. *Developmental psychobiology*, *48*(2), 121-132.
- Bryden, P. J., & Roy, E. A. (2006). Preferential reaching across regions of hemispace in adults and children. *Developmental Psychobiology*, *48*(2), 121-132. doi: 10.1002/dev.20120
- Butler, A. J., & James, K. H. (2011). Cross-modal versus within-modal recall: Differences in behavioral and brain responses. *Behavioural Brain Research*, *224*(2), 387-396. doi: 10.1016/j.bbr.2011.06.017
- Calvert, G. (1998). Quantifying hand preference using a behavioural continuum. *Laterality: Asymmetries of Body, Brain and Cognition*, *3*(3), 255-268.
- Calvert, G. A., & Bishop, D. V. (1998). Quantifying hand preference using a behavioural continuum. *Laterality*, *3*(3), 255-268. doi: 10.1080/713754307
- Carlier, M., Doyen, A. L., & Lamard, C. (2006). Midline crossing: Developmental trend from 3 to 10 years of age in a preferential card-reaching task. *Brain and cognition*, *61*(3), 255-261.
- Carlier, M., Doyen, A. L., & Lamard, C. (2006). Midline crossing: Developmental trend from 3 to 10 years of age in a preferential card-reaching task. *Brain and Cognition*, *61*(3), 255-261. doi: 10.1016/j.bandc.2006.01.007
- Connolly, J. D., & Goodale, M. A. (1999). The role of visual feedback of hand position in the control of manual prehension. *Experimental Brain Research*, *125*(3), 281-286.

- Craddock, M., & Lawson, R. (2008). Repetition priming and the haptic recognition of familiar and unfamiliar objects. *Perception & Psychophysics*, *70*(7), 1350-1365. doi: 10.3758/pp.70.7.1350
- De Renzi, E., Faglioni, P., & Scotti, G. (1969). Impairment of memory for position following brain damage. *Cortex*, *5*(3), 274-284. doi: 10.1016/S0010-9452(69)80035-3
- Easton, R., Greene, A., & Srinivas, K. (1997). Transfer between vision and haptics: Memory for 2-D patterns and 3-D objects. *Psychonomic Bulletin & Review*, *4*(3), 403-410. doi: 10.3758/BF03210801
- Fagard, J., & Marks, A. (2000). Unimanual and bimanual tasks and the assessment of handedness in toddlers. *Developmental Science*, *3*(2), 137-147. doi: 10.1111/1467-7687.00107
- Fagot, J., Hopkins, W. D., & Vauclair, J. (1993). Hand movements and hemispheric specialization in dichhaptic explorations. *Perception*, *22*(7), 847-853. doi: 10.1068/p220847
- Förster, J. (2011). Local and global cross-modal influences between vision and hearing, tasting, smelling, or touching. *Journal of Experimental Psychology: General*, *140*(3), 364.
- Gabbard, C., & Rabb, C. (2000). What determines choice of limb for unimanual reaching movements? *The Journal of General Psychology*, *127*(2), 178-184. doi: 10.1080/00221300009598577
- Gabbard, C., Tapia, M., & Helbig, C. R. (2003). Task complexity and limb selection in reaching. *International journal of neuroscience*, *113*(2), 143-152.
- Gonzalez, C. L., Whitwell, R. L., Morrissey, B., Ganel, T., & Goodale, M. A. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, *182*(2), 275-279. doi: 10.1007/s00221-007-1090-1
- Gottfried, A. W., Rose, S. A., & Bridger, W. H. (1977). Cross-modal transfer in human infants. *Child Development*, *48*(1), 118-123.
- Held, R. (2009). Visual-haptic mapping and the origin of cross-modal identity. *Optometry and Vision Science*, *86*(6), 595-598. doi: 10.1097/OPX.0b013e3181a72999
- Hupp, J. M., & Sloutsky, V. M. (2011). Learning to learn: From within-modality to cross-modality transfer during infancy. *Journal of Experimental Child Psychology*, *110*(3), 408-421. doi: 10.1016/j.jecp.2011.05.002
- Kritikos, A., & Beresford, M. (2002). Tactile interference in visually guided reach-to-grasp movements. *Experimental Brain Research*, *144*(1), 1-7. doi: 10.1007/s00221-002-1004-1
- Mamolo, C. M., Roy, E. A., Bryden, P. J., & Rohr, L. E. (2004). The effects of skill demands and object position on the distribution of preferred hand reaches. *Brain and Cognition*, *55*(2), 349-351. doi: 10.1016/j.bandc.2004.02.041
- Mamolo, C. M., Roy, E. A., Bryden, P. J., & Rohr, L. E. (2004). The effects of skill demands and object position on the distribution of preferred hand reaches. *Brain and cognition*, *55*(2), 349-351.
- Mamolo, C. M., Roy, E. A., Bryden, P. J., & Rohr, L. E. (2005). The performance of left-handed participants on a preferential reaching test. *Brain and cognition*, *57*(2), 143-145.

- Mamolo, C. M., Roy, E. A., Rohr, L. E., & Bryden, P. J. (2006). Reaching patterns across working space: The effects of handedness, task demands, and comfort levels. *Laterality, 11*(5), 465-492. doi: 10.1080/13576500600775692
- Mamolo, C. M., Roy, E. A., Rohr, L. E., & Bryden, P. J. (2006). Reaching patterns across working space: The effects of handedness, task demands, and comfort levels. *Laterality, 11*(5), 465-492.
- Melmoth, D. R., Finlay, A. L., Morgan, M. J., & Grant, S. (2009). Grasping deficits and adaptations in adults with stereo vision losses. *Investigative Ophthalmology & Visual Science, 50*(8), 3711-3720. doi: 10.1167/iovs.08-3229
- Millar, S., & Al-Attar, Z. (2005). What aspects of vision facilitate haptic processing? *Brain and Cognition, 59*(3), 258-268. doi: 10.1016/j.bandc.2005.07.005
- Milner, B., & Taylor, L. (1972). Right-hemisphere superiority in tactile pattern-recognition after cerebral commissurotomy: Evidence for nonverbal memory. *Neuropsychologia, 10*(1), 1-15. doi: 10.1016/0028-3932(72)90038-3
- Newell, F. N., Ernst, M. O., Tjan, B. S., & Bulthoff, H. H. (2001). Viewpoint dependence in visual and haptic object recognition. *Psychological Science, 12*(1), 37-42.
- Norman, J. F., Clayton, A. M., Norman, H. F., & Crabtree, C. E. (2008). Learning to perceive differences in solid shape through vision and touch. *Perception, 37*(2), 185-196. doi: 10.1068/p5679
- Pettypiece, C. E., Culham, J. C., & Goodale, M. A. (2009). Differential effects of delay upon visually and haptically guided grasping and perceptual judgments. *Experimental Brain Research, 195*(3), 473-479. doi: 10.1007/s00221-009-1807-4
- Reales, J. M., & Ballesteros, S. (1999). Implicit and explicit memory for visual and haptic objects: Cross-modal priming depends on structural descriptions. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 25*(3), 644-663. doi: 10.1037/0278-7393.25.3.644
- Riege, W. H., Metter, E. J., & Williams, M. V. (1980). Age and hemispheric asymmetry in nonverbal tactual memory. *Neuropsychologia, 18*(6), 707-710. doi: 10.1016/0028-3932(80)90112-8
- Sacrey, L. A., Karl, J. M., & Whishaw, I. Q. (2012). Development of rotational movements, hand shaping, and accuracy in advance and withdrawal for the reach-to-eat movement in human infants aged 6-12 months. *Infant Behavior & Development, 35*(3), 543-560. doi: 10.1016/j.infbeh.2012.05.006
- Sacrey, L. A. R., Karl, J. M., & Whishaw, I. Q. (2012). Development of rotational movements, hand shaping, and accuracy in advance and withdrawal for the reach-to-eat movement in human infants aged 6-12 months. *Infant Behavior and Development, 35*(3), 543-560.
- Schettino, L. F., Adamovich, S. V., & Poizner, H. (2003). Effects of object shape and visual feedback on hand configuration during grasping. *Experimental Brain Research, 151*(2), 158-166. doi: 10.1007/s00221-003-1435-3
- Serrien, D. J., Ivry, R. B., & Swinnen, S. P. (2006). Dynamics of hemispheric specialization and integration in the context of motor control. *Nature Reviews Neuroscience, 7*(2), 160-166. doi: 10.1038/nrn1849
- Squeri, V., Sciutti, A., Gori, M., Masia, L., Sandini, G., & Konczak, J. (2012). Two hands, one perception: How bimanual haptic information is combined by the brain. *Journal of Neurophysiology, 107*(2), 544-550. doi: 10.1152/jn.00756.2010

- Stone, K. D., Bryant, D. C., & Gonzalez, C. L. (2013). Hand use for grasping in a bimanual task: Evidence for different roles? *Experimental Brain Research*, 224(3), 455-467. doi: 10.1007/s00221-012-3325-z
- Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin*, 121(1), 20-42. doi: 10.1037/0033-2909.121.1.20
- Tomlinson, S. P., Davis, N. J., Morgan, H. M., & Bracewell, R. M. (2011). Hemispheric specialisation in haptic processing. *Neuropsychologia*, 49(9), 2703-2710. doi: 10.1016/j.neuropsychologia.2011.05.018
- Vallar, G. (1997). Spatial frames of reference and somatosensory processing: A neuropsychological perspective. *Philosophical Transactions of the Royal Society of London*, 352(1360), 1401-1409.
- Vogel, J. J., Bowers, C. A., & Vogel, D. S. (2003). Cerebral lateralization of spatial abilities: A meta-analysis. *Brain and Cognition*, 52(2), 197-204. doi: [http://dx.doi.org/10.1016/S0278-2626\(03\)00056-3](http://dx.doi.org/10.1016/S0278-2626(03)00056-3)
- Volcic, R., Wijntjes, M. A., Kool, E., & Kappers, A. L. (2010). Cross-modal visuo-haptic mental rotation: Comparing objects between senses. *Experimental Brain Research*, 203(3), 621-627. doi: 10.1007/s00221-010-2262-y
- Winges, S. A., Weber, D. J., & Santello, M. (2003). The role of vision on hand preshaping during reach to grasp. *Experimental Brain Research*, 152(4), 489-498. doi: 10.1007/s00221-003-1571-9
- Wismeijer, D. A., Gegenfurtner, K. R., & Drewing, K. (2012). Learning from vision-to-touch is different than learning from touch-to-vision. *Frontiers in Integrative Neuroscience*, 6. doi: 10.3389/fnint.2012.00105

APPENDIX 2

Grasping without Sight: Insights from the Congenitally Blind*

* **Stone, K. D., & Gonzalez, C. L.** (2014b). Grasping without sight: Insights from the congenitally blind. *PLoS ONE*, 9(10), e110175. doi: 10.1371/journal.pone.0110175

Abstract

We reach for and grasp different sized objects numerous times per day. Most of these movements are visually-guided, but some are guided by the sense of touch (i.e. haptically-guided), such as reaching for your keys in a bag, or for an object in a dark room. A marked right-hand preference has been reported during visually-guided grasping, particularly for small objects. However, little is known about hand preference for haptically-guided grasping. Recently, a study has shown a reduction in right-hand use in blindfolded individuals, and an absence of hand preference if grasping was preceded by a short haptic experience. These results suggest that vision plays a major role in hand preference for grasping. If this were the case, then one might expect congenitally blind (CB) individuals, who have never had a visual experience, to exhibit no hand preference. Two novel findings emerge from the current study: first, the results showed that contrary to our expectation, CB individuals used their right hand during haptically-guided grasping to the same extent as visually-unimpaired (VU) individuals did during visually-guided grasping. And second, object size affected hand use in an opposite manner for haptically- versus visually-guided grasping. Big objects were more often picked up with the right hand during haptically-guided, but less often during visually-guided grasping. This result highlights the different demands that object features pose on the two sensory systems. Overall the results demonstrate that hand preference for grasping is independent of visual experience, and they suggest a left-hemisphere specialization for the control of grasping that goes beyond sensory modality.

Introduction

We execute hundreds of reaching and grasping movements a day. Both vision and haptics (i.e. sense of touch) play an integral role in guiding these movements. For example, when reaching for an object, such as an apple, both visual and haptic cues are needed to successfully complete the movement. Initially vision is used to identify the apple (e.g. shape, size, colour) and haptics is used to assess properties such as object weight, temperature, and texture (Tomlinson, Davis, Morgan, & Bracewell, 2011; Withagen, Kappers, Vervloed, Knoors, & Verhoeven, 2013; Woods & Newell, 2004). Numerous studies have reported a preference to use the right hand during visually-guided grasping (Bishop, Ross, Daniels, & Bright, 1996; Bryden & Roy, 2006; Calvert & Bishop, 1998; Carlier, Doyen, & Lamard, 2006; Gabbard, Tapia, & Helbig, 2003; Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Sacrey, Karl, & Whishaw, 2012; Stone, Bryant, & Gonzalez, 2013), so it is likely one would choose this hand to pick up the apple. However, suppose you are searching for your keys in a bag, or a glass of water in the middle of the night. In these scenarios, only haptic cues would be used and essential to locate, recognize, and grasp the objects. Would the right-hand preference seen during visually-guided grasping persist in the absence of vision? To answer this question, Stone and Gonzalez (2014) asked sighted and blindfolded participants to reach for and grasp blocks scattered on a tabletop in order to construct 3D models. The results showed that participants used their right hand significantly more to grasp the blocks while sighted, but even so, a preference to grasp with the right hand persisted during the blindfolded trials. However, if these blindfolded trials were preceded by five minutes of haptic experience (without vision), equal use of the right and left hands was observed (Stone & Gonzalez, 2014). This finding suggests that haptics significantly influences hand preference for grasping and raises the possibility that individuals who have never had a visual experience (but a lifetime of haptic experience) would exhibit little to no hand preference.

A population absent of any visual experience are congenitally blind (CB) individuals. CB refers to an individual who was born without vision (or lost vision shortly thereafter) thus resulting in no recollection of a visual experience (Thinus-Blanc & Gaunet, 1997). These individuals use their sense of touch hundreds of times per day to identify, manipulate, and pick up objects, and therefore have had extensive experience using haptically-guided grasping. Hand preference for grasping in CB individuals, however, has only been reported anecdotally in children (Caliskan & Dane, 2009; Ittyerah, 1993, 2000, 2009) and these studies have shown mixed results. Hand preference for grasping in an adult CB population remains unknown. Based on the results of Stone and Gonzalez (2014) in which a brief haptic experience equalized hand use, one would predict no hand preference for grasping in CB individuals. Or perhaps, even a left-hand preference as several studies have shown a left-hand advantage during the haptic discrimination of objects (Benton, Varney, & Hamsher, 1978; Cormier & Tremblay, 2013; Harada et al., 2004; Kumar, 1977; O'Boyle, Van Wyhe-Lawler, & Miller, 1987; Tomlinson et al., 2011). In the present study we investigated these speculations. The *first goal* therefore, was to document hand preference for grasping in an adult CB population.

Hand preference for reaching and grasping is also influenced by the different motor programs that mediate these movements. It has been proposed that planning to reach for an object is guided by its spatial attributes (distance, position), whereas planning to grasp an object is guided by its intrinsic properties (size, shape; (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995)). With respect to grasping for example, when picking up the aforementioned apple, the motor program that mediates the grasp would assess its size and shape and transform this information into the appropriate grip type. In this case, most likely a grip that requires all five fingers (i.e. a power grasp) would be used. In contrast, if one were to pick up a grape, its small size would prompt the use of only the thumb and index finger (i.e. a precision grasp). That is, previous research has shown that object size significantly affects hand preference during visually-guided grasping. For example, Vainio, Ellis, Tucker, and Symes (2006) found a right-hand preference for precision grips and a left-hand preference for power grips. Similarly, other studies have shown that individuals will use their right hand more often to grasp small as opposed to big objects (Gonzalez & Goodale, 2009; Stone et al., 2013). It remains to be shown if this pattern persists for grasping without vision. Kinematic studies have shown that, in the absence of vision, visually-unimpaired individuals display disruptions in their movement including larger maximum grip apertures (Jackson, Jackson, & Rosicky, 1995; Pettypiece, Culham, & Goodale, 2009; Rand, Lemay, Squire, Shimansky, & Stelmach, 2007) and slower movement times (Schettino, Adamovich, & Poizner, 2003; Wings, Weber, & Santello, 2003). Interestingly, this does not seem to be the case for blind individuals. Kinematic analyses have shown that when reaching for an object, blind individuals *do* display differences in movement (i.e. a double opening and closing of the hand towards the target), but they still accurately scale to the size of the unseen object (in a manner similar to sighted individuals) (Bennett, Mucignat, Waterman, & Castiello; Castiello, Bennett, & Mucignat, 1993). In light of this evidence, we investigated if object size affects hand *preference* for those with lifelong deprivation of visual experience (CB individuals). Addressing this possibility was the *second goal* of the current study.

CB and visually unimpaired (VU) individuals were tested on the block building task (see (Gonzalez et al., 2007; Stone et al., 2013; Stone & Gonzalez, 2014)). Participants were asked to replicate models from a tabletop of evenly distributed building blocks. Participants built three models using small blocks and three models using big blocks to assess the effect of object size on hand preference. In Experiment One, CB and a group of age- and gender-matched VU participants (VU-Matched controls) were assessed for haptically-guided grasping (all participants were blindfolded). In Experiment Two, visually- and haptically-guided grasping were directly compared in two groups of VU students (VU-Sighted, VU-Blindfolded). In both experiments, hand preference for grasping was documented in ipsilateral (same side as the hand) and contralateral (opposite side of the hand) space as studies have found that reaching across the midline is a powerful indicator of hand preference (Bryden & Roy, 2006; Carlier et al., 2006; Gabbard, Helbig, & Gentry, 2001).

Experiment One

Methods and Procedures

Participants

With respect to the photographs of participants in Figure 1, each individual signed a consent form that read: “The results from this study will be reported in general terms in the form of speech, writing, photograph or video that may be presented in manuscripts submitted for publication in scientific journals, or oral and/or poster presentations at scientific meetings, seminars, and/or conferences.” Participants were therefore aware that their photograph may be used for a published manuscript when their signature was given on the consent form for the current experiment.

A priori power analysis suggested that with power at 0.95, effect size of 0.7, and statistical significance set at 0.05, the current study would require a total sample size of 16 participants (G*Power 3.1.9.2). A total of 24 participants were recruited for this experiment. Furthermore, it should be noted that participant’s gender was not balanced, as gender differences have not been reported in earlier studies involving a similar task (Gonzalez & Goodale, 2009).

