

**AN INVESTIGATION OF THE DISTORTED CHARACTERISTICS OF HAND
REPRESENTATION**

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Dedication

To David Astill, thank you for your support and encouragement.

Abstract

The internal perception of the hands has been found to be distorted. These distortions feature hand width that is overestimated and finger length that is underestimated. The purpose of this thesis was to explore the conditions in which hand perception is distorted. Two experiments were based on two hypotheses: 1) hand perception resembles its anatomical dimensions when perceived holistically; and 2) part of the distortion is as a result of different sensory modalities interfering with one another. The results confirmed the distorted characteristics, and both experiments had one group of participants that performed significantly more accurately. When participants pointed to their fingers in succession (experiment 1), the distortion was significantly reduced. In experiment 2, participants had better perception when using haptics but were more distorted when using vision or vision and haptics. This suggests that vision but not haptics interferes with having an anatomically accurate perception.

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List of Abbreviations

ANOVA: Analysis of Variance
IRED: Infra-red LED
fMRI: Functional Magnetic Resonance Imaging
MP Joint: Metacarpophalangeal joint
BA: Brodmann area
RA: Rapidly adapting afferents
RF: Receptor fields
SA1: Slowly adapting type 1 afferents
SI: Shape index
S1: Primary somatosensory cortex
S2: Secondary somatosensory cortex
VPL: Ventral posterior lateral nuclei

Chapter 1: Introduction to the Somatosensory System

1.1 Introduction

The somatosensory system is comprised of two distinct main areas of the brain, as well as several pathways that lead from the surface of the skin to the brain. Its main function is to receive and interpret sensory information; collected from the skin, joints, muscles and organs about size, position, temperature, and pain from these sources (Purves et al., 2012). The somatosensory system is responsible for several different senses including the sense of touch (haptics), proprioception (where the body is in space), temperature and nociception (feeling of pain), as well as the sub-modality of balance (through a unique system of receptors in the inner ear). These senses provide us with information about our bodies and what we are experiencing. Thus, it is through this system that an awareness of self-arises. Everyday our bodies are in constant interaction with our environments and it is the somatosensory system that allows us to interact with our environments. It is in this system where information about the position and size of the body is processed. This is important as the size of our bodies are used to guide our movements in our environments. Thus, through accurate perceptions about the position and size of our bodies the somatosensory system enables us to act in our environments. Both information internal to the body (leading to a sense of self) and external to the body (allowing for action) is processed by this system. The following sections will briefly discuss the organization of the somatosensory system.

1.2 The somatosensory periphery

Somatosensory signals that are perceived at the joints, muscles, skin, ligaments, and organs travel to the primary somatosensory cortex (S1) and the secondary somatosensory cortex (S2) through the somatosensory periphery. The signals remain relatively unprocessed as they travel through the periphery until they reach S1 (Gynther, Vickery, & Rowe, 1995; Sahai et al., 2006).

The somatosensory processing begins with mechanotransduction. This process involves converting a mechanical stimuli into somatosensory signals (Hertenstein & Weiss, 2011). For example, touch processing begins by a pattern of pressure on the skin transforming into a pattern of activity of the skin receptors (Hertenstein & Weiss, 2011; Johnson, 2001). The sensation of touch is as a result of mechanoreceptors on the skin. Mechanoreceptive afferents carry signals that contain information about the spatial patterns on the skin to the brain. This spatial information about the skin is taken to the brain through two types of afferents; slowly adapting type 1 (SA1) and rapidly adapting (RA) afferents (Hertenstein & Weiss, 2011). Individual SA1 and RA afferents are responsive to individual areas of skin and they only provide information about that specific area (Hertenstein & Weiss, 2011). This is how we can decipher when we are being touched on the thumb versus on the index finger, as two different individual afferents would respond to the two different locations. Skin receptors respond to three types of stimuli; the stretching of skin, stimuli on the skin, and proprioception (Horch, Tuckett, & Burgess, 1977; Nelson, 2001). For example, when the skin over the joints of the fingers is stretched, it creates the illusion that the fingers are moving (misproprioception), which suggests that these skin receptors

have a proprioceptive as well as tactile role (Collins & Prochazka, 1996; Edin & Johansson, 1995).