Congenitally blind (CB) participants: Ten self-reported right-handed CB individuals (8 males) and two late blind individuals (1 female) were recruited from the Canadian National Institute for the Blind (CNIB) in Lethbridge, Edmonton, Medicine Hat and Calgary (Alberta). These participants were between the ages of 20 and 76 years of age. The two late blind individuals suffered from retinitis pigmentosa. One had been totally blind for over 50 years and the other for 10 years, although this individual reported suffering from visual deprivation since childhood. Visually-unimpaired (VU)-Matched controls: Twelve self-reported right-handers (9 males) recruited from the Lethbridge area between the ages of 20 and 73 participated. For each CB participant, we tested one VU participant of the same gender and approximately the same age (± 3 years). The study was approved by the University of Lethbridge Human Subjects Research Committee (protocol #2011-22) and all participants gave written informed consent in accordance with the Declaration of Helsinki. Participants were naïve to the purposes of the study.

Apparatus and Stimuli

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. 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. CB participants were also asked about their diagnosed visual condition, ability to read Braille, and ability to function independently (i.e. yes or no). This information is included in Table 1.

Table 1 Information pertaining to each CB and Late Blind participants' (initials included) visual condition, hand used to read Braille, and ability to function independently.

Participant	Visual Condition	Hand used for Braille	Functions independently?
1 BV	Congenital glaucoma	Both	Yes
2 CM	Bilateral Retinoblastoma	Both	Yes
3 WR	Optic nerve hypoplasia	Both	Yes
4 BD	Retinopathy of prematurity	Both	Yes
5 CM	Leber Congenital Amaurosis	Both	Yes
6 EC	Leber Congenital Amaurosis	Both	Yes
7 GE	Optic Atrophy	Both	Yes
8 LP	Retinopathy of prematurity	Right	Yes
9 RG	Optic Nerve Hypoplasia	Unknown	Partial*
10 NS	Retinitis pigmentosa	Unknown	Yes
11 WB	Retinitis pigmentosa	Left	Yes
12 MH	Leber Congenital Amaurosis	Both	Yes

*resides in an assisted living home

Block Building Task: A total of six models built with MEGA BLOKS (big blocks) and LEGO (small blocks) were used for the experiment. Three models were built using big blocks (ranging in size from 3.1 L x 3.1 W x 2.0 cm H to 6.3 L x 3.1 W x 2.0 cm H) and three using small blocks (ranging in size from < 0.7 L x 0.7 W x 1.0 cm H to 6.3 L x 1.5 W x 1.0 cm H). Each model contained 10 blocks of various colours and shapes. Scattered on a table (122 L x 122 W x 74 cm H with a working space of 70 L x 122 W x 74 cm H) were all the blocks that made up the three models of each set (i.e. either 30 small blocks or 30 big blocks; see Figure 1A and 1B). The models were prepared ahead of time by the experimenter. The same six models were used with all participants. The same number of blocks were placed on the left and right side of the table. There was a fixed building plate (19L x 19cm 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.

Procedures

Participants were seated in front of the table facing the middle of the display that contained either “big blocks” or “small blocks”. Participants were notified that for the next three models they would be building with big *or* small blocks. In other words, participants were never presented with a table that contained small and big blocks at the same time. After the participant was comfortably seated, they were instructed to replicate the model as quickly and accurately as possible from the blocks given on the table. No other instruction was given. All participants were blindfolded prior to and during the task. Therefore, they were only able to use their sense of touch to identify the model and blocks. 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. Six models were built in total. Starting block size (small or big) was counterbalanced among participants. The task was recorded on a JVC HD Everio video recorder approximately 160cm away from the individual with a clear view of the tabletop, building blocks, and participants' hands.

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 for right-hand use (number of right grasps/total number of grasps X 100). The time in which it took participants to construct each model was recorded on a stopwatch and reported in seconds. Therefore, the dependent variables included percentage of overall right-hand use, percentage of hand use in contralateral space (contralateral grasps), and the time in seconds that it took participants to complete the models. Data were assessed and no violations for homogeneity of variance and normality were found prior to analysis. Partial Eta Squared values were used to show effect size (ES).

Data were analyzed using SPSS Statistics 18.0 for Windows (SPSS Inc., Chicago, IL, USA).

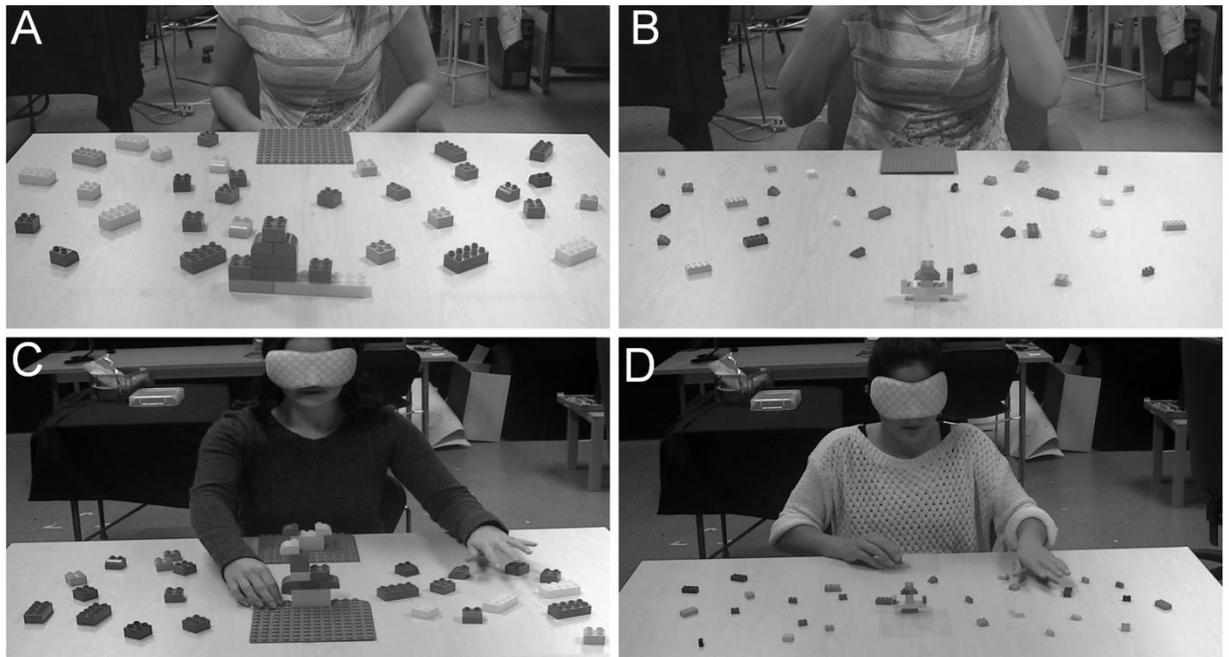


Fig. 1 Experimental setup with big blocks (A) Photograph of experimental setup with big blocks scattered across the tabletop. **Experimental setup with small blocks** (B) Photograph of experimental setup with small blocks scattered across the tabletop. **Power grasp formation for big blocks** (C) Photograph of blindfolded participant exhibiting an extension of all five fingers (resembling a power grasp) while reaching for a big block. **Power grasp formation for small blocks** (D) Photograph of blindfolded participant exhibiting an extension of all five fingers (resembling a power grasp) while reaching for a small block.

Results (Experiment One)

Handedness questionnaire

All participants self-reported as right-handers and this was confirmed by the handedness questionnaire. Congenitally Blind participants: Given that not all 22 questions applied to the CB participants, their scores were normalized to the traditional scale for this questionnaire (-44 to +44) regardless of how many questions they answered. To normalize the scores, we took the participant's total score (e.g. 25) divided by the total number of questions that participant answered (e.g. 19) and this value was then multiplied by 22, which is the total number of possible questions that could have been answered (and the total number of questions all of the VU individuals answered). On average, CB participants received an overall average score of 33.8 (± 1.0 SE; range +28 to +41.9) points out of a total possible score of -44/+44. VU-Matched controls: VU-Matched controls participants answered all 22 questions, and received an overall average score of 31.6 (± 2.0 SE range +17 to +40) points out of a total possible score of -44/+44. An independent samples t-test revealed that there was no significant difference between the two groups ($t(22) = 1.2$; $p = 0.2$).

Hand use for grasping

Analysis using a 2 (object size) X 2 (group) repeated measures ANOVA was performed on the percentage of right-hand use for grasping during the task. Object size (big, small) was a within subject factor and group (CB, VU-Matched controls) a between subject factor. Overall, we found a main effect of object size ($F(1, 22) = 26.2$; $p < 0.0001$, $ES = 0.54$). Participants used their right hand significantly more to grasp the big blocks ($59.6 \pm 1.4\%$) compared to the small blocks ($52.0 \pm 1.5\%$). There was also a main effect of group ($F(1, 22) = 8.1$; $p = 0.009$, $ES = 0.26$). Participants in the CB group used their right hands significantly more to grasp the blocks ($59.5 \pm 1.8\%$) than the VU-Matched controls ($52.2 \pm 1.8\%$), regardless of object size. The interaction between group and size was not significant ($p = 0.42$). Both groups displayed the same pattern of hand preference for both big and small blocks. CB participants used their right hand $62.7 \pm 2.0\%$ when grasping big blocks and $56.3 \pm 2.1\%$ when grasping small blocks. VU-Matched controls used their right hand $56.6 \pm 2.0\%$ when grasping big blocks, and $47.8 \pm 2.1\%$ when grasping small blocks (see Figure 2A).

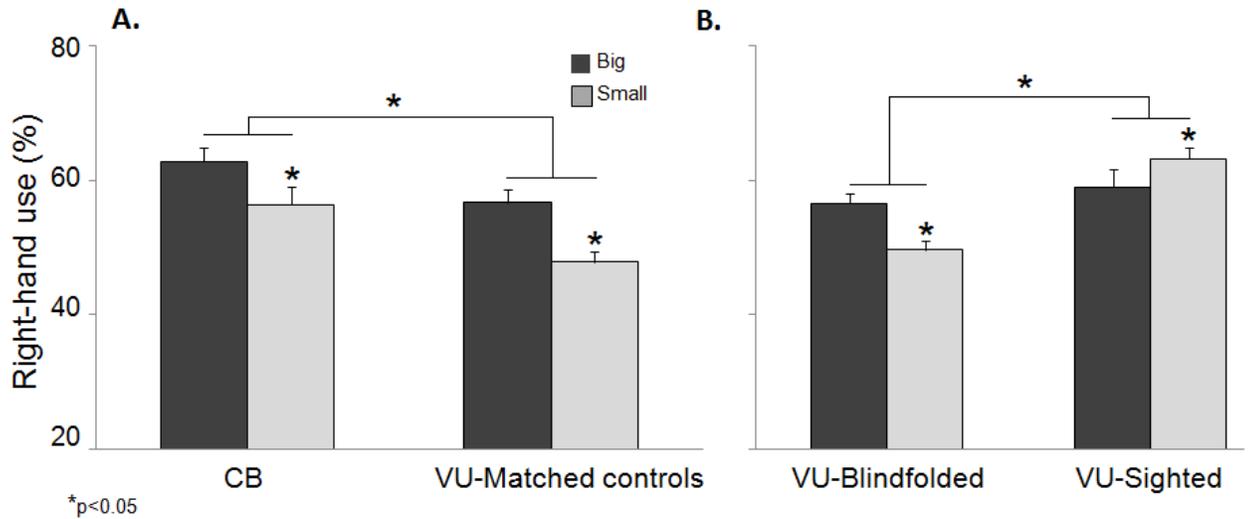


Fig.2 Hand use for grasping for big and small blocks in Experiment One (A)

This graph demonstrates right-hand use as a function of object size for the two groups: CB and VU-Matched controls (Experiment One). The dark grey bars represent the big blocks. The light grey bars represent the small blocks. Note the significant difference between the CB and VU-Matched controls, as well as reduction in right-hand use for the small blocks seen in both groups. **Hand use for grasping for big and small blocks in Experiment Two (B)**

This graph demonstrates right-hand use as a function of object size for the two groups: VU-Blindfolded and VU-Sighted groups (Experiment Two). The dark grey bars represent the big blocks. The light grey bars represent the small blocks. Note the significant difference between the VU-Sighted and VU-Blindfolded participants, as well as the opposite pattern of hand use exhibited for object size within the two groups.

Contralateral grasps: Analysis using a 2 (object size) X 2 (hand) X 2 (group) repeated measures ANOVA was performed on the percentage of contralateral grasps made during the task. Object size (big, small) and hand (right, left) were within factors and group (CB, VU-Matched controls) the between factor. Analyses did not show a significant effect of object size ($F(1, 22) = 0.6; p = 0.42, ES = 0.02$), therefore data were collapsed across this variable. A 2 (hand) X 2 (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 (CB, VU-Matched controls) a between subject factor. There was no main effect of hand ($F(1, 22) = 2.8; p = 0.1, ES = 0.11$). There was no main effect of group ($p = 0.2$). However, the group by hand interaction was significant ($F(1, 22) = 5.2; p = 0.03, ES = 0.19$). Post hoc analysis (paired samples t-test) revealed that the CB group made significantly more right-handed grasps into left contralateral space ($6.1 \pm 2.0\%$) than left-handed grasps into right contralateral space ($1.6 \pm 0.5\%$; $t(11) = 2.2; p = 0.04$). This was not the case for the VU-Matched controls (2.4% versus 3.3%; $t(11) = -0.6; p = 0.55$).

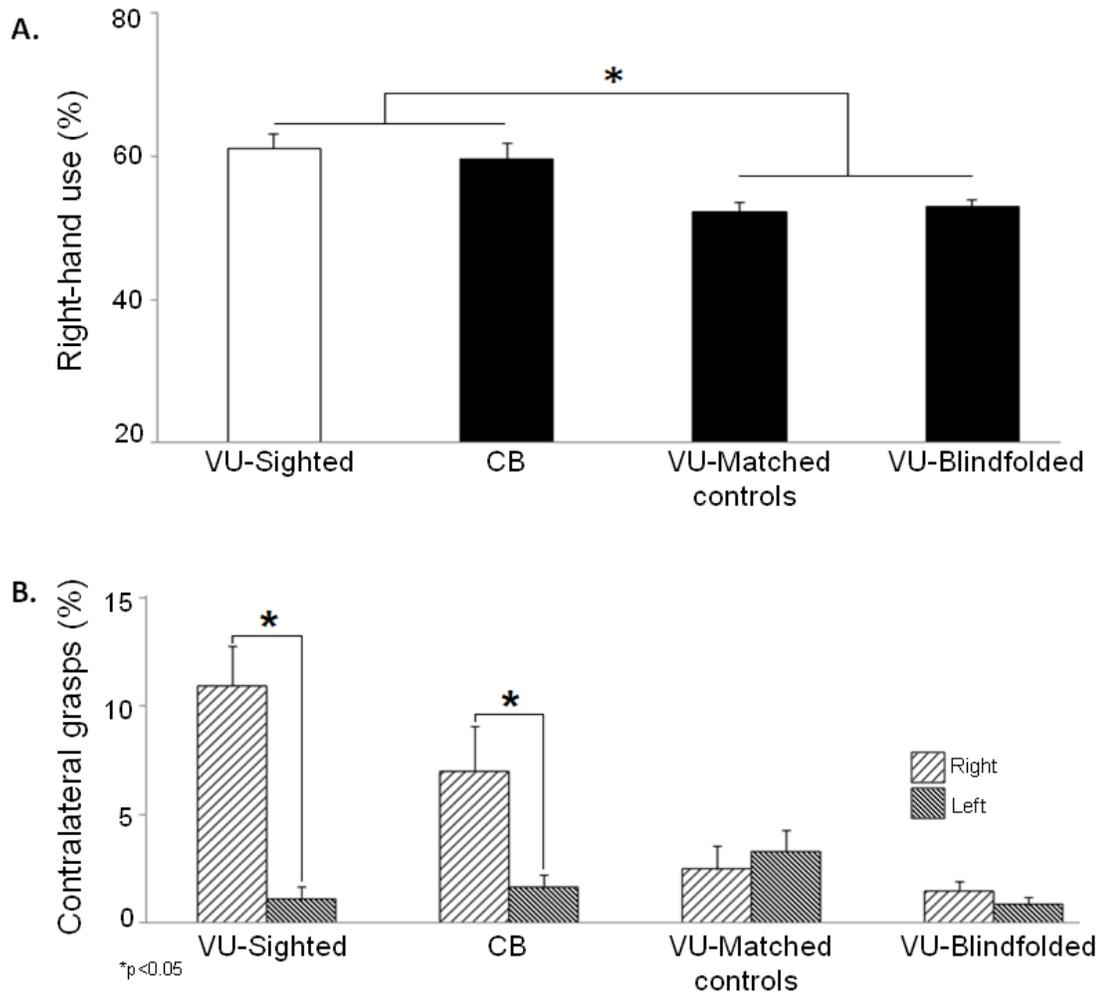


Fig.3 Overall hand use for grasping across all groups (A) This graph demonstrates overall right-hand use (across object size) in percentage for groups in Experiment One (CB, VU-Matched controls) and Experiment Two (VU-Sighted, VU-Blindfolded). White bars signify that the participants had vision for the duration of the task. Black bars signify that the participants had no vision (blind or blindfolded). Note that there is *no* significant difference in right-hand use between VU-Sighted and CB participants, but these groups are different from the VU-Blindfolded and VU-Matched controls. **Hand use for contralateral grasps across all groups (B)** This graph demonstrates the average percentage of contralateral grasps made with the left and right hand for the VU-Sighted, CB, VU-Matched controls, and VU-Blindfolded groups. The spaced rightward diagonal bars represent the right hand and the compressed leftward diagonal bars represent the left hand. Note the significant difference in contralateral grasps made with each hand for the VU-Sighted and CB groups but not for the VU-Matched controls. Note also, that the VU-Sighted and CB groups behaved similarly.

Build times for models

Analysis using a 2 (object size) X 2 (group) repeated measures ANOVA was performed on the average time in seconds it took for participants to complete one model. Object size (big, small) was a within subject factor and group (CB, VU-Matched controls) a between subject factor. Overall, we found a main effect of object size ($F(1, 22) = 14.2$; $p = 0.001$, $ES = 0.39$). Participants were faster at completing one model made of big blocks ($175.7 \pm 11.9s$) compared to one model made of small blocks (213.0 ± 14.2). There was no main effect of group ($F(1, 22) = 0.8$; $p = 0.53$, $ES = 0.01$). The interaction between size and group reached significance however ($F(1, 22) = 4.1$; $p = 0.05$). Post hoc analysis (paired samples t-test) revealed that VU-Matched controls were significantly faster at completing one model made of big blocks ($173.2 \pm 12.6s$) compared to one model made of small blocks ($230.7 \pm 21.2s$; $t(11) = -3.7$; $p = 0.003$). No such difference was found in the CB group, who completed one model made of big blocks in approximately the same time as one model made of small blocks ($178.1 \pm 16.9s$ and $195.2 \pm 20.1s$ respectively; $t(11) = -1.3$; $p = 0.1$).

Discussion (Experiment One)

Although the majority of the participants were congenitally blind ($n=10$), we recognize that two of them were late blind individuals. These individuals, however, reported suffering a lifetime of visual impairment, and had experienced total blindness for a significant number of years. Hand preference for grasping for these individuals was indistinguishable from that of CB individuals, and the results remained unaffected when the two participants are removed, thus they were included in the current study.

Overall the results yielded two interesting findings. First, CB participants preferred their right hand significantly more for grasping the blocks compared to the VU-Matched controls. Second, object size affected hand preference for grasping in both the CB and VU-Matched controls groups. Participants used the right hand more to grasp the big blocks when compared to the small blocks. This effect seen in haptically-guided grasping is opposite to what has previously been reported during visually-guided grasping. Thus, to contrast the effect that object size could have in haptically- versus visually-guided grasping, we tested a group of blindfolded young adult controls (VU-Blindfolded) and a group of sighted young adult controls (VU-Sighted). This last group was presented with the exact same task as the haptically-guided group but they completed the task using vision.

Experiment Two Methods and Procedures

Participants

A priori power analysis suggested that with power at 0.95, effect size of 0.7, and statistical significance set at 0.05, the current study would require a total sample size of 16 participants (G*Power 3.1.9.2). A total of 24 participants were recruited for this experiment.

VU-Blindfolded participants: Twelve self-reported right-handers (4 males) from the University of Lethbridge, between the ages of 19 and 31, participated. VU-Sighted participants: Twelve self-reported right-handed individuals (4 males) from the University of Lethbridge, between the ages of 19 and 23, participated. The study was approved by the University of Lethbridge Human Subjects Research Committee (protocol #2011-22) and all participants gave written informed consent in accordance with the Declaration of Helsinki. Participants were naïve to the purposes of the study.

Apparatus and Stimuli

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

Procedures

All procedures were identical to those in Experiment One, with one alteration: those in the VU-Sighted group did not wear a blindfold during the task. In turn, the task was haptically-guided (as in Experiment One) for the VU-Blindfolded group and visually-guided for the VU-Sighted group.

Data Analysis

Data analysis was the same as Experiment One. Bonferroni correction was applied to all multiple group comparisons.

Results (Experiment Two)

Handedness questionnaire

All participants self-reported as right-handers and this was confirmed by the handedness questionnaire. VU-Blindfolded: The average score was +30.4 (± 1.7 SE; range +21 to +39) out of a total possible score of -44/+44. VU-Sighted: The average score was +32.2 (± 1.9 SE; range +22 to +43) out of a total possible score of -44/+44. An independent samples t-test revealed that there was no significant difference between the two groups ($t(22) = -0.7$; $p = 0.4$).

Hand use for grasping

Analysis using a 2 (object size) X 2 (group) repeated measures ANOVA was performed on the percentage of right-hand use for grasping during the task. Object size (big, small) was a within subject factor and group (VU-Sighted, VU-Blindfolded) a between subject factor. There was no main effect of object size ($F(1, 22) = 0.4$; $p = 0.52$, $ES = 0.01$) but a main effect of group ($F(1, 22) = 13.8$; $p = 0.001$, $ES = 0.38$). Consistent with Stone and Gonzalez (2014), blindfolded participants used their right hand significantly less for grasping ($53.0 \pm 1.5\%$) than sighted individuals ($61.1 \pm 1.5\%$), regardless of object size. A significant interaction between object size and group was found ($F(1, 22) = 17.1$; $p < 0.0001$, $ES = 0.43$). Post hoc analysis (paired samples t-tests) revealed that, just as in Experiment One, VU-Blindfolded individuals used their right hand more to grasp big blocks ($56.5 \pm 1.5\%$) compared to small blocks ($49.6 \pm 1.2\%$; $t(11) = 3.1$; $p = 0.009$). However, VU-Sighted individuals used their right hand more to grasp small blocks ($63.6 \pm 1.6\%$) compared to big blocks ($58.6 \pm 2.5\%$; $t(11) = -2.6$; $p = 0.02$), as shown in Figure 2B. Noteworthy, the values of hand use for the VU-Blindfolded individuals were identical to those of the VU-Matched controls in Experiment One.

Contralateral grasps: Analysis using a 2 (object size) X 2 (hand) X 2 (group) repeated measures ANOVA was performed on the percentage of contralateral grasps made during the task. Object size (big, small) and hand (right, left) were within factors and group (VU-Blindfolded, VU-Sighted) the between factor. As in Experiment One, analyses did not show a significant effect of object size therefore data were collapsed across this variable ($F(1, 22) = 2.8$; $p = 0.1$, $ES = 0.11$). Therefore, a 2 (hand) X 2 (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 (VU-Blindfolded, VU-Sighted) a between subject factor. There was a main effect of hand ($F(1, 22) = 28.3$; $p < 0.0001$, $ES = 0.56$). Both groups made significantly more contralateral grasps with the right ($6.2 \pm 0.9\%$) versus the left ($0.9 \pm 0.3\%$) hand. There was a main effect of group ($F(1, 22) = 49.0$; $p < 0.0001$, $ES = 0.69$). The VU-Sighted group made significantly more contralateral grasps than the VU-Blindfolded group (6.0% versus 1.1%, respectively). The group by hand interaction was also significant ($F(1, 22) = 21.7$; $p < 0.0001$, $ES = 0.49$). Post hoc analysis (paired samples t-tests) revealed that the VU-Sighted group made significantly more right-handed grasps in the left contralateral space ($10.9 \pm 1.8\%$) than left-handed grasps in the right contralateral space ($0.8 \pm 0.3\%$; $t(11) = 5.2$; $p < 0.0001$). This was not the case for the VU-Blindfolded group ($1.5 \pm .4\%$ versus $0.8 \pm 0.3\%$; $t(11) = 1.1$; $p = 0.2$).

Build times for models

Given that the VU-Sighted group built the models substantially faster than the VU-Blindfolded group (likely due to visual availability; $p < 0.0001$), the two groups were compared separately. A paired samples t-test revealed that VU-Sighted participants completed the task with the big blocks significantly faster

than with the small blocks ($t(11) = -3.8$; $p = 0.003$). Participants completed one model made of big blocks in approximately 22.6 ± 0.9 s and one model made of small blocks in 25.7 ± 1.2 s. Similarly to the results of Experiment One, the VU-Blindfolded group completed one model made of big blocks significantly faster than one model made of small blocks ($t(11) = -2.7$; $p = 0.01$; Mean time = 128.3 ± 9.2 s and 153.6 ± 15.4 s for big and small blocks respectively).

Comparison between Experiment One and Experiment Two

We performed an analysis using a 2 (object size) X 4 (group) repeated measures ANOVA on the percentage of overall right-hand use for grasping. Object size (big, small) was a within subject factor and group (CB, VU-Matched controls, VU-Blindfolded, and VU-Sighted) a between subject factor. We found a main effect of size ($F(1, 44) = 17.0$; $p < 0.0001$, $ES = 0.28$). Again, participants used the right hand more often to grasp big ($58.6 \pm 1.0\%$), as opposed to small ($54.3 \pm 0.9\%$) blocks. There was also a main effect of group ($F(3, 44) = 7.1$; $p < 0.0001$, $ES = 0.32$). The CB group used their right hands significantly more for grasping than the VU-Blindfolded ($p = 0.05$) and the VU-Matched controls ($p = 0.02$). Interestingly, however, the CB group behaved similarly to the VU-Sighted group ($p = 1.0$). That is, both groups used their right hand to the same extent during the grasping task. Importantly, as depicted in Figure 3A, the VU-Matched controls and VU-Blindfolded groups differed from the VU-Sighted group ($p = 0.003$; $p = 0.009$, respectively). The VU-Matched controls and VU-Blindfolded group did not differ from each other ($p = 1.0$). The size by group interaction was also significant ($F(3, 44) = 9.2$; $p < 0.0001$, $ES = 0.38$). Post hoc analysis (independent samples t-test) revealed that the VU-Sighted group used the right hand significantly more than the VU-Blindfolded ($t(22) = -6.7$; $p < 0.0001$), VU-Matched controls ($t(22) = -6.9$; $p < 0.0001$), and CB ($t(22) = -2.3$; $p = 0.03$) groups when grasping small blocks. This was not the case for the big blocks, however (all comparisons $p > 0.1$). This result reflects the different effect that object size poses on haptically- versus visually-guided grasping, particularly for small objects. In other words, small objects were more often picked up with the right hand during visually-guided, but less often during haptically-guided grasping. This is not surprising as we have previously shown less pronounced right-hand use for grasping big blocks (Gonzalez & Goodale, 2009; Stone et al., 2013).

Contralateral grasps:

Analysis using a 2 (object size) X 2 (hand) X 4 (group) repeated measures ANOVA was performed on the percentage of contralateral grasps made during the task. Object size (big, small) and hand (right, left) were within factors and group (CB, VU-Matched controls, VU-Blindfolded, VU-Sighted) the between factor. Again, analyses did not show a significant effect of object size therefore data were collapsed across this variable ($F(1,44) = 3.0$; $p = 0.1$, $ES = 0.05$). Therefore, a 2 (hand) X 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 (CB, VU-Matched controls, VU-Blindfolded, VU-Sighted) a between subject factor. There was a main effect of hand ($F(1, 44) = 20.1$; $p < 0.0001$, $ES = 0.31$). Participants made significantly more right-handed grasps in the left contralateral space ($5.4 \pm 0.7\%$) compared to left-handed grasps in the right contralateral space ($1.7 \pm 0.3\%$). In other words, participants were more likely to reach across to the left contralateral space to grasp a block with the right hand compared to reaching into the right contralateral space to grasp a block with the left hand. There was a main effect of group ($F(3, 44) = 6.4$; $p = 0.001$, $ES = 0.30$). The VU-Sighted group made significantly more right-handed grasps in left contralateral space than the VU-Blindfolded ($p = 0.001$) and the VU-Matched controls ($p = 0.05$). No differences emerged between the VU-Sighted and CB groups ($p = 0.8$). The hand by group interaction was also significant ($F(3, 44) = 8.4$; $p < 0.0001$, $ES = 0.36$). Post hoc analysis (paired samples t-tests) revealed that the VU-Sighted group made significantly more right-handed grasps in the left contralateral space ($10.9 \pm 1.8\%$) than left-handed grasps in the right contralateral space ($1.0 \pm 0.5\%$; $t(11) = 5.2$; $p < 0.0001$). The CB also made significantly more right-handed grasps in the left contralateral space ($6.1 \pm 2.0\%$) than left-handed grasps in the right contralateral space ($1.6 \pm 0.5\%$; $t(11) = 2.2$; $p = 0.04$). However, this was not the case for the VU-Matched controls ($2.4 \pm 1.0\%$ versus $3.3 \pm 0.9\%$; $t(11) = -0.6$; $p = 0.55$) nor for the VU-Blindfolded group (1.5 ± 1.5 versus $0.8 \pm 1.2\%$; $t(11) = 1.1$; $p = 0.27$; see Figure 3B). Furthermore, independent samples t-test revealed that the VU-Matched controls made significantly more left-handed grasps in the right contralateral space than the VU-Blindfolded (3.3% versus 0.8% ; $t(22) = 2.4$; $p = 0.02$). All remaining comparisons between hand and group were not significant. To emphasize, independent samples t-test results showed no significant difference in percentage of right-handed grasps completed in the left contralateral space between the CB and the VU-Sighted group ($t(22) = -1.4$) $p > 0.1$). Thus, in terms of grasping in contralateral space, the CB group displayed similar behaviour to the VU-Sighted group.

General Discussion

The present study had two main goals: first, to document hand preference for grasping in a congenitally blind (CB) population and second, to investigate how object properties, specifically object size, would influence hand preference during haptically-guided grasping. CB and visually unimpaired (VU: Sighted and Blindfolded/Matched controls) individuals were asked to replicate 3D models using small or large blocks scattered on a tabletop. Results showed that CB individuals exhibit a right-hand preference for grasping, and this preference was significantly greater than the VU-Matched controls and VU-Blindfolded group. Furthermore, this right-hand preference in CB individuals was not different from the VU-Sighted group, which was further confirmed by the analysis of contralateral grasps. These results suggest that, regardless of visual experience, hand preference for grasping is lateralized to the right hand. A second finding was the influence that object size exerted on hand preference. Consistent with previous studies (Gonzalez & Goodale, 2009; Stone et al., 2013) VU-Sighted participants used their right hand more often to grasp the small, as opposed to the big blocks. However, when blindfolded, VU participants demonstrated the opposite pattern: they

preferred their right hand to grasp the big, versus the small, blocks. This result was also seen in the CB participants. Overall, these findings suggest first, a left-hemisphere specialization for grasping regardless of lifetime visual *or* haptic experience; and second, that object properties such as size pose different demands on visually- versus haptically-guided grasping.

Studies exploring hand use in blind individuals have focused on haptically-guided tasks such as reading Braille (Grant, Thiagarajah, & Sathian, 2000; Hermelin & O'Connor, 1971; Millar, 1987) or identifying: geometrical shapes (Theurel, Frileux, Hatwell, & Gentaz, 2012; Withagen et al., 2013), tactile pictures (Heller, Calcaterra, Burson, & Tyler, 1996; Lederman, Klatzky, Chataway, & Summers, 1990; Theurel, Witt, Claudet, Hatwell, & Gentaz, 2013), or spatial targets (Collignon & De Volder, 2009). These studies have highlighted the ability, and in some cases, the advantage that CB individuals exhibit over VU participants during tactile recognition tasks. In some studies, this advantage was specific to one hand. For example, when CB participants were asked to read Braille they were more proficient when using their left hand (Hermelin & O'Connor, 1971). Another study showed that when sorting different objects, CB individuals were faster with their left hand than VU participants were with either hand (Ittyerah, 2000). None of these studies however, specifically investigated hand preference for grasping in CB adults. In the present investigation, we document CB individuals' right-hand preference for grasping. Interestingly, this right-hand preference was similar to that of sighted individuals when using vision. A previous study has shown a reduction of right-hand use during haptically-guided grasping in VU individuals (Stone & Gonzalez, 2014) which was replicated in the current study. CB participants however, used their right hand to the same extent as the sighted VU participants. In fact, the analysis of contralateral grasps confirmed that CB behave virtually identical to VU-Sighted individuals in terms of hand use. When reaching across the midline, both groups showed a marked right-hand preference over the left for grasping the blocks. These results suggest that the mechanisms of hand preference for grasping develop *independently* of visual experience. In an investigation of hand preference and ability in CB children, Ittyerah suggests that hand preference might not be determined by vision (Ittyerah, 2009). Furthermore, based on 39 neuroimaging studies, Ricciardi, Bonino, Pellegrini, and Pietrini (2013) argue that brain functional organization is to a large extent independent from visual experience. For example, sighted and CB individuals were asked to tactically recognize different objects (bottles, shoes, and masks of faces) while brain activation was measured through functional MRI (Pietrini et al., 2004). The results showed that category-relative object activation in occipito-temporal areas (ventral stream), was similar for sighted and CB individuals. Likewise, overlapping activation patterns in the dorsal stream have been shown during kinesthetically guided hand movements in both sighted and CB individuals (Fiehler, Burke, Bien, Roder, & Rosler, 2009). Our results of hand use during grasping are in line with these previous studies in that CB individuals behaved virtually identical to sighted individuals.

Another finding of the present investigation was the effect that object size exerted on hand preference during grasping. Studies have shown that the kinematics of prehensile movements are contingent upon object size. Movement time, peak velocity and grip

apertures all respond to changes in object size. For instance, the larger the object to be grasped, the longer it takes to reach maximum grip aperture (Connolly & Goodale, 1999; Jakobson & Goodale, 1991; Paulignan, Frak, Toni, & Jeannerod, 1997). When reaching for smaller objects, individuals exhibit lower and earlier peak velocities and longer deceleration phases when compared to reaching for larger objects (Gentilucci et al., 1991; Heath, Hodges, Chua, & Elliott, 1998; Kudoh, Hattori, Numata, & Maruyama, 1997; Marteniuk, Leavitt, MacKenzie, & Athenes, 1990). Interestingly, grip scaling in blind individuals is accurate and indistinguishable from sighted individuals when reaching for different sized objects (Castiello et al., 1993). These results illustrate how object size influences kinematics of reaching and grasping, even in the absence of vision. With respect to hand preference, previous investigations (Gonzalez & Goodale, 2009; Stone et al., 2013) have also highlighted the influence of object size and have shown that when grasping small objects, there is an increase in right-hand use. In the current investigation we replicated this finding for visually-guided grasping. Interestingly, during haptically-guided grasping, both CB and VU individuals used the right hand more often for grasping the large objects. This finding suggests that object characteristics affect patterns of hand use differently for haptically- versus visually-guided grasping.

We offer two non-mutually exclusive explanations for this phenomenon. First, it is possible that, as we have argued before (Stone & Gonzalez, 2014), hand use during haptically-guided grasping could be influenced by the known advantage of this hand for haptic discrimination. Several studies have shown a left-hand advantage for object discrimination when guided by haptics (Benton, Levin, & Varney, 1973; Dodds, 1978; Fagot, Hopkins, & Vauclair, 1993; Heller & Joyner, 1993; Milner & Taylor, 1972; O'Boyle et al., 1987; Riege, Metter, & Williams, 1980; Squeri et al., 2012; Tomlinson et al., 2011; Varney & Benton, 1975). For instance, Benton et al. (1973) applied tactile stimulation to the hands of individuals and asked them to identify the direction of the stimulus. Participants were significantly more accurate when the stimulation was applied to their left hand. In a series of experiments, Fagot and colleagues have demonstrated a left-hand superiority for recognizing shapes when given a discrimination task. Accordingly, they also found a left-hand advantage in terms of overall time the left hand explored the given objects for these tasks (Fagot, Hopkins, et al., 1993; Fagot, Lacreuse, & Vauclair, 1993, 1994). Fagot's results demonstrate that the left hand is better at encoding haptic information. Support for this evidence was provided via personal communication with the CB individuals in the present study. Upon reviewing the CB testimonials collected during and after our visit we encountered two statements that speak to this matter. When asking the participants if one hand was better for touch, one individual responded, "Well... I might look for more detail with the left". A second CB individual responded to the question similarly: "My left hand is more focused towards the two fingers, feeling the spatial [properties of the object], and I use my right hand to pick up [the object]." It appears then, that there is a division of labour between the hands when identifying (left hand) and grasping (right hand) an object that one cannot see.