The mechanoreceptors in the skin and joints are positioned in areas that are capable of providing proprioceptive feedback. The receptors in the joints provide information about limb position and movement for only the extremes of motion or for the full range of motion, either when rapidly and slowly moving, or over the entire range and speed of the movement (Nelson, 2001). Therefore, at every position of the joint at least one receptor is firing (Nelson, 2001). Receptors fire at different stages of a movement, and will overlap with one another. The brain assesses joint position by determining which receptors are firing. The number of joint mechanoreceptors that signal a movement are relatively low in comparison to the muscles and skin receptors that respond to the same movement (Ferrell, 1980).

Skin mechanoreceptors that are located in the outer (epidermis) or inner (dermis) layer of the skin are referred to as cutaneous receptors. These receptors contribute to proprioceptive information about the extremities. The cutaneous receptors located in the joints and muscles are either always active or respond specifically to movement (Nelson, 2001). It has been suggested that these receptors also contribute to proprioception of the extremities (Edin, 1992, 2001; Edin & Abbs, 1991; Edin & Johansson, 1995). Thus, information about the location of the hands and feet is provided by specific receptors in the skin and joints that respond when the limb is still and when is moving.

1.3 Somatosensory pathways

There are two main somatosensory pathways that travel from the periphery to the brain. The two somatosensory pathways are referred to as the dorsal medial lemniscal pathway and the spinothalamic tract (Kandel, Schwartz, & Jessell, 2000). The two pathways transmit different types of information and take slightly different paths to the brain. The first pathway is the dorsal column medial lemniscal pathway and this is the pathway that transmits information about proprioception and haptics (Kolb & Whishaw, 2009). The sensory information that travels in the dorsal column medial lemniscal pathway's neurons travel from the body into the spinal cord (see Figure 1). The axons enter the spinal cord through either the gracile or cuneate fasciculus (depending on where on the body this signal is coming from). The pathway ascends the spinal cord into the brainstem, until it reaches the ventral posterior lateral nuclei (VPL) of the thalamus (Kandel et al., 2000). The VPL then sends signals to the primary somatosensory cortex (S1) as well as the primary motor cortex. The second pathway is referred to as the spinothalamic tract. The spinothalamic tract carries nociceptive (pain) and temperature information from the spinal cord to the cortex (Kolb & Whishaw, 2009). The cells in the dorsal medial lemniscal pathway and the spinothalamic tract are also different, as the cells in the dorsal medial lemniscal pathway are larger and more heavily myelinated (Kolb & Whishaw, 2009).

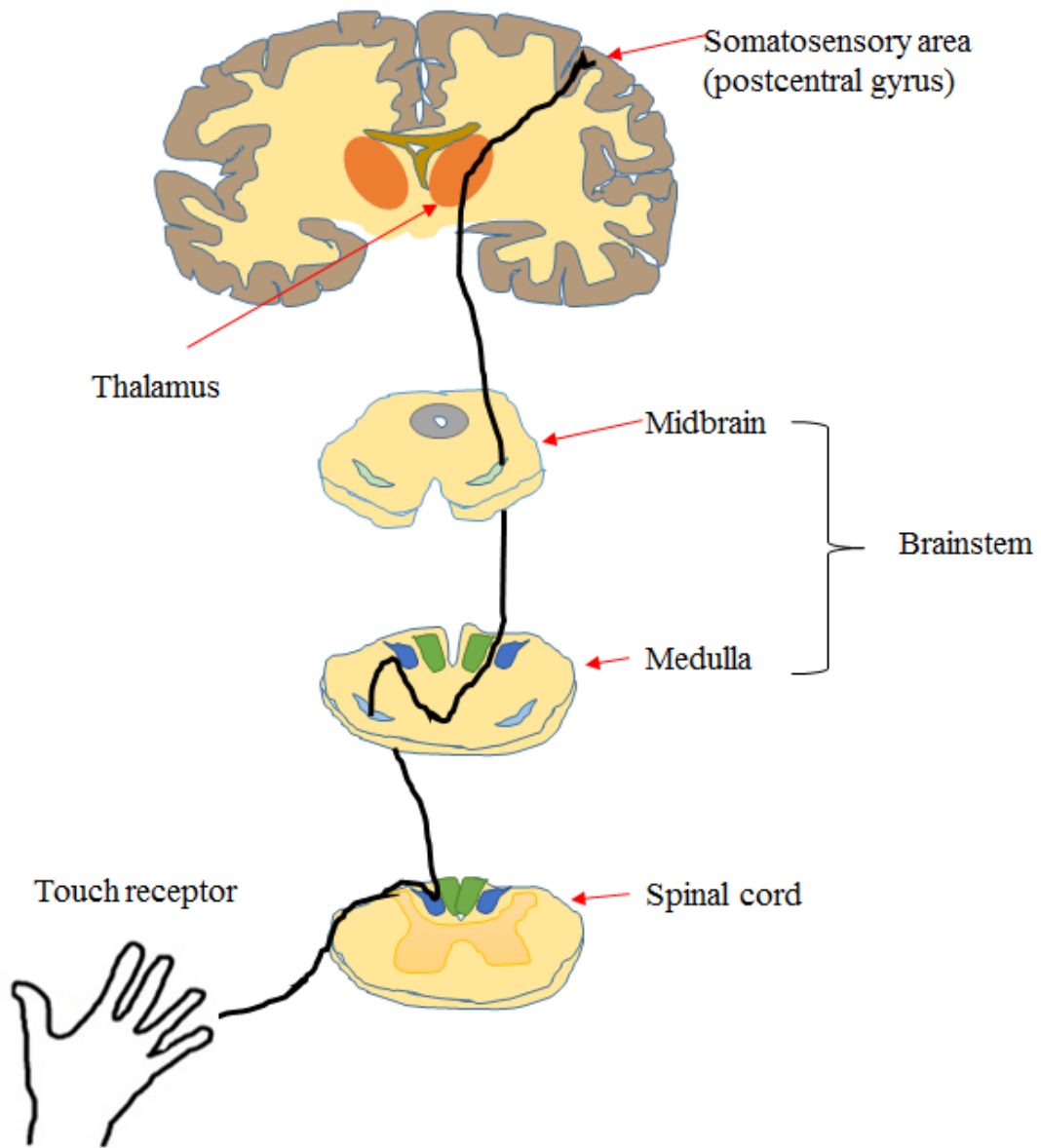


Figure 1. A representation of the dorsal medial lemniscal tract. The figure depicts how haptic information (from the hand) travels from the hand to the brain through the periphery (adapted from Kolb & Whishaw, 2009).

1.4 The somatosensory cortex

The somatosensory cortex consists of two main areas; the primary somatosensory cortex (S1) and the secondary somatosensory cortex (S2) (see Figure 2). S1 is located in the postcentral gyrus and is comprised of four interconnected areas specifically Brodmann areas 3a, 3b, 1, and 2 (Hertenstein & Weiss, 2011; Kaas, Nelson, Sur, Lin, & Merzenich, 1979; Kaas, Nelson, Sur, & Merzenich, 1981). Each of these areas responds to a different type of stimulation. Stimulation on the skin causes area 3b and area 1 to respond, whereas changes to position sense (limb position and posture) causes area 3a to respond (Hertenstein & Weiss, 2011). Area 2 responds to both, stimulation of the skin and changes in position sense. Signals from S1 travel to two different locations in the cortex. Somatosensory information travels to S2, whereas motor planning information reaches the posterior parietal cortex, specifically areas 5 and 7 (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975). The four areas of S1 process information at different times (see Figure 3). Areas 3a and 3b process skin stimulation and position sense before those signals are funnelled to areas 1 and 2. Lastly this information is sent to S2 (Hertenstein & Weiss, 2011).