The second possibility that could have contributed to the object size effect is the initial grasp formation. A previous study has shown facilitation of right-handed responses for pincer grasps (i.e. thumb and index finger) and facilitation of left-handed responses for power grasps (Vainio et al., 2006). Similarly, it has been shown that visually-guided

grasps requiring more precision (pincer grasping) are more often executed with the right hand as opposed to grasps that require the whole hand (i.e. power grasps), even in left-handers (Begliomini, Nelini, Caria, Grodd, & Castiello, 2008; Gonzalez & Goodale, 2009; Stone et al., 2013). In the current experiments we observed that all haptically-guided reaching movements (regardless of the block's size) exhibited an extension of all five fingers (see Figure 1C and 1D) resembling a power grasp (see (Karl, Schneider, & Whishaw, 2013) for similar results). It is possible that this power grasp formation, which favours left-handed grasps, affected the selection of hand use while grasping the small blocks. In fact, Overvliet, Anema, Brenner, Dijkerman, and Smeets (2011) found that individuals were better at localizing tactile stimuli when the fingers were spread apart (similar to a power grasp formation) compared to when they were close together. We speculate that the decrease in right-hand use seen for haptically-guided grasping stems in part from an increase of left-hand use during haptic discrimination, particularly for the small objects. Although this might not explain the increase in right-hand use seen when grasping the *big* blocks, it provides a preliminary explanation for change in hand use for grasping the small blocks. Furthermore, it remains unknown if these findings would persist in a population of left-handed individuals, which is a limitation of the current study. These possibilities warrant further investigation.

In conclusion, the results indicate that visual availability, but not visual experience, determines hand use in response to object size. Furthermore, the results suggest a left-hemisphere/right-hand specialization for grasping, regardless of visual experience.

References

- Begliomini, C., Nelini, C., Caria, A., Grodd, W., & Castiello, U. (2008). Cortical activations in humans grasp-related areas depend on hand used and handedness. *PLoS ONE*, *3*(10), e3388. doi: 10.1371/journal.pone.0003388
- Bennett, K. M., Mucignat, C., Waterman, C., & Castiello, U. (1994). Vision and the reach to grasp movement. In K. M. Bennett & U. Castiello (Eds.), *Insights into the reach to grasp movement* (pp. 390). North-Holland: Elsevier Science B.V.
- Benton, A. L., Levin, H. S., & Varney, N. R. (1973). Tactile perception of direction in normal subjects: Implications for hemispheric cerebral dominance. *Neurology*, *23*(11), 1248-1250. doi: 10.1212/WNL.23.11.1248
- Benton, A. L., Varney, N. R., & Hamsher, K. S. (1978). Lateral differences in tactile directional perception. *Neuropsychologia*, *16*(1), 109-114.
- Bishop, D. V., Ross, V. A., Daniels, M. S., & Bright, P. (1996). The measurement of hand preference: A validation study comparing three groups of right-handers. *British Journal of Psychology*, *87* (Pt 2), 269-285. doi: 10.1111/j.2044-8295.1996.tb02590.x
- Brown, S. G., Roy, E. A., Rohr, L. E., & Bryden, P. J. (2006). Using hand performance measures to predict handedness. *Laterality*, *11*(1), 1-14. doi: 10.1080/1357650054200000440
- Bryden, P. J., & Roy, E. A. (2006). Preferential reaching across regions of hemispace in adults and children. *Developmental Psychobiology*, *48*(2), 121-132. doi: 10.1002/dev.20120
- Caliskan, E., & Dane, S. (2009). Left-handedness in blind and sighted children. *Laterality*, *14*(2), 205-213. doi: 10.1080/13576500802586251
- Calvert, G. A., & Bishop, D. V. (1998). Quantifying hand preference using a behavioural continuum. *Laterality*, *3*(3), 255-268. doi: 10.1080/713754307
- Carlier, M., Doyen, A. L., & Lamard, C. (2006). Midline crossing: Developmental trend from 3 to 10 years of age in a preferential card-reaching task. *Brain and Cognition*, *61*(3), 255-261. doi: 10.1016/j.bandc.2006.01.007
- Castiello, U., Bennett, K. M., & Mucignat, C. (1993). The reach to grasp movement of blind subjects. *Experimental Brain Research*, *96*(1), 152-162. doi: 10.1007/BF00230448
- Collignon, O., & De Volder, A. G. (2009). Further evidence that congenitally blind participants react faster to auditory and tactile spatial targets. *Canadian Journal of Experimental Psychology*, *63*(4), 287-293. doi: 10.1037/a0015415
- Connolly, J. D., & Goodale, M. A. (1999). The role of visual feedback of hand position in the control of manual prehension. *Experimental Brain Research*, *125*(3), 281-286.
- Cormier, J. M., & Tremblay, F. (2013). Asymmetry in corticomotor facilitation revealed in right-handers in the context of haptic discrimination. *Laterality*, *18*(3), 365-383. doi: 10.1080/1357650x.2012.701631
- Dodds, A. G. (1978). Hemispheric differences in tactuo-spatial processing. *Neuropsychologia*, *16*(2), 247-250. doi: 10.1016/0028-3932(78)90115-X
- Fagot, J., Hopkins, W. D., & Vauclair, J. (1993). Hand movements and hemispheric specialization in dichhaptic explorations. *Perception*, *22*(7), 847-853. doi: 10.1068/p220847

- Fagot, J., Lacreuse, A., & Vauclair, J. (1993). Haptic discrimination of nonsense shapes: Hand exploratory strategies but not accuracy reveal laterality effects. *Brain and Cognition*, 21(2), 212-225. doi: 10.1006/brcg.1993.1017
- Fagot, J., Lacreuse, A., & Vauclair, J. (1994). Hand-movement profiles in a tactual-tactual matching task: Effects of spatial factors and laterality. *Perception & Psychophysics*, 56(3), 347-355. doi: 10.3758/BF03209768
- Fiehler, K., Burke, M., Bien, S., Roder, B., & Rosler, F. (2009). The human dorsal action control system develops in the absence of vision. *Cerebral Cortex*, 19(1), 1-12. doi: 10.1093/cercor/bhn067
- Gabbard, C., Helbig, C. R., & Gentry, V. (2001). Lateralized effects on reaching by children. *Developmental Neuropsychology*, 19(1), 41-51. doi: 10.1207/s15326942dn1901_4
- Gabbard, C., Tapia, M., & Helbig, C. R. (2003). Task complexity and limb selection in reaching. *The International Journal of Neuroscience*, 113(2), 143-152. doi: 10.1080/00207450390161994
- Gentilucci, M., Castiello, U., Corradini, M. L., Scarpa, M., Umiltà, C., & Rizzolatti, G. (1991). Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia*, 29(5), 361-378.
- Gonzalez, C. L., & Goodale, M. A. (2009). Hand preference for precision grasping predicts language lateralization. *Neuropsychologia*, 47(14), 3182-3189. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2009.07.019>
- Gonzalez, C. L., Whitwell, R. L., Morrissey, B., Ganel, T., & Goodale, M. A. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, 182(2), 275-279. doi: 10.1007/s00221-007-1090-1
- Grant, A. C., Thiagarajah, M. C., & Sathian, K. (2000). Tactile perception in blind Braille readers: A psychophysical study of acuity and hyperacuity using gratings and dot patterns. *Perception & Psychophysics*, 62(2), 301-312.
- Harada, T., Saito, D. N., Kashikura, K., Sato, T., Yonekura, Y., Honda, M., & Sadato, N. (2004). Asymmetrical neural substrates of tactile discrimination in humans: A functional magnetic resonance imaging study. *The Journal of Neuroscience*, 24(34), 7524-7530. doi: 10.1523/jneurosci.1395-04.2004
- Heath, M., Hodges, N. J., Chua, R., & Elliott, D. (1998). On-line control of rapid aiming movements: Unexpected target perturbations and movement kinematics. *Canadian Journal of Experimental Psychology*, 52(4), 163-173.
- Heller, M. A., Calcaterra, J. A., Burson, L. L., & Tyler, L. A. (1996). Tactual picture identification by blind and sighted people: Effects of providing categorical information. *Perception & Psychophysics*, 58(2), 310-323. doi: 10.3758/BF03211884
- Heller, M. A., & Joyner, T. D. (1993). Mechanisms in the haptic horizontal-vertical illusion: Evidence from sighted and blind subjects. *Perception & Psychophysics*, 53(4), 422-428.
- Hermelin, B., & O'Connor, N. (1971). Functional asymmetry in the reading of Braille. *Neuropsychologia*, 9(4), 431-435. doi: 10.1016/0028-3932(71)90007-8
- Ittyerah, M. (1993). Hand preferences and hand ability in congenitally blind children. *The Quarterly Journal of Experimental Psychology*, 46(1), 35-50.

- Ittyerah, M. (2000). Hand skill and hand preference in blind and sighted children. *Laterality*, 5(3), 221-235. doi: 10.1080/713754379
- Ittyerah, M. (2009). Hand ability and practice in congenitally blind children. *Journal of Developmental and Physical Disabilities*, 21(5), 329-344. doi: 10.1007/s10882-009-9146-8
- Jackson, S. R., Jackson, G. M., & Rosicky, J. (1995). Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. *Experimental Brain Research*, 102(3), 519-530. doi: 10.1007/BF00230656
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research*, 86(1), 199-208. doi: 10.1007/BF00231054
- Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: The cortical mechanisms of visuomotor transfer. *Trends in Neuroscience*, 18(7), 314-320. doi: 10.1016/0166-2236(95)93921-j
- Karl, J. M., Schneider, L. R., & Whishaw, I. Q. (2013). Nonvisual learning of intrinsic object properties in a reaching task dissociates grasp from reach. *Experimental Brain Research*, 225(4), 465-477. doi: 10.1007/s00221-012-3386-z
- Kudoh, N., Hattori, M., Numata, N., & Maruyama, K. (1997). An analysis of spatiotemporal variability during prehension movements: Effects of object size and distance. *Experimental Brain Research*, 117(3), 457-464.
- Kumar, S. (1977). Short term memory for a nonverbal tactual task after cerebral commissurotomy. *Cortex*, 13(1), 55-61. doi: 10.1016/S0010-9452(77)80053-1
- Lederman, S. J., Klatzky, R. L., Chataway, C., & Summers, C. D. (1990). Visual mediation and the haptic recognition of two-dimensional pictures of common objects. *Perception & Psychophysics*, 47(1), 54-64.
- Marteniuk, R. G., Leavitt, J. L., MacKenzie, C. L., & Athenes, S. (1990). Functional relationships between grasp and transport components in a prehension task. *Human Movement Science*, 9(2), 149-176. doi: [http://dx.doi.org/10.1016/0167-9457\(90\)90025-9](http://dx.doi.org/10.1016/0167-9457(90)90025-9)
- Millar, S. (1987). The perceptual "window" in two-handed braille: Do the left and right hands process text simultaneously? *Cortex*, 23(1), 111-122.
- Milner, B., & Taylor, L. (1972). Right-hemisphere superiority in tactile pattern-recognition after cerebral commissurotomy: Evidence for nonverbal memory. *Neuropsychologia*, 10(1), 1-15. doi: 10.1016/0028-3932(72)90038-3
- O'Boyle, M. W., Van Wyhe-Lawler, F., & Miller, D. A. (1987). Recognition of letters traced in the right and left palms: Evidence for a process-oriented tactile asymmetry. *Brain and Cognition*, 6(4), 474-494. doi: 10.1016/0278-2626(87)90141-2
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97-113.
- Overvliet, K. E., Anema, H. A., Brenner, E., Dijkerman, H. C., & Smeets, J. B. (2011). Relative finger position influences whether you can localize tactile stimuli. *Experimental Brain Research*, 208(2), 245-255. doi: 10.1007/s00221-010-2475-0

- Paulignan, Y., Frak, V. G., Toni, I., & Jeannerod, M. (1997). Influence of object position and size on human prehension movements. *Experimental Brain Research*, *114*(2), 226-234.
- Pettypiece, C. E., Culham, J. C., & Goodale, M. A. (2009). Differential effects of delay upon visually and haptically guided grasping and perceptual judgments. *Experimental Brain Research*, *195*(3), 473-479. doi: 10.1007/s00221-009-1807-4
- Pietrini, P., Furey, M. L., Ricciardi, E., Gobbini, M. I., Wu, W. H., Cohen, L., . . . Haxby, J. V. (2004). Beyond sensory images: Object-based representation in the human ventral pathway. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(15), 5658-5663. doi: 10.1073/pnas.0400707101
- Rand, M. K., Lemay, M., Squire, L. M., Shimansky, Y. P., & Stelmach, G. E. (2007). Role of vision in aperture closure control during reach-to-grasp movements. *Experimental Brain Research*, *181*(3), 447-460. doi: 10.1007/s00221-007-0945-9
- Ricciardi, E., Bonino, D., Pellegrini, S., & Pietrini, P. (2013). Mind the blind brain to understand the sighted one! Is there a supramodal cortical functional architecture? *Neuroscience and Biobehavioral Reviews*. doi: 10.1016/j.neubiorev.2013.10.006
- Riege, W. H., Metter, E. J., & Williams, M. V. (1980). Age and hemispheric asymmetry in nonverbal tactual memory. *Neuropsychologia*, *18*(6), 707-710. doi: 10.1016/0028-3932(80)90112-8
- Sacrey, L. A., Karl, J. M., & Whishaw, I. Q. (2012). Development of rotational movements, hand shaping, and accuracy in advance and withdrawal for the reach-to-eat movement in human infants aged 6-12 months. *Infant Behavior & Development*, *35*(3), 543-560. doi: 10.1016/j.infbeh.2012.05.006
- Schettino, L. F., Adamovich, S. V., & Poizner, H. (2003). Effects of object shape and visual feedback on hand configuration during grasping. *Experimental Brain Research*, *151*(2), 158-166. doi: 10.1007/s00221-003-1435-3
- Squeri, V., Sciutti, A., Gori, M., Masia, L., Sandini, G., & Konczak, J. (2012). Two hands, one perception: How bimanual haptic information is combined by the brain. *Journal of Neurophysiology*, *107*(2), 544-550. doi: 10.1152/jn.00756.2010
- Stone, K. D., Bryant, D. C., & Gonzalez, C. L. (2013). Hand use for grasping in a bimanual task: Evidence for different roles? *Experimental Brain Research*, *224*(3), 455-467. doi: 10.1007/s00221-012-3325-z
- Stone, K. D., & Gonzalez, C. L. (2014). Grasping with the eyes of your hands: Haptics and vision modulate hand preference. *Experimental Brain Research*, *232*(2), 385-393. doi: 10.1007/s00221-013-3746-3
- Theurel, A., Frileux, S., Hatwell, Y., & Gentaz, E. (2012). The haptic recognition of geometrical shapes in congenitally blind and blindfolded adolescents: Is there a haptic prototype effect? *PLoS ONE*, *7*(6), e40251. doi: 10.1371/journal.pone.0040251
- Theurel, A., Witt, A., Claudet, P., Hatwell, Y., & Gentaz, E. (2013). Tactile picture recognition by early blind children: The effect of illustration technique. *Journal of Experimental Psychology. Applied*, *19*(3), 233-240. doi: 10.1037/a0034255
- Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin*, *121*(1), 20-42. doi: 10.1037/0033-2909.121.1.20

- Tomlinson, S. P., Davis, N. J., Morgan, H. M., & Bracewell, R. M. (2011). Hemispheric specialisation in haptic processing. *Neuropsychologia*, *49*(9), 2703-2710. doi: 10.1016/j.neuropsychologia.2011.05.018
- Vainio, L., Ellis, R., Tucker, M., & Symes, E. (2006). Manual asymmetries in visually primed grasping. *Experimental Brain Research*, *173*(3), 395-406. doi: 10.1007/s00221-006-0378-x
- Varney, N. R., & Benton, A. L. (1975). Tactile perception of direction in relation to handedness and familial handedness. *Neuropsychologia*, *13*(4), 449-454. doi: [http://dx.doi.org/10.1016/0028-3932\(75\)90068-8](http://dx.doi.org/10.1016/0028-3932(75)90068-8)
- Winges, S. A., Weber, D. J., & Santello, M. (2003). The role of vision on hand preshaping during reach to grasp. *Experimental Brain Research*, *152*(4), 489-498. doi: 10.1007/s00221-003-1571-9
- Withagen, A., Kappers, A. M., Vervloed, M. P., Knoors, H., & Verhoeven, L. (2013). The use of exploratory procedures by blind and sighted adults and children. *Attention, Perception & Psychophysics*. doi: 10.3758/s13414-013-0479-0
- Woods, A. T., & Newell, F. N. (2004). Visual, haptic and cross-modal recognition of objects and scenes. *Journal of Physiology Paris*, *98*(1-3), 147-159. doi: 10.1016/j.jphysparis.2004.03.006

APPENDIX 3

Manual preferences for visually- and haptically-guided grasping*

* **Stone, K. D.**, & Gonzalez, C. L. (2015a). Manual preferences for visually- and haptically-guided grasping. *Acta Psychologica*, *160*, 1-10. doi: 10.1016/j.actpsy.2015.06.004

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).

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, 1993). 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; P. J. Bryden & Roy, 2006; Calvert & Bishop, 1998; Gabbard & Rabb, 2000; Gonzalez & Goodale, 2009; Jacquet, Esseily, Rider, & Fagard, 2012; Stone, Bryant, & Gonzalez, 2013; Stone & Gonzalez, 2014a). 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; Keyzers, 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?

We recently investigated this question using the block building task (Gonzalez & Goodale, 2009; Stone et al., 2013; Stone & Gonzalez, 2014a, 2014b) 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, 2014b). 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 et al. 1987, including Braille: e.g. Hermelin and O'Connor 1971, Wilkinson and 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, 1993; Fagot, Lacreuse, & Vauclair, 1993), 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, 2014b), 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, 2002; 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 et al. 2007; Stone et al. 2013; Stone and Gonzalez 2014a) . 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)

Methods and Procedures

2.1. 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.

2.2. Apparatus and Stimuli

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.

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 x 0.7 W x 1.0 cm H to 3.1 L x 1.5 W x 1.0 cm H. Each model contained 10 blocks of various colours and shapes (see supplementary material for a picture of models used). Scattered on a table (122 L x 122 W x 74 cm H with a working space of 70 L x 122 W x 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 (19L x 19cm 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).