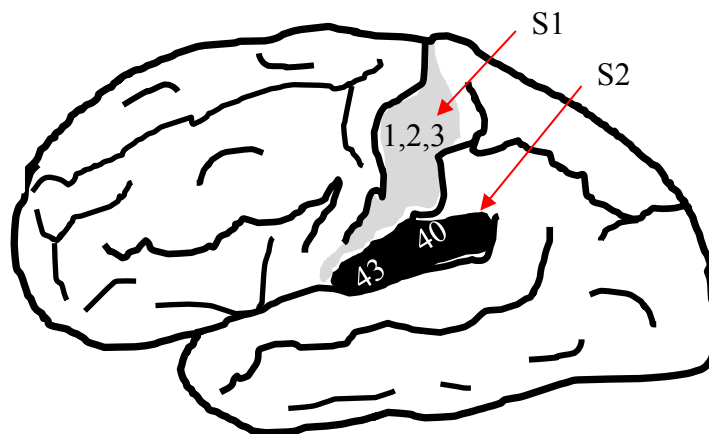


Figure 2. A representation of the two areas of the somatosensory cortex. S1 is comprised of areas 1, 2 and 3, and S2 is comprised of areas 40 and 43 (adapted from Purves et al., 2012).

S2 is located further down the somatosensory processing pathway (Hertenstein & Weiss, 2011; Pons, Garraghty, Friedman, & Mishkin, 1987; Pons, Garraghty, & Mishkin, 1992). S2 is made up of Brodmann areas 40 and 43. These areas respond to touch on the skin and/or proprioceptive information (Fitzgerald, Lane, Thakur, & Hsiao, 2004). From S2 projections are sent to the insular cortex, and once there projections are sent to the frontal and temporal lobe regions (Augustine, 1996; Hertenstein & Weiss, 2011).

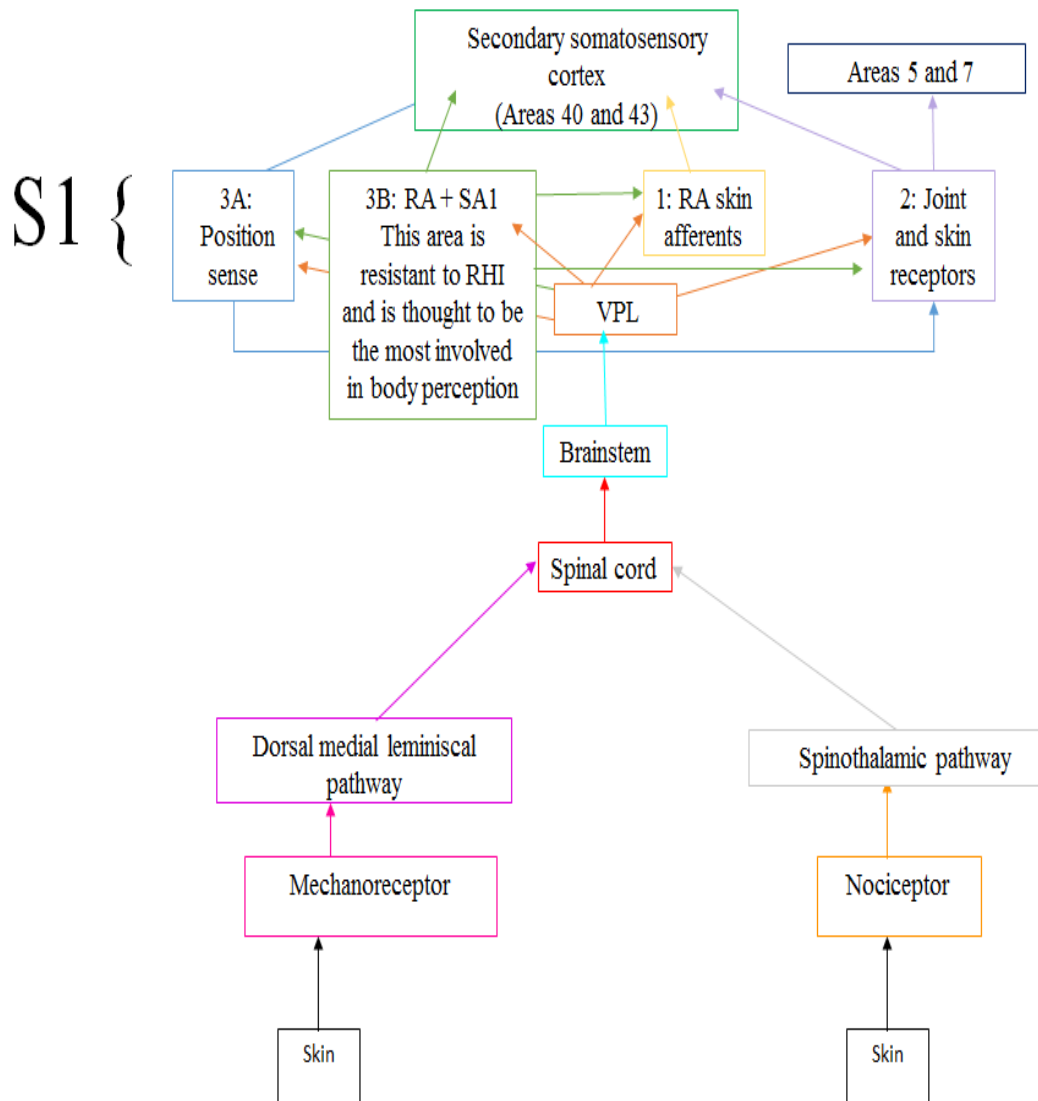


Figure 3: How both fine touch and nociceptive information travel from the skin to the brain.

1.5 The homunculus

Research has found that within S1 and S2 an entire representation of the body is stored. This representation is called the “Homunculus”. The homunculus is Latin for “little man”. Wilder Penfield first characterized the homunculus when he stimulated the sensory cortex of human epileptic patients (Kolb & Whishaw, 2009; Penfield & Boldrey, 1937). He stimulated different sections of the somatosensory cortex and asked the participants to report where on the body they felt a sensation. From this information Penfield detailed a map of the body in S1, this map became known as the homunculus (see Figure 4). Further studies in non-human primates have found that the somatosensory cortex could possibly contain a number of homunculi, one for each of its four different areas; 3a, 3b, 1, and 2 (Kaas et al., 1979; Kolb & Whishaw, 2009).

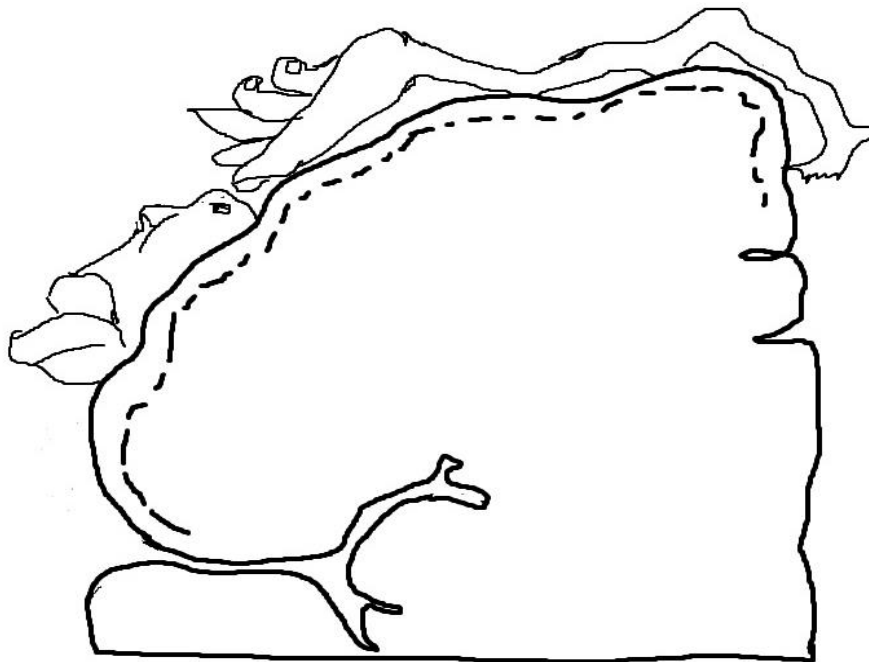


Figure 4. This is a representation of the homunculus, and how different amounts of cortical area respond to each body part.