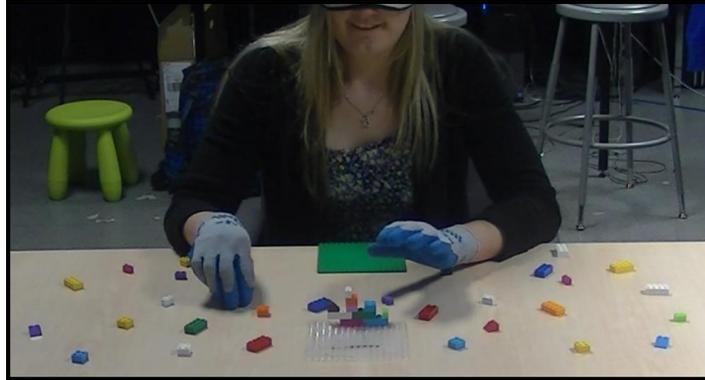


Fig. 1 Photograph of a participant in the NV/Constrained-H group completing the task. Please note that the participant is wearing a blindfold as well as a pair of gloves. The model to be replicated is located on the clear plate. Using the blocks on the table, the participant will complete a replica of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

2.3. 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 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 160cm away from the individual with a clear view of the tabletop, building blocks, and participants' hands.

2.4. 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 X 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 & Shapiro-Wilk) 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 (P. J. Bryden & Huszczyński, 2011; P.

J. Bryden, Pryde, & Roy, 2000; P. J. Bryden & Roy, 2006; Cavill & Bryden, 2003; de Bruin, Bryant, & Gonzalez, 2014; Sacrey, Arnold, Whishaw, & Gonzalez, 2013; Stone et al., 2013; Stone & Gonzalez, 2014a, 2014b).

Results

2.5. 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 ($F(3, 79) = 0.7$; $p = 0.5$).

2.6. 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 ($M = 24.8 \pm 0.8s$ versus $M = 35.0 \pm 1.7s$, ($t(38) = -5.3$; $p < 0.0001$)). **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 ($M = 160.8 \pm 11.5s$ versus $M = 313.6 \pm 14.7s$, ($t(38) = -8.1$; $p < 0.0001$)). 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).

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.

Right-handers			
Visual Availability	Group	Mean (sec)	Standard Error (sec)
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

** $p < 0.0001$

2.7. 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 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 ($81.2 \pm 3.3\%$) significantly more than the V/H group ($63.5 \pm 1.6\%$), the NV/H group ($51.3 \pm 1.2\%$), and the NV/Constrained-H group ($58.2 \pm 1.7\%$; $p < 0.0001$ 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.

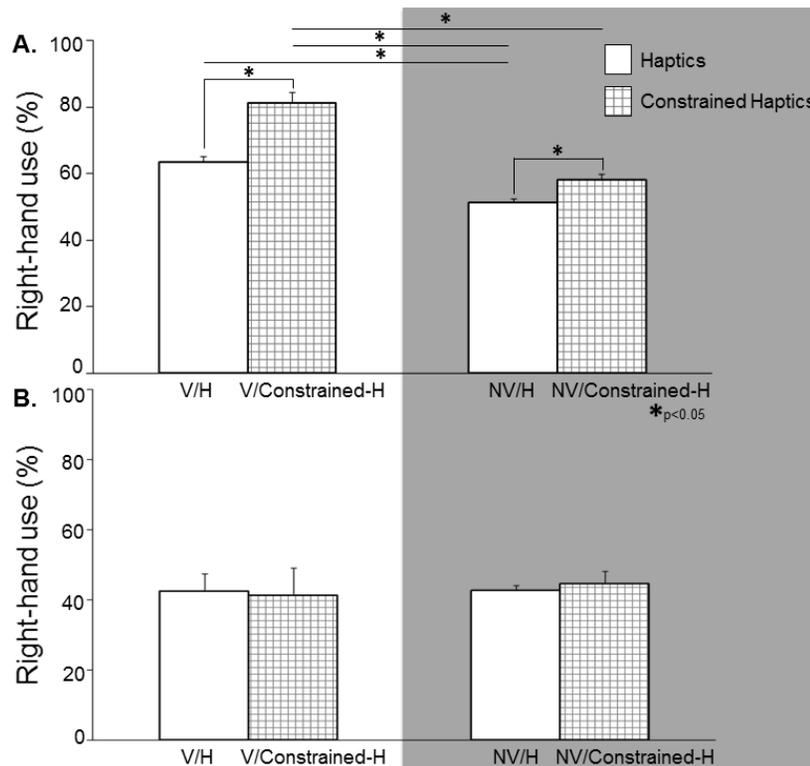


Fig. 2 A) Overall hand use in right-handers: This graph demonstrates right-hand use for all four groups (V/H, V/Constrained-H, NV/H, NV/Constrained-H) in Experiment One. White bars represent the groups who had normal haptics for the duration of the task (V/H, NV/H). The bars filled with the grey grid 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 grey background) represent 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.

Comparison to 50%: To examine if hand use for grasping was significantly different from chance (Gonzalez et al. 2007 and Stone and 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.

2.8. Analysis of contralateral grasps

Analysis using a 2 (hand) X 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 ($12.7 \pm 1.0\%$) than left-handed grasps into right contralateral space ($1.0 \pm 0.2\%$). 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 ($15.4 \pm 1.0\%$) than the V/H ($7.7 \pm 1.0\%$), NV/H ($1.7 \pm 1.0\%$), and NV/Constrained-H ($2.8 \pm 1.0\%$) 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 ($30.3 \pm 2.0\%$) than the V/H ($13.8 \pm 2.0\%$), NV/H ($2.0 \pm 2.0\%$), and NV/Constrained-H ($4.8 \pm 2.0\%$) groups ($p < 0.0001$ 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 vision reduces contralateral grasps. See Fig. 3A for these results.

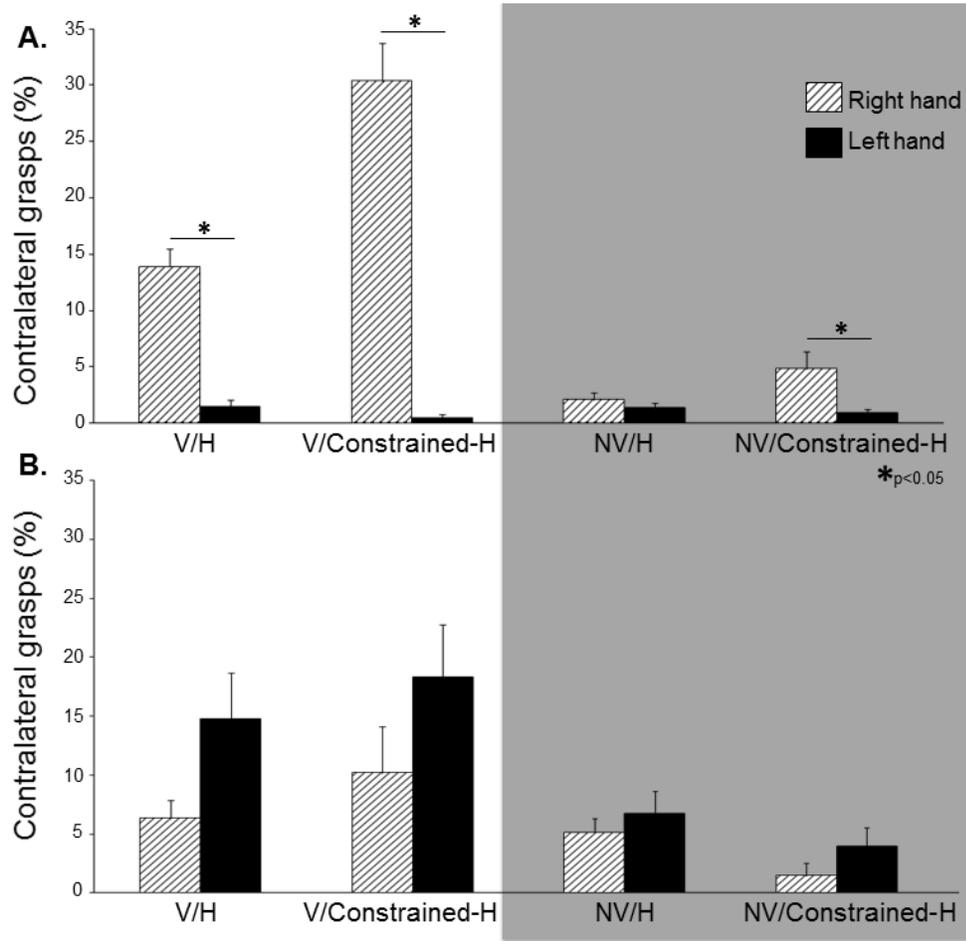


Fig. 3 A) Contralateral grasps in right-handers: The following graphs demonstrate right- and left-handed contralateral grasps for all four groups (V/H, V/Constrained-H, NV/H, NV/Constrained-H) in Experiment One. The bars filled with the diagonal pattern represent the right-hand. The bars filled with 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 grey background) represent 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.

2.9. 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, Ganel, & Goodale, 2006; Gonzalez & Goodale, 2009; Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Goodale, 1988; Janssen, Meulenbroek, & Steenbergen, 2011; Netelenbos & Gonzalez, 2015; Serrien, Ivry, & Swinnen, 2006; Stone et al., 2013).

3. Experiment Two (Left-handers)

Methods and Procedures

3.1. 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.

3.2. Apparatus and Stimuli

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

3.3. Procedures

All procedures were identical to those used in Experiment One.

3.4. Data Analysis

Data analysis was the same as Experiment One.

Results

3.5. 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 ($F(3, 59) = 0.1$; $p = 0.9$).

3.6. 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 ($M = 21.2 \pm 4.8s$ versus $M = 31.8 \pm 4.6s$, ($t(28) = -6.0$; $p < 0.0001$). **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 ($M = 166.3 \pm 16.1s$ versus $M = 303.6 \pm 24.0s$, ($t(28) = -4.7$; $p < 0.0001$). 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.

3.7. 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.

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.

3.8. Analysis of contralateral grasps

Analysis using a 2 (hand) X 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 ($10.9 \pm 1.5\%$) than right-handed grasps into left contralateral space ($5.7 \pm 1.1\%$). 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 ($14.2 \pm 1.4\%$) than the NV/H ($5.8 \pm 1.4\%$) and NV/Constrained-H ($2.7 \pm 1.4\%$) groups ($p = 0.006$ and $p < 0.0001$, respectively), but not the V/H ($10.5 \pm 1.4\%$) 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, 2014b) 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 et al., 2006; Gonzalez & Goodale, 2009; Gonzalez et al., 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, et al., 1993; Fagot, Lacreuse, et al., 1993; 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; P. J. Bryden & Huszczyński, 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 (M. P. Bryden, Hecaen, & DeAgostini, 1983; Gur et al., 1982; Levy & Reid, 1978; Mazoyer et al., 2014; Steinmetz, Volkman, 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.

References

- Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology*, 61(3), 303-321.
- Atkinson, J. (2002). *The developing visual brain*. Oxford: Oxford University Press.
- Babinsky, E., Braddick, O., & Atkinson, J. (2012). The effect of removing visual information on reach control in young children. *Experimental Brain Research*, 222(3), 291-302. doi: 10.1007/s00221-012-3216-3
- Benton, A. L., Levin, H. S., & Varney, N. R. (1973). Tactile perception of direction in normal subjects: Implications for hemispheric cerebral dominance. *Neurology*, 23(11), 1248-1250. doi: 10.1212/WNL.23.11.1248
- Bishop, D. V., Ross, V. A., Daniels, M. S., & Bright, P. (1996). The measurement of hand preference: A validation study comparing three groups of right-handers. *British Journal of Psychology*, 87 (Pt 2), 269-285. doi: 10.1111/j.2044-8295.1996.tb02590.x
- Brown, S. G., Roy, E. A., Rohr, L. E., & Bryden, P. J. (2006). Using hand performance measures to predict handedness. *Laterality*, 11(1), 1-14. doi: 10.1080/1357650054200000440
- Bryden, M. P., Hecaen, H., & DeAgostini, M. (1983). Patterns of cerebral organization. *Brain and Language*, 20(2), 249-262.
- Bryden, P. J., & Huszczyński, J. (2011). Under what conditions will right-handers use their left hand? The effects of object orientation, object location, arm position, and task complexity in preferential reaching. *Laterality*, 16(6), 722-736. doi: 10.1080/1357650x.2010.514344
- Bryden, P. J., Pryde, K. M., & Roy, E. A. (2000). A performance measure of the degree of hand preference. *Brain and Cognition*, 44(3), 402-414. doi: 10.1006/brcg.1999.1201
- Bryden, P. J., & Roy, E. A. (2006). Preferential reaching across regions of hemispace in adults and children. *Developmental Psychobiology*, 48(2), 121-132. doi: 10.1002/dev.20120
- Calvert, G. A., & Bishop, D. V. (1998). Quantifying hand preference using a behavioural continuum. *Laterality*, 3(3), 255-268. doi: 10.1080/713754307
- Cannon, A., & Benton, A. L. (1969). Tactile perception of direction and number in patients with unilateral cerebral disease. *Neurology*, 19(6), 525. doi: 10.1212/wnl.19.6.525
- Carey, D. P., & Hutchinson, C. V. (2013). Looking at eye dominance from a different angle: Is sighting strength related to hand preference? *Cortex*, 49(9), 2542-2552. doi: 10.1016/j.cortex.2012.11.011
- Castiello, U. (2005). The neuroscience of grasping. *Nature Reviews Neuroscience*, 6(9), 726-736. doi: 10.1038/nrn1744
- Cavill, S., & Bryden, P. (2003). Development of handedness: Comparison of questionnaire and performance-based measures of preference. *Brain and Cognition*, 53(2), 149-151. doi: 10.1016/S0278-2626(03)00098-8
- Cormier, J. M., & Tremblay, F. (2013). Asymmetry in corticomotor facilitation revealed in right-handers in the context of haptic discrimination. *Laterality*, 18(3), 365-383. doi: 10.1080/1357650x.2012.701631

- de Bruin, N., Bryant, D. C., & Gonzalez, C. L. (2014). "Left neglected," but only in far space: Spatial biases in healthy participants revealed in a visually guided grasping task. *Frontiers in Neurology*, 5, 4. doi: 10.3389/fneur.2014.00004
- De Renzi, E., Faglioni, P., & Scotti, G. (1969). Impairment of memory for position following brain damage. *Cortex*, 5(3), 274-284. doi: 10.1016/S0010-9452(69)80035-3
- Dodds, A. G. (1978). Hemispheric differences in tactuo-spatial processing. *Neuropsychologia*, 16(2), 247-250. doi: 10.1016/0028-3932(78)90115-X
- Elias, L. J., & Saucier, D. M. (2006). *Neuropsychology: Clinical and experimental foundations*: Pearson/Allyn & Bacon.
- Fagot, J., Hopkins, W. D., & Vauclair, J. (1993). Hand movements and hemispheric specialization in dichhaptic explorations. *Perception*, 22(7), 847-853. doi: 10.1068/p220847
- Fagot, J., Lacreuse, A., & Vauclair, J. (1993). Haptic discrimination of nonsense shapes: Hand exploratory strategies but not accuracy reveal laterality effects. *Brain and Cognition*, 21(2), 212-225. doi: 10.1006/brcg.1993.1017
- Flindall, J. W., Stone, K. D., & Gonzalez, C. L. R. (2014). Evidence for right-hand feeding biases in a left-handed population. *Laterality: Asymmetries of Body, Brain and Cognition*, 1-19. doi: 10.1080/1357650X.2014.961472
- Fontenot, D. J., & Benton, A. L. (1971). Tactile perception of direction in relation to hemispheric locus of lesion. *Neuropsychologia*, 9(1), 83-88. doi: 10.1016/0028-3932(71)90065-0
- Gabbard, C., & Rabb, C. (2000). What determines choice of limb for unimanual reaching movements? *The Journal of General Psychology*, 127(2), 178-184. doi: 10.1080/00221300009598577
- Gonzalez, C. L., Ganel, T., & Goodale, M. A. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of Neurophysiology*, 95(6), 3496-3501. doi: 10.1152/jn.01187.2005
- Gonzalez, C. L., & Goodale, M. A. (2009). Hand preference for precision grasping predicts language lateralization. *Neuropsychologia*, 47(14), 3182-3189. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2009.07.019>
- Gonzalez, C. L., Whitwell, R. L., Morrissey, B., Ganel, T., & Goodale, M. A. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, 182(2), 275-279. doi: 10.1007/s00221-007-1090-1
- Goodale, M. A. (1983). Vision as a sensorimotor system. In T. E. Robinson (Ed.), *Behavioral Approaches to Brain Research* (pp. 41-61). New York: Oxford University Press.
- Goodale, M. A. (1988). Hemispheric differences in motor control. *Behavioural Brain Research*, 30(2), 203-214. doi: 10.1016/0166-4328(88)90149-0
- Grunwald, M. (2008). *Human haptic perception: Basics and applications*. Basel, Boston, Berlin: Birkhäuser.
- Gur, R. C., Gur, R. E., Obrist, W. D., Hungerbuhler, J. P., Younkin, D., Rosen, A. D., . . . Reivich, M. (1982). Sex and handedness differences in cerebral blood flow during rest and cognitive activity. *Science*, 217(4560), 659-661.
- Harada, T., Saito, D. N., Kashikura, K., Sato, T., Yonekura, Y., Honda, M., & Sadato, N. (2004). Asymmetrical neural substrates of tactile discrimination in humans: A

- functional magnetic resonance imaging study. *The Journal of Neuroscience*, 24(34), 7524-7530. doi: 10.1523/jneurosci.1395-04.2004
- Heller, M. A., Rogers, G. J., & Perry, C. L. (1990). Tactile pattern recognition with the Optacon: Superior performance with active touch and the left hand. *Neuropsychologia*, 28(9), 1003-1006. doi: 10.1016/0028-3932(90)90114-4
- Hermelin, B., & O'Connor, N. (1971). Functional asymmetry in the reading of Braille. *Neuropsychologia*, 9(4), 431-435. doi: 10.1016/0028-3932(71)90007-8
- Ittyerah, M. (1993). Hand preferences and hand ability in congenitally blind children. *The Quarterly Journal of Experimental Psychology*, 46(1), 35-50.
- Ittyerah, M. (2009). Hand ability and practice in congenitally blind children. *Journal of Developmental and Physical Disabilities*, 21(5), 329-344. doi: 10.1007/s10882-009-9146-8
- Jackson, S. R., Jackson, G. M., & Rosicky, J. (1995). Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. *Experimental Brain Research*, 102(3), 519-530. doi: 10.1007/BF00230656
- Jacquet, A. Y., Esseily, R., Rider, D., & Fagard, J. (2012). Handedness for grasping objects and declarative pointing: A longitudinal study. *Developmental Psychobiology*, 54(1), 36-46. doi: 10.1002/dev.20572
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research*, 86(1), 199-208. doi: 10.1007/BF00231054
- Janssen, L., Meulenbroek, R. G., & Steenbergen, B. (2011). Behavioral evidence for left-hemisphere specialization of motor planning. *Experimental Brain Research*, 209(1), 65-72. doi: 10.1007/s00221-010-2519-5
- Judge, J., & Stirling, J. (2003). Fine motor skill performance in left- and right-handers: Evidence of an advantage for left-handers. *Laterality*, 8(4), 297-306. doi: 10.1080/13576500342000022
- Karl, J. M., Sacrey, L. A., Doan, J. B., & Whishaw, I. Q. (2012). Hand shaping using haptics resembles visually guided hand shaping. *Experimental Brain Research*, 219(1), 59-74. doi: 10.1007/s00221-012-3067-y
- Keefe, B. D., & Watt, S. J. (2009). The role of binocular vision in grasping: A small stimulus-set distorts results. *Experimental Brain Research*, 194(3), 435-444. doi: 10.1007/s00221-009-1718-4
- Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, 11(6), 417-428. doi: 10.1038/nrn2919
- Klatzky, R. L., Loomis, J. M., Lederman, S. J., Wake, H., & Fujita, N. (1993). Haptic identification of objects and their depictions. *Perception & Psychophysics*, 54(2), 170-178.
- Kolb, B., & Whishaw, I. Q. (2001). *An introduction to brain and behavior*: Worth Publishers.
- Kolb, B., & Whishaw, I. Q. (2009). *Fundamentals of human neuropsychology*: Macmillan.
- Lakatos, S., & Marks, L. E. (1999). Haptic form perception: Relative salience of local and global features. *Perception & Psychophysics*, 61(5), 895-908.

- Lederman, S. J., & Klatzky, R. L. (2004). Haptic identification of common objects: Effects of constraining the manual exploration process. *Perception & Psychophysics*, *66*(4), 618-628.
- Lederman, S. J., & Klatzky, R. L. (2009). Haptic perception: A tutorial. *Attention, Perception & Psychophysics*, *71*(7), 1439-1459. doi: 10.3758/app.71.7.1439
- Lederman, S. J., Klatzky, R. L., Chataway, C., & Summers, C. D. (1990). Visual mediation and the haptic recognition of two-dimensional pictures of common objects. *Perception & Psychophysics*, *47*(1), 54-64.
- Levy, J., & Reid, M. (1978). Variations in cerebral organization as a function of handedness, hand posture in writing, and sex. *Journal of Experimental Psychology: General*, *107*(2), 119.
- Mazoyer, B., Zago, L., Jobard, G., Crivello, F., Joliot, M., Percey, G., . . . Tzourio-Mazoyer, N. (2014). Gaussian mixture modeling of hemispheric lateralization for language in a large sample of healthy individuals balanced for handedness. *PLoS ONE*, *9*(6), e101165.
- Michel, G. F. (1981). Right-handedness: A consequence of infant supine head-orientation preference? *Science*, *212*(4495), 685-687. doi: 10.1126/science.7221558
- Milner, B., & Taylor, L. (1972). Right-hemisphere superiority in tactile pattern-recognition after cerebral commissurotomy: Evidence for nonverbal memory. *Neuropsychologia*, *10*(1), 1-15. doi: 10.1016/0028-3932(72)90038-3
- Morange-Majoux, F. (2011). Manual exploration of consistency (soft vs hard) and handedness in infants from 4 to 6 months old. *Laterality*, *16*(3), 292-312. doi: 10.1080/13576500903553689
- Netelenbos, N., & Gonzalez, C. L. (2015). Is that graspable? Let your right hand be the judge. *Brain and Cognition*, *93*, 18-25. doi: 10.1016/j.bandc.2014.11.003
- O'Boyle, M. W., Van Wyhe-Lawler, F., & Miller, D. A. (1987). Recognition of letters traced in the right and left palms: Evidence for a process-oriented tactile asymmetry. *Brain and Cognition*, *6*(4), 474-494. doi: 10.1016/0278-2626(87)90141-2
- Ocklenburg, S., Burger, C., Westermann, C., Schneider, D., Biedermann, H., & Gunturkun, O. (2010). Visual experience affects handedness. *Behavioural Brain Research*, *207*(2), 447-451. doi: 10.1016/j.bbr.2009.10.036
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97-113.
- Rand, M. K., Lemay, M., Squire, L. M., Shimansky, Y. P., & Stelmach, G. E. (2007). Role of vision in aperture closure control during reach-to-grasp movements. *Experimental Brain Research*, *181*(3), 447-460. doi: 10.1007/s00221-007-0945-9
- Riege, W. H., Metter, E. J., & Williams, M. V. (1980). Age and hemispheric asymmetry in nonverbal tactual memory. *Neuropsychologia*, *18*(6), 707-710. doi: 10.1016/0028-3932(80)90112-8
- Rock, I., & Victor, J. (1964). Vision and touch: An experimentally created conflict between the two senses. *Science*, *143*(3606), 594-596.
- Sacrey, L. A., Arnold, B., Wishaw, I. Q., & Gonzalez, C. L. (2013). Precocious hand use preference in reach-to-eat behavior versus manual construction in 1- to 5-year-old children. *Developmental Psychobiology*, *55*(8), 902-911. doi: 10.1002/dev.21083

- Saunders, J. A., & Knill, D. C. (2003). Humans use continuous visual feedback from the hand to control fast reaching movements. *Experimental Brain Research*, *152*(3), 341-352. doi: 10.1007/s00221-003-1525-2
- Schettino, L. F., Adamovich, S. V., & Poizner, H. (2003). Effects of object shape and visual feedback on hand configuration during grasping. *Experimental Brain Research*, *151*(2), 158-166. doi: 10.1007/s00221-003-1435-3
- Serrien, D. J., Ivry, R. B., & Swinnen, S. P. (2006). Dynamics of hemispheric specialization and integration in the context of motor control. *Nature Reviews Neuroscience*, *7*(2), 160-166. doi: 10.1038/nrn1849
- Squeri, V., Sciutti, A., Gori, M., Masia, L., Sandini, G., & Konczak, J. (2012). Two hands, one perception: How bimanual haptic information is combined by the brain. *Journal of Neurophysiology*, *107*(2), 544-550. doi: 10.1152/jn.00756.2010
- Steinmetz, H., Volkman, J., Jancke, L., & Freund, H. J. (1991). Anatomical left-right asymmetry of language-related temporal cortex is different in left- and right-handers. *Annals of Neurology*, *29*(3), 315-319. doi: 10.1002/ana.410290314
- Stone, K. D., Bryant, D. C., & Gonzalez, C. L. (2013). Hand use for grasping in a bimanual task: Evidence for different roles? *Experimental Brain Research*, *224*(3), 455-467. doi: 10.1007/s00221-012-3325-z
- Stone, K. D., & Gonzalez, C. L. (2014a). Grasping with the eyes of your hands: Haptics and vision modulate hand preference. *Experimental Brain Research*, *232*(2), 385-393. doi: 10.1007/s00221-013-3746-3
- Stone, K. D., & Gonzalez, C. L. (2014b). Grasping without sight: Insights from the congenitally blind. *PLoS ONE*, *9*(10), e110175. doi: 10.1371/journal.pone.0110175
- Szaflarski, J. P., Binder, J. R., Possing, E. T., McKiernan, K. A., Ward, B. D., & Hammeke, T. A. (2002). Language lateralization in left-handed and ambidextrous people: fMRI data. *Neurology*, *59*(2), 238-244.
- Tapley, S. M., & Bryden, M. P. (1985). A group test for the assessment of performance between the hands. *Neuropsychologia*, *23*(2), 215-221.
- Tomlinson, S. P., Davis, N. J., Morgan, H. M., & Bracewell, R. M. (2011). Hemispheric specialisation in haptic processing. *Neuropsychologia*, *49*(9), 2703-2710. doi: 10.1016/j.neuropsychologia.2011.05.018
- Tremblay, L., Hansen, S., Kennedy, A., & Cheng, D. T. (2013). The utility of vision during action: Multiple visuomotor processes? *Journal of Motor Behavior*, *45*(2), 91-99. doi: 10.1080/00222895.2012.747483
- Westwood, D. A., Heath, M., & Roy, E. A. (2003). No evidence for accurate visuomotor memory: Systematic and variable error in memory-guided reaching. *Journal of Motor Behavior*, *35*(2), 127-133. doi: 10.1080/00222890309602128
- Wilkinson, J. M., & Carr, T. H. (1987). Strategic hand use preferences and hemispheric specialization in tactual reading: Impact of the demands of perceptual encoding. *Brain and Language*, *32*(1), 97-123. doi: 10.1016/0093-934X(87)90119-2
- Willems, R. M., Van der Haegen, L., Fisher, S. E., & Francks, C. (2014). On the other hand: Including left-handers in cognitive neuroscience and neurogenetics. *Nature Reviews Neuroscience*, *15*(3), 193-201. doi: 10.1038/nrn3679

- Wing, A. M., Turton, A., & Fraser, C. (1986). Grasp size and accuracy of approach in reaching. *Journal of Motor Behavior*, 18(3), 245-260. doi: 10.1080/00222895.1986.10735380
- Winges, S. A., Weber, D. J., & Santello, M. (2003). The role of vision on hand preshaping during reach to grasp. *Experimental Brain Research*, 152(4), 489-498. doi: 10.1007/s00221-003-1571-9
- Yahagi, S., & Kasai, T. (1999). Motor evoked potentials induced by motor imagery reveal a functional asymmetry of cortical motor control in left- and right-handed human subjects. *Neuroscience Letters*, 276(3), 185-188.
- Zaidel, D., & Sperry, R. W. (1973). Performance on the raven's colored progressive matrices test by subjects with cerebral commissurotomy. *Cortex*, 9(1), 34-39. doi: [http://dx.doi.org/10.1016/S0010-9452\(73\)80015-2](http://dx.doi.org/10.1016/S0010-9452(73)80015-2)

APPENDIX 4

Sensory Modulation of Hand Preference for Grasping in Children*

* **Stone K.D.**, Gonzalez C.L.R. (2015). Sensory modulation of hand preference grasping in children. Submitted to *Journal of Experimental Child Psychology*

Abstract

Studies on the development of handedness have demonstrated a right-hand preference for grasping in pre-schoolers. But what factors contribute to the development of this right-hand preference? Since grasping an object requires processing visual and haptic information, sensory feedback must play a pivotal role in the establishment of hand preference. Recent studies on right-handed adults have shown a right-hand preference for visually-guided grasping, but an increased preference to use the left hand for haptically-guided grasping. This result suggests distinct hemispheric specializations for sensory processing that guide hand selection for grasping. However, little is known about the development of such specializations. We asked children (5-8 years old) to replicate 3D models from a tabletop of building blocks under different sensory (visual or haptic) conditions and recorded the hand used to grasp each block. Results showed clear differences in hand preference for grasping when vision was occluded or haptics was constrained: a right-hand preference for visually-guided grasping, and a significant increase in left-hand use for haptically-guided grasping. The results support the view of hemispheric asymmetries in sensory processing for grasping which is apparent as early as five years of age. Moreover, the results suggest that hand preference for grasping develops from the interplay between the visual and haptic systems.

Introduction

Handedness is one of the most widely studied cerebral asymmetries. A salient and observable component of handedness is preference, which refers to the hand favoured for completing actions (e.g. grasping an object; Gabbard & Rabb 2000). Hand preference for grasping has been used as a model to investigate the development of cerebral asymmetries. Babies will begin to reach as early as 12 weeks of age (Hopkins & Prechtl, 1984; Claes von Hofsten, 1984) and to grasp around 5 months (C. von Hofsten, 1983; Wallace & Whishaw, 2003). A right-hand preference for grasping has been reported in numerous developmental studies (Cavill & Bryden, 2003; Fagard & Marks, 2000; Ferre, Babik, & Michel, 2010; Gesell & Ames, 1947; Hinojosa, Sheu, & Michel, 2003; Jacobsohn, Rodrigues, Vasconcelos, Corbetta, & Barreiros, 2014; Kotwica, Ferre, & Michel, 2008; Marschik et al., 2008; Michel, 1981; Michel, Tyler, Ferre, & Sheu, 2006; Nelson, Campbell, & Michel, 2013; Ramsay, 1980; Sacrey, Arnold, Whishaw, & Gonzalez, 2013). This preference has been documented in infants between 6-18 months of age (Carlson & Harris, 1985; Corbetta & Thelen, 1999; Fagard, 1998; Fagard & Lockman, 2005; Ferre et al., 2010; Hinojosa et al., 2003; Jacobsohn et al., 2014; Jacquet, Esseily, Rider, & Fagard, 2012; McCormick & Maurer, 1988; Michel, Ovrut, & Harkins, 1985; Michel et al., 2006; Morange-Majoux, Peze, & Bloch, 2000; Nelson et al., 2013; Ronnqvist & Domellof, 2006; Sacrey et al., 2013). Yet, it appears that consistent preference for the right hand is not robust until around four or five years of age (Bryden & Roy, 2006; Gesell & Ames, 1947; C. L. Gonzalez, Flindall, & Stone, 2015; Hill & Khanem, 2009; McManus et al., 1988; Sacrey et al., 2013). The studies investigating the development of hand preference have asked children to pick up: toys (Fagard & Marks, 2000; Ramsay, 1980), building blocks (C. L. Gonzalez et al., 2015; C. L. Gonzalez et al., 2014; Sacrey et al., 2013), food (Kastner-Koller, Diemann, & Bruckner, 2007; Marschik et al., 2008; Sacrey et al., 2013), geometrical shapes (Kotwica et al., 2008), and tools (Marschik et al., 2008; McManus et al., 1988). These actions are visually-guided. Grasping, however, is multisensory in nature, insofar that both visual and haptic cues are used to complete the action (Buckingham, Ranger, & Goodale, 2012; Castiello, 2005; Chang, Flanagan, & Goodale, 2008; Endo, Wing, & Bracewell, 2011; Kritikos & Beresford, 2002; Pettypiece, Goodale, & Culham, 2010; Stone & Gonzalez, 2014a). Although these developmental reports emphasize a right-hand preference for visually-guided actions, the contributions of the haptic system to this development are largely unknown.

Some studies have investigated the development of haptics (the integration of cutaneous and kinesthetic feedback during object manipulation) in infants and children. One study showed that pre-term infants are able to haptically identify wooden objects placed in their hand (only tested the left hand) in the first few days of life (Marcus, Lejeune, Berne-Audeoud, Gentaz, & Debillon, 2012). By three months of age, infants can haptically discriminate between object properties such as hardness or softness (Rochat, 1987). Yet, it is not until around five years of age that most children display a developed strategy for identifying objects using touch alone (Hoop, 1971).

With respect to hand preference for haptic processing, infants as young as two months of age will retain haptic information better if it is exposed to the left versus the

right hand (Lhote & Streri, 1998). Moreover, at four months of age infants will display a left-hand preference for “feeling” (touching and manipulating) objects (Morange-Majoux, 2011). Some studies have also shown this left-hand haptic advantage during cross-modal transfer (haptics to vision). Rose (1984) asked 2- and 3-year-olds to visually identify objects that the child had previously explored haptically with either the right or left hand, and found better recognition when the object had been explored with the left hand. In fact, some of the oldest reports on hand superiority for haptics revealed that children aged 6-12 years show an advantage for visually identifying objects that were previously manipulated with the left, rather than the right, hand (D. F. Witelson, 1976; S. F. Witelson, 1974). Moreover, Goble, Lewis, Hurvitz, and Brown (2005) demonstrated that children are better with their left arm at matching passively-guided arm movements, emphasizing the role of the right hemisphere in haptic feedback. In sum, these studies suggest a left-hand/right-hemisphere specialization for haptic processing. None of these studies however, have investigated how this left-hand advantage for haptics influences hand preference for grasping.

In adults, studies have shown that hand preference for grasping is modulated by both vision and haptics (Stone & Gonzalez, 2014a, 2014b). In a recent study (Stone & Gonzalez, 2015), young adults were asked to replicate block models from a tabletop while sighted (vision and haptics are available), sighted and wearing a pair of textured, fitted gloves (vision available but haptics constrained) or solely blindfolded (haptics available). Participants displayed a right-hand preference for grasping while sighted (~65%), a substantial increase in right-hand use when haptics was constrained (~80%) and no preference when blindfolded (~50%). These results demonstrate how manipulating sensory information modulates hand preference for grasping. What remains unknown is whether this sensory modulation is present in children. In the present study, right-handed children between 5-8 years of age were tested on the “block-building task” (C. L. Gonzalez & Goodale, 2009; C. L. Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Stone, Bryant, & Gonzalez, 2013; Stone & Gonzalez, 2014a, 2014b). Similar to Stone and Gonzalez (2015) participants were asked to replicate block models from a tabletop of evenly distributed building blocks. Each child completed the task under three separate sensory conditions: 1) while sighted (Vision/Haptics), 2) while sighted and wearing a pair of gloves (Vision/Constrained-Haptics), and 3) while blindfolded (No Vision/Haptics). Hand preference for grasping the blocks in ipsilateral and contralateral space was documented for all trials. We predicted that if these visual and haptic asymmetries are present early in development, then children should show similar hand preferences for grasping as adults do in response to changes in sensory information.

Methods and Procedures

1.1. Participants

Thirty-two right-handed (by parent or guardian report) children (16 males) between the ages of 5 and 8 years were recruited from the community of Lethbridge for this study. An equal number of children ($n = 8$) in each age group (5-, 6-, 7-, and 8-years-old) took part in the study. The parent or guardian of each child gave written informed consent in accordance with the Declaration of

Helsinki and the approval of the University of Lethbridge Human Subjects Research Committee (protocol #2014-046) before participating in the study. Participants were naïve to the purposes of the study and able to withdraw at any time without consequence.

1.2. Apparatus and Stimuli

Handedness Questionnaire: A modified version of the Edinburgh (Oldfield, 1971) and Waterloo (Brown, Roy, Rohr, & Bryden, 2006) handedness questionnaires were given to the parent or guardian of all children during the testing session. This version included questions on hand preference for 17 different tasks. Parents/guardians had to rate which hand their child preferred 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, 0, -1, or -2) and a total score was obtained by adding all values. Possible scores range from +34 for exclusive right-hand use to -34 for exclusive left-hand use.

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 x 0.7 W x 1.0 cm H to 3.1 L x 1.5 W x 1.0 cm H. Each model contained 10 blocks of various colours and four different shapes. Scattered on a table (60L x 120 W x 55 cm H with a working space of 45 L x 65 W x 55 cm H) were all the blocks (n = 30) that made up the three models. The models were prepared ahead of time by the experimenter. The same three models were used with all children and for all three parts of the study. The same number of blocks was placed on the left and right side of the table. There was a fixed building plate (19L x 19cm W) the front and center of the child. The plate served as a location for the construction of the new model and/or placement of the blocks while blindfolded. See Figure 1 for set-up.