The homunculus is topographical in nature with the mouth and eyes being located in the ventral part of S1, the hand and fingers represented in the middle, and the feet represented in the dorsal areas (Kolb & Whishaw, 2009). The homunculus is not an anatomically accurate representation of the body, but rather a representation that corresponds to the amount of sensory receptors located on a specific body part (see Figure 3) (Penfield & Boldrey, 1937). This is why the largest cortical area is devoted to our hands and lips/mouths. We have lots of sensory receptors in these areas as we primarily manipulate our environment with our hands, and we talk and taste with our lips/mouths. Conversely, the trunk and the legs had the smallest representation as they are the least sensitive part of the human body. Therefore, the homunculus can also be thought of as a map that represents how we interact with our environments.

Interestingly, not all the digits on the hand are represented by the same amount of cortical area in S1 and S2. The thumb was found to have larger cortical representation than the other digits, each represented by the same amount of cortical area (Penfield & Boldrey, 1937; Sutherling, Levesque, & Baumgartner, 1992). This is likely related to how the thumb (as it is opposable) affords us the possibility to interact with the environment (as we could not grasp objects with the four fingers alone). The distance between each knuckle (metacarpalphalangeal joints) pairing on the hand is also misrepresented in the somatosensory cortex. One study found the distance between the thumb and index finger to be the same as the distance between the index finger and middle finger, or the middle finger and ring finger (even though anatomically, the distance between thumb and index finger is greater than the distance between the other two pairings (Martuzzi, van der Zwaag, Farthouat, Gruetter, & Blanke, 2014)). The functional relevance of this misrepresentation remains to be solved.

Chapter 2. Introduction to Studies on Body Perception

2.1 Body representation, perception and the somatosensory system

In this thesis body representation refers to “the many distributed processing systems in the brain that encode a person's body” (Romano, Llobera, & Blanke, 2016). Body perception refers to the individual’s account for that neural representation (see Figure 5). Body perception involves both constantly updating sensorimotor representations, as well as the remembered metrics of the body, (Dijkerman & de Haan, 2007; Haggard, Kitadono, Press, & Taylor-Clarke, 2006; Keizer et al., 2013). The information of where our bodies are located in space (i.e position sense) is processed through different types of afferent signals (joint receptors, muscle spindles, and the skin) located in the somatosensory periphery (Proske & Gandevia, 2012). These peripheral signals are transformed into a perception of body posture (Graziano & Botvinick, 2002). While these afferent signals provide information about the angles of each joint, they do not provide information about the exact location of a body part (Longo, 2015a; Longo & Haggard, 2010). As there are no direct signals to inform the brain about the size and shape of each body part, the information from the afferent signals is combined with a stored representation of the body. Thus it is through body perception that we register how different individual body parts are united to form a perception of the entire body.

While body perception informs us about the location and shape of our bodies it also allows us to decipher what parts are our own and what parts are not. Studies have found that participants can be tricked into thinking that non-corporeal objects are a part of their bodies, leading to a temporary disorder of body perception. A transitory disorder of body perception can be induced via the rubber hand illusion. This illusion works by occluding one of the participant’s hands and then placing a rubber hand somewhere in the proximity of the participant. The participant’s

occluded hand and the rubber hand are stroked simultaneously. The participant then feels as if the rubber hand is a part of their body. This feeling of embodiment over the hand appears quickly, and it could even be incorporated into motor planning. This transitory disorder of body perception can be so powerful that participants would be drawn to protect it (as they would do with their actual hands) during threatening situations (Armel & Ramachandran, 2003; Ehrsson, Holmes, & Passingham, 2005).