Figure 1. Photograph of task set-up for the three sensory conditions: (A) Vision/Haptics; (B) Vision/Constrained-Haptics (note the child is wearing a pair of gloves); (C) No Vision/Haptics (note the child is wearing a blindfold).

1.3. Procedures

Children were seated in front of the table facing the middle of the display. Each child completed the same three block models under three different sensory

conditions (Vision/Haptics, Vision/Constrained-Haptics, No Vision/Haptics). The presentation of models was counterbalanced within children and the starting order of sensory condition was counterbalanced between children. During the Vision/Haptics (V/H) condition, a 3D block model (sample) was placed centrally, approximately at arm's length away from the child. The children were encouraged to build with the available blocks in order to make a model that looked exactly like the sample. They were asked to build it as quickly as they could but to pay attention to detail. Once the model was replicated, both models were removed from the table and a new model was given. Children were praised for their work at the end of each replication. No blocks were replaced after each model was completed. For the Vision/Constrained Haptics (V/Constrained-H) condition, the child put on a pair of child-sized gardening gloves (to constrain haptic input) prior to the initiation of the task. Besides that manipulation, procedures for the V/Constrained-H trials were the same as for the V/H trials. For the No Vision/Haptics (NV/H) condition, the child put on a blindfold (to occlude visual input) prior to the initiation of the task. Because in a pilot sample children had great difficulties replicating the model without vision, in this condition, the experimenter called out the blocks that made up each model, one shape at a time (e.g. square). The children were then asked to haptically locate and grasp the shape, and to bring it to the building plate in the front of them (i.e. same location that the models in V/H and V/Constrained-H were built). After the 10 blocks that made a model were placed on the building plate, these were cleared and the next trial started. The same thirty blocks that made up the three models in V/H and V/Constrained-H were haptically identified and picked up during the NV/H condition.

All tasks were recorded on a JVC HD Everio video recorder approximately 160cm away from the individual with a clear view of the tabletop, building blocks, and participants' hands.

1.4. Data Analysis

All recorded videos were analyzed offline. Each grasp was recorded as a left or right hand grasp in the child's ipsilateral or contralateral space. The total number of grasps was calculated to determine a percent for right-hand use (number of right grasps/total number of grasps X 100). The time in which it took participants to construct each model was recorded on a stopwatch and reported in seconds. Data were assessed and no violations for homogeneity of variance and normality were found prior to analysis. Partial Eta Squared values were used to show effect size (ES). Data were analyzed using SPSS Statistics 18.0 for Windows (SPSS Inc., Chicago, IL, USA). Bonferroni correction was applied to comparisons where applicable.

Results

1.5. Handedness questionnaire

All participants were right-handed and this was confirmed by the handedness questionnaire filled out by the parent or guardian. The average score was 24.5 ± 1.0 (ranging from 14 to 34) of a total possible score of +34/-34.

1.6. Overall hand use for grasping

Analysis using a 2 (Sex) X 4 (Age Group) X 3 (Sensory Condition) repeated measures ANOVA was performed on the percentage of right-hand use for grasping during the task. Sex (male, female) and Age Group (5-, 6-, 7-, or 8-years-old) were the between subject factors and Sensory Condition (V/H, V/Constrained-H, NV/H) was the within subject factor. There was no main effect of Sex ($F(1, 24) = 0.4$; $p = 0.5$, $ES = 0.01$) or Age Group ($F(3, 24) = 0.2$; $p = 0.8$, $ES = 0.02$). There was, however, a main effect of Sensory Condition ($F(2, 48) = 43.2$; $p < 0.0001$, $ES = 0.64$). During the V/H condition, children used their right hand significantly more for grasping ($68.1 \pm 2.7\%$) compared to the NV/H condition (51.9 ± 2.1 ; $p < 0.0001$) but significantly *less* for grasping compared to the V/Constrained-H group ($76.6 \pm 2.5\%$; $p = 0.005$; see Figure 2A). The comparison between the NV/H versus the V/Constrained-H group was also significant ($p < 0.0001$). No interactions reached significance ($p > 0.2$ for all comparisons).

1.7. Analysis of contralateral grasps

Because there were no main effects of sex or age group nor any significant interactions in hand use for grasping ($p > 0.6$ for all analyses), these factors were collapsed for analysis of contralateral grasps. Therefore, analysis using a 2 (Hand) X 3 (Sensory Condition) repeated measures ANOVA on the percentage of contralateral grasps made during the task was performed. Hand (right, left) and Sensory Condition (V/H, V/Constrained-H, NV/H) were the within subject factors. There was a main effect of Hand ($F(1, 31) = 56.9$; $p < 0.001$, $ES = 0.64$), in that the children made significantly more right-handed grasps into left contralateral space than left-handed grasps into right contralateral space ($19.4 \pm 1.6\%$ versus $3.9 \pm 0.5\%$, respectively). There was a main effect of Sensory Condition ($F(2, 62) = 26.8$; $p < 0.001$, $ES = 0.46$), in that children made significantly more contralateral grasps during the V/Constrained-H condition ($15.7 \pm 1.0\%$) compared to the V/H ($11.8 \pm 1.0\%$; $p = 0.001$) and NV/H ($7.5 \pm 0.6\%$; $p < 0.0001$) conditions. Contralateral grasps made in V/H condition were also different when compared to the NV/H condition ($p = 0.003$). The Hand X Sensory Condition interaction was also significant ($F(2, 62) = 36.6$; $p < 0.0001$, $ES = 0.54$). Post-hoc analyses (paired-samples t-test) revealed that children made significantly more right-handed grasps in the left contralateral space during the V/Constrained-H ($28.2 \pm 2.3\%$) than during the V/H ($20.1 \pm 2.2\%$; $t(31) = -4.1$; $p < 0.0001$) and the NV/H ($9.9 \pm 1.4\%$; $t(31) = 7.9$; $p < 0.0001$). This was not the case for the left hand, which showed similar percentage of contralateral grasps regardless of sensory condition ($p > 0.05$ for all comparisons). See Figure 2B.

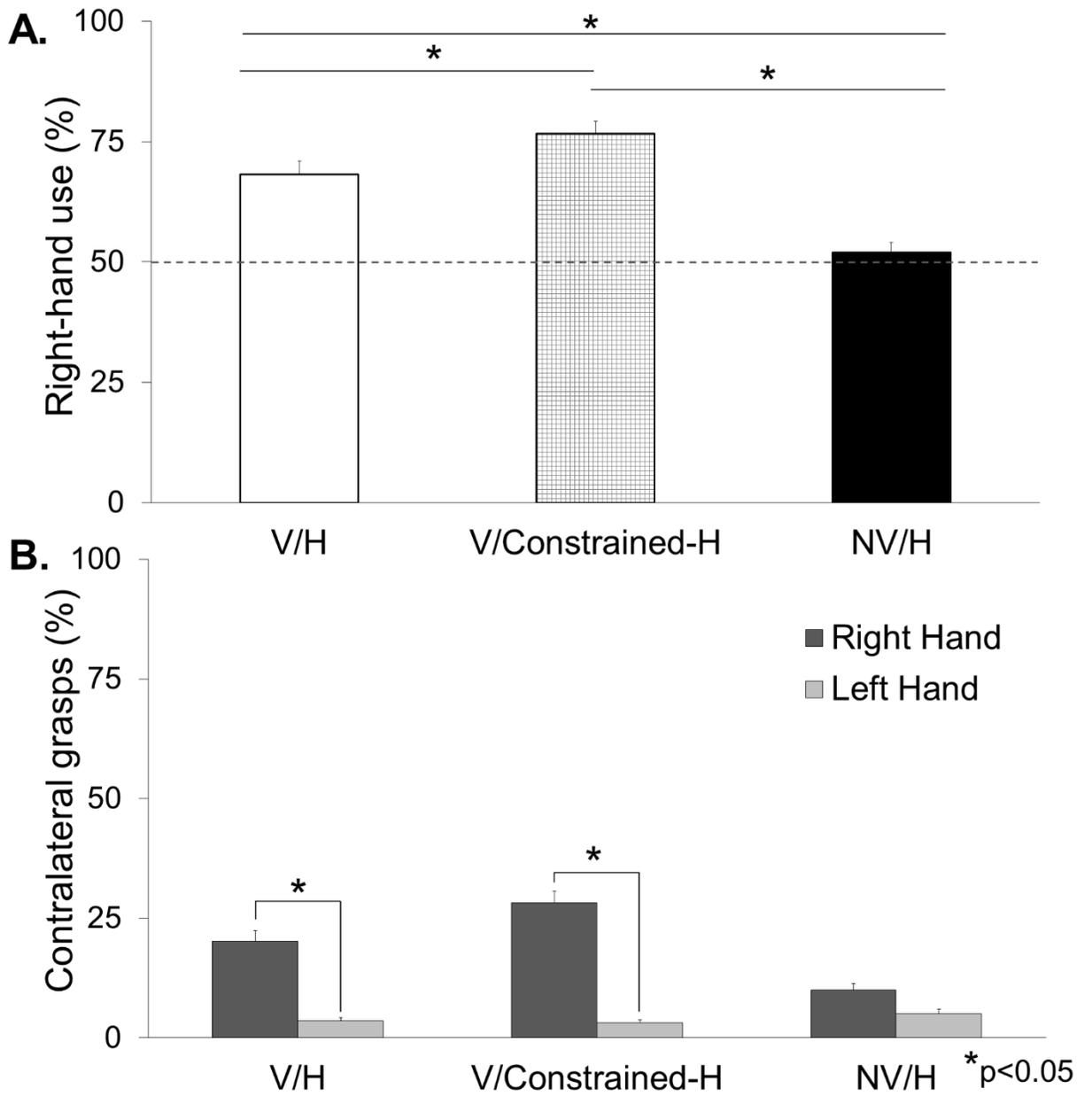


Figure 2. (A) Graph demonstrating right-hand use in percentage for the three conditions: V/H, V/Constrained-H, and NV/H. The dashed grey line denotes 50% right-hand use. Note the significant difference in hand use across all three

conditions. **(B)** Graph demonstrating percentage of contralateral grasps for the three conditions. Dark grey bars represent the right hand and light grey bars represent the left hand. Note that significant difference between the hands for the visually-guided, but not the haptically-guided, portions of the task.

1.8. Build times for models

Analysis using a 2 (Sex) X 4 (Age Group) X 3 (Sensory Condition) repeated measures ANOVA was performed on the average time it took (in seconds) to complete one model. Sex (male, female) and Age Group (5-, 6-, 7-, or 8-years-old) were the between subject factors and Sensory Condition (V/H, V/Constrained-H, NV/H) was the within subject factor. There was no main effect of Sex ($F(1, 24) = 0.7; p = 0.3, ES = 0.03$). There was a main effect of Age Group ($F(3, 24) = 6.2; p = 0.003, ES = 0.44$), in that the 5-year-olds were significantly slower at completing the tasks ($98.5 \pm 5.9s$) compared to both the 7- ($71.1 \pm 5.7s, p = 0.01$) and 8-year-olds ($65.5 \pm 5.7s, p = 0.003$), but not the 6-year-olds ($83.1 \pm 5.9s, p = 0.4$). The 6-year-olds were not different from the 7- ($p = 0.9$) or 8- (0.2) year-olds. Moreover, the 7-year-olds were not different from the 8-year-olds ($p = 1.0$). There was also a main effect of Sensory Condition ($F(2, 48) = 86.5; p < 0.0001, ES = 0.78$), in that children were significantly slower at completing the task during the blindfolded trials (NV/H; $103.2 \pm 3.1s$) when compared to the V/H ($55.3 \pm 2.8s$) and the V/Constrained-H ($80.2 \pm 3.1s$) trials. Time to complete the V/H and V/Constrained-H trials were also significantly different ($p < 0.0001$ for all pairwise comparisons). The interaction between Sensory Condition and Age Group was also significant ($F(6, 48) = 3.2; p = 0.009, ES = 0.29$). Post-hoc analyses (independent samples t-tests) revealed that the 8-year-olds were significantly faster at completing the blindfolded (NV/H) trials than the 5-year-olds ($t(14) = 5.4; p < 0.0001$), 6-year-olds ($t(14) = 2.2; p = 0.03$), and 7-year-olds ($t(14) = 2.3; p = 0.03$). So it appears that children become faster at haptically identifying and grasping the blocks as they get older. See Table 1.

Table 1. Average time it took each age group to complete one model in each condition. Means and standard error are reported in seconds.

Age Group	Sensory Condition		
	V/H	V/Constrained-H	NV/H
5-years old	67.8 (5.8)	97.9 (9.1)	129.9 (6.4)
6-years old	61.6 (5.8)	91.5 (9.1)	96.2 (6.4)
7-years old	44.7 (5.6)	64.1 (8.8)	104.5 (6.2)
8-years old	47.1 (5.6)	67.1 (8.8)	82.2 (6.2)

Discussion

The present study sought to explore if children's hand preference for grasping is sensitive to changes in sensory feedback. Children were asked to replicate 3D models from a tabletop of building blocks 1) while vision and haptics were available, 2) while vision was available but haptics was constrained, and 3) while blindfolded, but with full haptics. Results showed that, regardless of age or sex, there was a right-hand preference for grasping when both vision and haptics were available to the child (~68%). When the child completed the same task with the gloves on (V/Constrained-H), there was a significant increase in right-hand preference (~76%). In contrast, when vision was occluded but haptics was available, children showed a significant increase in left-hand use to the point that no hand preference was observed (~50%). These results highlight the key role that haptics plays in shaping hand preference for grasping. Furthermore, they suggest an early establishment of hemispheric differences in sensory processing.

Hand preference for grasping in children has been assessed in a multitude of natural grasping tasks. Children have been observed picking up objects such as toys (Campbell, Marcinowski, Latta, & Michel, 2015; Jacquet et al., 2012; Kotwica et al., 2008; Michel et al., 2006; Nelson et al., 2013; Ramsay, 1980), food (Cavill & Bryden, 2003; Sacrey et al., 2013), small pegs (Geerts, Einspieler, Dibiasi, Garzarolli, & Bos, 2003), blocks (C. L. Gonzalez et al., 2014; Mills, Rousseau, & Gonzalez, 2014; Morange-Majoux et al., 2000; Sacrey et al., 2013), cards (Hill & Khanem, 2009; Souza, Coelho, & Teixeira, 2014) or tools (Marschik et al., 2008; McManus et al., 1988). These studies have reported a preference to use the right hand that may emerge as early as six months of age and is largely established by five years of age. Our results align with this previous literature: children in the V/H condition displayed a clear right-hand preference for grasping the blocks. Worth noting is that the block-building task is bimanual in nature because one hand usually grasps the blocks while the other hand holds the model being replicated (Stone et al., 2013). Because the current study used a fixed plate to support the model being built, the child had equal opportunity to use either hand to pick up the blocks. The results of hand preference in this bimanual task were not different from previous studies that have utilized unimanual tasks, highlighting the robustness of this right-hand preference for grasping.

A unique contribution of the present study was the investigation of hand preference under different sources of sensory feedback. Very few studies have investigated hand preference in children when vision is unavailable. In two studies, Ittyerah (2000, 2009) tested sighted-blindfolded and congenitally blind children (ranging in age from 5 to 15 years) on various motor tasks. Some of these tasks involved grasping (e.g. reach for a toy), whereas others did not (e.g. snap your fingers). Both sighted-blindfolded and congenitally blind were reported to have an overall right-hand preference for these tasks, but the extent to which the right hand was preferred or differences in preference for the various types of actions were not specified. In our study, we used a bimanual task to investigate manual preference and found that the use of the right hand increases with visual reliance whereas use of the left hand increases with haptic demand. This was shown in two ways. First, when vision was available but haptics was constrained by wearing the gloves (V/Constrained-H), there was a pronounced increase in right-hand use. This demonstrates that vision is a powerful driver of right-hand preference. But it

also suggests that haptics plays a pivotal role in modulating hand use. If haptic feedback did not play a role, then hand preference in the V/Constrained-H and V/H should have been similar. Further support for the role of haptics in hand preference comes from the results of the NV/H condition. When vision was not available to the child and they had to rely on haptics to complete the task, there was no longer a preference to use the right hand. The results of both conditions (V/Constrained-H and NV/H) suggest a right-hand specialization for visually-guided grasping and the important role that right hemisphere (left hand) plays during haptically-guided grasping.

Remarkably, the rate to which children used their right hands under the different sensory conditions was virtually identical to that found in adults (Stone and Gonzalez, 2015). This finding suggests that the visual and haptic modulation of hand preference is fully developed early in childhood. This notion is supported by Kalagher and Jones (2011) who found that 5-year-old children demonstrate the same exploratory procedures for haptically identifying object properties as adults do. Exploratory procedures are stereotyped patterns of hand movements used to extract object information during haptic recognition (Lederman & Klatzky, 2009). In Kalagher and Jones (2011), children and adults were asked to haptically match 3D shapes from an array based on different properties such as shape, texture, hardness. The children used the same optimal strategies as adults for identifying these objects. Yet in that study, hand preference was not assessed and both hands were used to feel the objects. Based on our current results we suspect that a left-hand preference would ensue these strategies. Furthermore, our findings also coincide with studies demonstrating a left-hand advantage for haptic processing early in childhood (Lhote & Streri, 1998; Morange-Majoux, 2011; Morange-Majoux, Cougnot, & Bloch, 1997; Rose, 1984; D. F. Witelson, 1976; S. F. Witelson, 1974). For example, Morange-Majoux et al. (1997) showed that children as young as four months of age show a left-hand preference for the exploration and extraction of haptic object properties of cylindrical objects. They conclude that by four months of age, children display a left-hand/right-hemisphere specialization for spatial arrangements and tactile processing. Together with the results of the current investigation, these findings maintain a view of left-hand/right-hemisphere specialization for haptics.

A limitation of the current study is the age of the children. Although the results suggest that by age five, sensory information modulates hand preference, it remains unknown when this modulation emerges. Some studies have shown that (particularly for haptically-guided actions), there is an advantage to use the left hand as early as a few months of age (Lhote & Streri, 1998; Marcus et al., 2012; Morange-Majoux, 2011). Other studies, however, have suggested that haptic skill does not emerge and/or is not proficient until at least five years of age (Bleyenheuft, Cols, Arnould, & Thonnard, 2006; Bushnell & Baxt, 1999; Kalagher & Jones, 2011). For example, in Kalagher and Jones' study, although 5-year-olds reached adult-like behaviour for haptic discrimination this was not achieved by 3- and 4-year-olds. In our study, children younger than five years of age (pilot study) demonstrated great difficulty with the procedures used in the task (e.g. they did not like having a blindfold or gloves on). However, modifications to our current design could be made in the future in order to test younger children (using a curtain instead of a blindfold, for example).