Neuroimaging studies have found that the effects of the rubber hand illusion are associated with brain activity in the parietal cortex, the insula, and the somatosensory cortex particularly area 3b (Cardini, Longo, & Haggard, 2011; Dieguez, Mercier, Newby, & Blanke, 2009; Ehrsson et al., 2005; Ehrsson, Spence, & Passingham, 2004; Ionta et al., 2011; Kammers et al., 2009; Kanayama, Sato, & Ohira, 2007; Lenggenhager, Halje, & Blanke, 2011; Schaefer, Flor, Heinze, & Rotte, 2006; Schaefer, Xu, Flor, & Cohen, 2009; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007). The rubber hand illusion has been useful to study body perception and representation as it allows for an examination of neural changes when body perception is distorted. For example, one study found that areas 1 and 2 would respond to the rubber hand as if it were a real hand, whereas area 3b would not (Martuzzi et al., 2015). Thus, area 3b was not influenced by the illusion, demonstrating that this area is less susceptible to changes in body perception.

It has been proposed that there are two types of body perception: body image and body schema. Body image is defined as the “off-line” representation of the body that is based on stored knowledge (i.e. experience and memory) of the body and is used for perceptual judgements (such as estimating height). Body schema is the “online” body perception that uses constantly updating sensory information to form a representation (Gallagher, 2005; Paillard, 1999). Body schema is

updated through movement and is used for understanding the relative position of the body with respect to other objects (e.g. stepping over an object). Body perception encompasses both body image and body schema, as the representation of the body relies on both a stored perception of size and shape as well as the online sensory information to form an updated perception of the body. This proposal is based on neuropsychological studies of brain-damaged patients (Anema et al., 2009; Paillard, 1999). For example, in one study, two patients were tapped somewhere on their hands and then were asked to indicate on their hand or on a picture the location where they felt the stimulus (Anema et al, 2009). One patient who had damage to the left side of her middle cerebral artery was able to correctly identify where on her own body she had been touched but she was unable to identify the location on a picture of a hand. A different patient who had damage to his ventral posterior lateral nuclei (VPL) of the right thalamus showed the opposite pattern. He was able to correctly identify where he had been touched using a picture of the hand but was unable to decipher where on his own body he had been touched. This double-dissociation highlights the differences between the two proposed perceptions of the body. Body schema integrates vision, proprioception, touch, and motor feedback to form a perception of the body. Thus, the patient who could correctly identify on the picture the location where she had been touched, but was unable to point at the location on her own where on her own body she had been touched, had knowledge of body image but no knowledge of body schema. On the other hand, the participant who could correctly identify where he had been touched on his body, but was unable to transfer that knowledge to a picture of the hand had accurate body schema but not body image.

Body representation: the neural processing systems dedicated to encrypting the body.

Body image: “off-line” perception that is formed from memory and experience. Used in perceptual judgments.

Body perception: refers to the individuals account for that neural representation.

Body schema: “on-line” perception that is formed from updating sensory information. Updated through movement. Used to assess the bodies relative location in comparison to the environment.

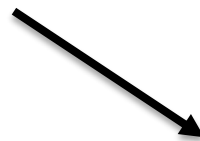
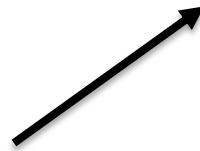


Figure 5: The definitions of body representation and body perception used in this thesis. Body perception can be broken into body image and body schema.

2.2 Studies on body perception

Having an anatomically accurate perception of one’s body is what allows us to interact efficiently with the environment. This is because we use our bodies as a metric guide for our actions. Tasks such as walking through a doorway, reaching for an object or stepping over an object, all rely on having a representation that matches the anatomical structure of these body

parts. For the most part, studies have found this to be the case (Berlucchi & Aglioti, 1997; Berlucchi & Aglioti, 2010; Bolognini, Casanova, Maravita, & Vallar, 2012; Guardia et al., 2010; Keizer et al., 2013; Linkenauger, Witt, Bakdash, Stefanucci, & Proffitt, 2009; Sposito, Bolognini, Vallar, & Maravita, 2012; Sposito, Bolognini, Vallar, Posteraro, & Maravita, 2010; Wagman, Thomas, McBride, & Day, 2013; Warren & Whang, 1987). For example, one study asked participants to identify what they perceived to be their maximum reaching capability (Wagman et al., 2013). They completed this by indicating to the experimenter when they believed an object was placed at their maximum vertical reach. Results showed a slight underestimation but anatomically accurate representation of maximum body length. This finding is unsurprising as if we had inaccurate representation of our body sizes, navigating through our environment and performing novel tasks would be difficult if not impossible.