The results of the present study revealed that the ability to use haptics to guide one's movement in the absence of vision is present early in development. Furthermore they demonstrate sensory-modality specific asymmetries that influence hand preference for grasping as early as five years of age. When exactly these sensory specializations emerge and interact to shape manual preferences warrants future investigation.

References

- Bleyenheuft, Y., Cols, C., Arnould, C., & Thonnard, J. L. (2006). Age-related changes in tactile spatial resolution from 6 to 16 years old. *Somatosensory and Motor Research*, 23(3-4), 83-87. doi: 10.1080/08990220600816440
- Brown, S. G., Roy, E. A., Rohr, L. E., & Bryden, P. J. (2006). Using hand performance measures to predict handedness. *Laterality*, 11(1), 1-14. doi: 10.1080/1357650054200000440
- Bryden, P. J., & Roy, E. A. (2006). Preferential reaching across regions of hemispace in adults and children. *Developmental Psychobiology*, 48(2), 121-132. doi: 10.1002/dev.20120
- Buckingham, G., Ranger, N. S., & Goodale, M. A. (2012). Handedness, laterality and the size-weight illusion. *Cortex*, 48(10), 1342-1350. doi: 10.1016/j.cortex.2011.09.007
- Bushnell, E. W., & Baxt, C. (1999). Children's haptic and cross-modal recognition with familiar and unfamiliar objects. *Journal of Experimental Psychology: Human Perception and Performance*, 25(6), 1867-1881.
- Campbell, J. M., Marcinowski, E. C., Latta, J., & Michel, G. F. (2015). Different assessment tasks produce different estimates of handedness stability during the eight to 14 month age period. *Infant Behavior & Development*, 39(0), 67-80. doi: <http://dx.doi.org/10.1016/j.infbeh.2015.02.003>
- Carlson, D. F., & Harris, L. J. (1985). Development of the infant's hand preference for visually directed reaching: Preliminary report of a longitudinal study. *Infant Mental Health Journal*, 6(3), 158-174. doi: 10.1002/1097-0355(198523)6:33.0.CO;2-X
- Castiello, U. (2005). The neuroscience of grasping. *Nature Reviews Neuroscience*, 6(9), 726-736. doi: 10.1038/nrn1744
- Cavill, S., & Bryden, P. (2003). Development of handedness: Comparison of questionnaire and performance-based measures of preference. *Brain and Cognition*, 53(2), 149-151. doi: 10.1016/S0278-2626(03)00098-8
- Chang, E. C., Flanagan, J. R., & Goodale, M. A. (2008). The intermanual transfer of anticipatory force control in precision grip lifting is not influenced by the perception of weight. *Experimental Brain Research*, 185(2), 319-329. doi: 10.1007/s00221-007-1156-0
- Corbetta, D., & Thelen, E. (1999). Lateral biases and fluctuations in infants' spontaneous arm movements and reaching. *Developmental Psychobiology*, 34(4), 237-255. doi: 10.1002/(SICI)1098-2302(199905)34:23.3.CO;2-R
- Endo, S., Wing, A. M., & Bracewell, R. M. (2011). Haptic and visual influences on grasp point selection. *Journal of Motor Behavior*, 43(6), 427-431. doi: 10.1080/00222895.2011.621996
- Fagard, J. (1998). *Changes in grasping skills and the emergence of bimanual coordination during the first year of life*. Londres: Mac Keith Press.
- Fagard, J., & Lockman, J. J. (2005). The effect of task constraints on infants' (bi)manual strategy for grasping and exploring objects. *Infant Behavior & Development*, 28(3), 305-315. doi: <http://dx.doi.org/10.1016/j.infbeh.2005.05.005>

- Fagard, J., & Marks, A. (2000). Unimanual and bimanual tasks and the assessment of handedness in toddlers. *Developmental Science*, 3(2), 137-147. doi: 10.1111/1467-7687.00107
- Ferre, C. L., Babik, I., & Michel, G. F. (2010). Development of infant prehension handedness: A longitudinal analysis during the 6- to 14-month age period. *Infant Behavior & Development*, 33(4), 492-502. doi: 10.1016/j.infbeh.2010.06.002
- Gabbard, C., & Rabb, C. (2000). What determines choice of limb for unimanual reaching movements? *The Journal of General Psychology*, 127(2), 178-184. doi: 10.1080/00221300009598577
- Geerts, W. K., Einspieler, C., Dibiasi, J., Garzarolli, B., & Bos, A. F. (2003). Development of manipulative hand movements during the second year of life. *Early Human Development*, 75(1-2), 91-103.
- Gesell, A., & Ames, L. B. (1947). The development of handedness. *The Pedagogical Seminary and Journal of Genetic Psychology*, 70(2), 155-175. doi: 10.1080/08856559.1947.10533403
- Goble, D. J., Lewis, C. A., Hurvitz, E. A., & Brown, S. H. (2005). Development of upper limb proprioceptive accuracy in children and adolescents. *Human Movement Science*, 24(2), 155-170. doi: 10.1016/j.humov.2005.05.004
- Gonzalez, C. L., Flindall, J. W., & Stone, K. D. (2015). Hand preference across the lifespan: Effects of end-goal, task nature, and object location. *Frontiers in Psychology*, 5, 1579. doi: 10.3389/fpsyg.2014.01579
- Gonzalez, C. L., & Goodale, M. A. (2009). Hand preference for precision grasping predicts language lateralization. *Neuropsychologia*, 47(14), 3182-3189. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2009.07.019>
- Gonzalez, C. L., Mills, K. J., Genee, I., Li, F., Piquette, N., Rosen, N., & Gibb, R. (2014). Getting the right grasp on executive function. *Frontiers in Psychology*, 5, 285. doi: 10.3389/fpsyg.2014.00285
- Gonzalez, C. L., Whitwell, R. L., Morrissey, B., Ganel, T., & Goodale, M. A. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, 182(2), 275-279. doi: 10.1007/s00221-007-1090-1
- Hill, E. L., & Khanem, F. (2009). The development of hand preference in children: The effect of task demands and links with manual dexterity. *Brain and Cognition*, 71(2), 99-107. doi: 10.1016/j.bandc.2009.04.006
- Hinojosa, T., Sheu, C.-F., & Michel, G. F. (2003). Infant hand-use preferences for grasping objects contributes to the development of a hand-use preference for manipulating objects. *Developmental Psychobiology*, 43(4), 328-334. doi: 10.1002/dev.10142
- Hoop, N. H. (1971). Haptic perception in preschool children. I. Object recognition. *The American Journal of Occupational Therapy*, 25(7), 340-344.
- Hopkins, B., & Prechtl, H. F. (1984). A qualitative approach to the development of movements during early infancy. In H. F. Prechtl (Ed.), *Continuity of neural functions from prenatal to postnatal life* (Vol. 94). Blackwell: Oxford.
- Ittyerah, M. (2000). Hand skill and hand preference in blind and sighted children. *Laterality*, 5(3), 221-235. doi: 10.1080/713754379

- Ittyerah, M. (2009). Hand ability and practice in congenitally blind children. *Journal of Developmental and Physical Disabilities, 21*(5), 329-344. doi: 10.1007/s10882-009-9146-8
- Jacobsohn, L., Rodrigues, P., Vasconcelos, O., Corbetta, D., & Barreiros, J. (2014). Lateral manual asymmetries: A longitudinal study from birth to 24 months. *Developmental Psychobiology, 56*(1), 58-72. doi: 10.1002/dev.21091
- Jacquet, A. Y., Esseily, R., Rider, D., & Fagard, J. (2012). Handedness for grasping objects and declarative pointing: A longitudinal study. *Developmental Psychobiology, 54*(1), 36-46. doi: 10.1002/dev.20572
- Kalagher, H., & Jones, S. S. (2011). Developmental change in young children's use of haptic information in a visual task: The role of hand movements. *Journal of Experimental Child Psychology, 108*(2), 293-307. doi: 10.1016/j.jecp.2010.09.004
- Kastner-Koller, U., Diemann, P., & Bruckner, J. (2007). Assessing handedness in pre-schoolers: Construction and initial validation of a hand preference test for 4-6-year-olds. *Psychology Science, 49*(3), 239-254.
- Kotwica, K. A., Ferre, C. L., & Michel, G. F. (2008). Relation of stable hand-use preferences to the development of skill for managing multiple objects from 7 to 13 months of age. *Developmental Psychobiology, 50*(5), 519-529. doi: 10.1002/dev.20311
- Kritikos, A., & Beresford, M. (2002). Tactile interference in visually guided reach-to-grasp movements. *Experimental Brain Research, 144*(1), 1-7. doi: 10.1007/s00221-002-1004-1
- Lederman, S. J., & Klatzky, R. L. (2009). Haptic perception: A tutorial. *Attention, Perception & Psychophysics, 71*(7), 1439-1459. doi: 10.3758/app.71.7.1439
- Lhote, M., & Streri, A. (1998). Haptic memory and handedness in 2-month-old infants. *Laterality, 3*(2), 173-192. doi: 10.1080/713754298
- Marcus, L., Lejeune, F., Berne-Audeoud, F., Gentaz, E., & Debillon, T. (2012). Tactile sensory capacity of the preterm infant: Manual perception of shape from 28 gestational weeks. *Pediatrics, 130*(1), e88-94. doi: 10.1542/peds.2011-3357
- Marschik, P. B., Einspieler, C., Strohmeier, A., Plienegger, J., Garzarolli, B., & Prechtel, H. F. (2008). From the reaching behavior at 5 months of age to hand preference at preschool age. *Developmental Psychobiology, 50*(5), 511-518. doi: 10.1002/dev.20307
- McCormick, C. M., & Maurer, D. M. (1988). Unimanual hand preferences in 6-month-olds: Consistency and relation to familial-handedness. *Infant Behavior & Development, 11*(1), 21-29. doi: 10.1016/S0163-6383(88)80013-4
- McManus, I. C., Sik, G., Cole, D. R., Mellon, A. F., Wong, J., & Kloss, J. (1988). The development of handedness in children. *British Journal of Developmental Psychology, 6*(3), 257-273. doi: 10.1111/j.2044-835X.1988.tb01099.x
- Michel, G. F. (1981). Right-handedness: A consequence of infant supine head-orientation preference? *Science, 212*(4495), 685-687. doi: 10.1126/science.7221558
- Michel, G. F., Ovrut, M. R., & Harkins, D. A. (1985). Hand-use preference for reaching and object manipulation in 6- through 13-month-old infants. *Genetic, Social, and General Psychology Monographs, 111*(4), 407-427.
- Michel, G. F., Tyler, A. N., Ferre, C., & Sheu, C. F. (2006). The manifestation of infant hand-use preferences when reaching for objects during the seven-to thirteen-

- month age period. *Developmental Psychobiology*, 48(6), 436-443. doi: 10.1002/dev.20161
- Mills, K. J., Rousseau, B. R., & Gonzalez, C. L. (2014). A cross-sectional developmental examination of the SNARC effect in a visually-guided grasping task. *Neuropsychologia*, 58, 99-106. doi: 10.1016/j.neuropsychologia.2014.04.001
- Morange-Majoux, F. (2011). Manual exploration of consistency (soft vs hard) and handedness in infants from 4 to 6 months old. *Laterality*, 16(3), 292-312. doi: 10.1080/13576500903553689
- Morange-Majoux, F., Peze, A., & Bloch, H. (2000). Organisation of left and right hand movement in a prehension task: A longitudinal study from 20 to 32 weeks. *Laterality*, 5(4), 351-362. doi: 10.1080/713754386
- Morange-Majoux, F., Cougnot, P., & Bloch, H. (1997). Hand tactual exploration of textures in infants from 4 to 6 months. *Early Development and Parenting*, 6(3-4), 127-136. doi: 10.1002/(SICI)1099-0917(199709/12)6:3/43.0.CO;2-G
- Nelson, E. L., Campbell, J. M., & Michel, G. F. (2013). Unimanual to bimanual: Tracking the development of handedness from 6 to 24 months. *Infant Behavior & Development*, 36(2), 181-188. doi: 10.1016/j.infbeh.2013.01.009
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97-113.
- Pettypiece, C. E., Goodale, M. A., & Culham, J. C. (2010). Integration of haptic and visual size cues in perception and action revealed through cross-modal conflict. *Experimental Brain Research*, 201(4), 863-873. doi: 10.1007/s00221-009-2101-1
- Ramsay, D. S. (1980). Onset of unimanual handedness in infants. *Infant Behavior & Development*, 3, 377-385. doi: [http://dx.doi.org/10.1016/S0163-6383\(80\)80045-2](http://dx.doi.org/10.1016/S0163-6383(80)80045-2)
- Rochat, P. (1987). Mouthing and grasping in neonates: Evidence for the early detection of what hard or soft substances afford for action. *Infant Behavior & Development*, 10(4), 435-449. doi: [http://dx.doi.org/10.1016/0163-6383\(87\)90041-5](http://dx.doi.org/10.1016/0163-6383(87)90041-5)
- Ronnqvist, L., & Domellof, E. (2006). Quantitative assessment of right and left reaching movements in infants: A longitudinal study from 6 to 36 months. *Developmental Psychobiology*, 48(6), 444-459. doi: 10.1002/dev.20160
- Rose, S. A. (1984). Developmental changes in hemispheric specialization for tactual processing in very young children: Evidence from cross-modal transfer. *Developmental Psychology*, 20(4), 568. doi: 10.1037/0012-1649.20.4.568
- Sacrey, L. A., Arnold, B., Whishaw, I. Q., & Gonzalez, C. L. (2013). Precocious hand use preference in reach-to-eat behavior versus manual construction in 1- to 5-year-old children. *Developmental Psychobiology*, 55(8), 902-911. doi: 10.1002/dev.21083
- Souza, R. M., Coelho, D. B., & Teixeira, L. A. (2014). Modulation of manual preference induced by lateralized practice diffuses over distinct motor tasks: Age-related effects. *Frontiers in Psychology*, 5, 1406. doi: 10.3389/fpsyg.2014.01406
- Stone, K. D., Bryant, D. C., & Gonzalez, C. L. (2013). Hand use for grasping in a bimanual task: Evidence for different roles? *Experimental Brain Research*, 224(3), 455-467. doi: 10.1007/s00221-012-3325-z
- Stone, K. D., & Gonzalez, C. L. (2014a). Grasping with the eyes of your hands: Hapsis and vision modulate hand preference. *Experimental Brain Research*, 232(2), 385-393. doi: 10.1007/s00221-013-3746-3

- Stone, K. D., & Gonzalez, C. L. (2014b). Grasping without sight: Insights from the congenitally blind. *PLoS ONE*, *9*(10), e110175. doi: 10.1371/journal.pone.0110175
- Stone, K. D., & Gonzalez, C. L. (2015). Manual preferences for visually- and haptically-guided grasping. *Acta Psychologica*, *160*, 1-10. doi: 10.1016/j.actpsy.2015.06.004
- von Hofsten, C. (1983). Catching skills in infancy. *Journal of Experimental Psychology: Human Perception and Performance*, *9*(1), 75-85.
- von Hofsten, C. (1984). Developmental changes in the organization of prereaching movements. *Developmental Psychology*, *20*(3), 378-388. doi: 10.1037/0012-1649.20.3.378
- Wallace, P. S., & Whishaw, I. Q. (2003). Independent digit movements and precision grip patterns in 1-5-month-old human infants: Hand-babbling, including vacuous then self-directed hand and digit movements, precedes targeted reaching. *Neuropsychologia*, *41*(14), 1912-1918.
- Witelson, D. F. (1976). Sex and the single hemisphere: Specialization of the right hemisphere for spatial processing. *Science*, *193*(4251), 425-427. doi: 10.1007/BF02653735
- Witelson, S. F. (1974). Hemispheric specialization for linguistic and nonlinguistic tactual perception using a dichotomous stimulation technique. *Cortex*, *10*(1), 3-17.

APPENDIX 5

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 left hand? If so, please explain:

APPENDIX 6

PERMISSION TO USE APPENDICES 1, 2, AND 3 AS PART OF THESIS

Appendix 1 was published in Experimental Brain Research, and as per the following License Agreement, I retain my rights as an author to include this article in my thesis.

“With reference to your request to reprint in your thesis material on which Springer Science and Business Media control the copyright, permission is granted, free of charge, for the use indicated in your enquiry.”

SPRINGER LICENSE
TERMS AND CONDITIONS

May 31, 2015

This is a License Agreement between Kayla Stone (“You”) and Springer (“Springer”) provided by Copyright Clearance Center (“CCC”). The license consists of your order details, the terms and conditions provided by Springer, and the payment terms and conditions.

All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

License Number	3627420799370
License date	May 13, 2015
Licensed content publisher	Springer
Licensed content publication	Experimental Brain Research
Licensed content title	Grasping with the eyes of your hands: Hapsis and vision modulate hand preference
Licensed content author	Kayla D. Stone
Licensed content date	Jan 1, 2013
Volume number	232
Issue number	2
Type of Use	Thesis/Dissertation
Portion	Full text
Number of copies	1
Author of this Springer article	Yes and you are a contributor of the new work
Order reference number	None
Title of your thesis / dissertation	Vision and haptics: How sensorimotor interactions influence grasping
Expected completion date	Aug 2015
Estimated size(pages)	200
Total	0.00 CAD
Terms and Conditions	

Appendix 2 was published in PLoS ONE and as per the following, I retain my rights as an author to include this article in my thesis.

“I would like to re-use/incorporate some of my published work in something else, can I?”

“Answer: Because we are an Open Access journal, you have the right, after a paper has been successfully published, to use it in any way you like so long as you use the appropriate citation to the original work. You do not need to request our permission for any kind of re-use.”

<http://blogs.plos.org/everyone/authors/qa/>

Appendix 3 was published in Acta Psychologica (under Elsevier). See the following.

RETENTION OF RIGHTS FOR SCHOLARLY PURPOSES

I understand that I retain or am hereby granted (without the need to obtain further permission) the Retained Rights (see description below), and that no rights in patents, trademarks or other intellectual property rights are transferred to Elsevier B.V. .

The Retained Rights include:

- » the right to use the [Preprint](#) or [Accepted Author Manuscript](#) for [Personal Use](#), [Internal Institutional Use](#) and for [Permitted Scholarly Posting](#) and
- » the right to use the [Published Journal Article](#) for [Personal Use](#) and [Internal Institutional Use](#).

but in each case as noted in the Definitions' clause excluding [Commercial Use](#) or [Systematic Distribution](#) (unless expressly agreed in writing by Elsevier B.V.).

“Theses and dissertations which contain embedded Published Journal Articles as part of the formal submission can be posted publicly by the awarding institution with DOI links back to the formal publications on ScienceDirect”

<http://www.elsevier.com/about/company-information/policies/sharing>