Not only has body perception been shown to be accurate, research has found that the perception of our own bodies is more accurate than the perception of non-corporeal objects, (Sposito et al., 2012). For example, Sposito (2012) asked participants to indicate the midpoint of their forearms and of a similarly shaped cylindrical object. Participants were significantly more accurate at estimating their own forearms midpoint than they were for the object. Perhaps, this is because we have proprioceptive, visual, and tactile information about the forearm, whereas we only have visual information about the object.

Interestingly, body perception can be manipulated through tool use. Studies that have investigated reaching capabilities before and after tool use have shown participants incorporate the size of a tool into their own body perception (Cardinali et al., 2009; Maravita & Iriki, 2004; Sposito et al., 2012). For example, one study asked participants to indicate the midpoint of their

forearms both before and after using a 60 cm long stick (Sposito et al., 2012). After using the tool participants perceived the midpoint of their forearms as being more distal (closer to their hand) than before using the stick. This finding supports the idea that although body perception reflects the anatomical size it can be altered through action-based affordances (incorporation of a tool to attain a goal). Body perception is also altered when different outcomes of an activity are expected by the participant (Wagman & Morgan, 2010). In this study, participants were asked to report their perceived maximum vertical reaching height while subjected to four different conditions: 1) walking; 2) sitting on the floor; 3) standing on a stool; and 4) using a stick to reach for the object. The participant verbally instructed the experimenter to move an object (that was hung from the ceiling) up or down until it was at the maximum height they believed they could reach, if they stood in the designated area below the object. For the stool condition and stick condition, the stool and stick were placed in the middle of the floor. The results were appropriate for the condition. For example, participants' perceived maximum reach height was greatest in the stick condition so participants incorporated the metrics of each of the conditions into their body representation. These findings indicated that body perception is plastic and can change depending on the situation.

2.3 Studies on hand perception

The hands are the primary physical tools that we use to explore our environments, and so one would expect accurate perception of this body part. However, studies investigating how we perceive our hands have produced conflicting results. For example, one study investigated how long and wide participants perceive their hands to be (Linkenauger et al., 2009). In this

experiment, the experimenter would either lengthen or shorten a retractable measuring tool (with no metric information visible to the participant) and the participants were instructed to inform the experimenter when the measuring tool had reached either the width or length of the participant's hands. Hand width was defined as the distance between the little finger and index finger, and length was defined as the distance between the crease at the bottom of the wrist and the longest fingertip. The results showed that participants were very good at estimating the size of their hands, with right handers perceiving their right hands accurately and their left hands as being slightly underestimated. Left handers perceived both hands accurately. These results are somewhat unsurprising, as one would expect that the body part that we use the most to explore the environment with would be accurately perceived.

In contrast, a different study investigated hand perception through testing participants position sense over ten landmarks on their hands (Longo & Haggard, 2010). In this study participants completed two tasks; a localization task and a body image task. For the localization task, the participants would place their hands underneath a table top (so their hands were hidden from view). The researchers would then instruct the participants to point using a stylus five times to each of the ten locations on their hands (the tips and knuckles of each of their five fingers), in a random order. Between each point the participants would return the stylus to a home spot that was located outside of the span of the hand. Each point (estimation) by the participant was photographed, and from these photos the researchers were able to map out a picture of the participants representations of their hands. Interestingly, these representations were not anatomically accurate and followed several key characteristics: the hand width was overestimated (measured from the knuckles) and the finger lengths (measured as the distance between the tip

and base of each finger) were underestimated. The authors also analyzed hand shape by using a modified version of Napier's shape index (hand width/hand length*100). The results showed a hand shape that was nearly double the size of the participants' real hands, indicating that the estimated hand shape was wider than it was long. The second task involved participants identifying a picture of their hand out of an array of photos of hands (which were distorted as either larger or smaller than their real hands). Participants were able to correctly identify their hand size for this task. Therefore, the body image task produced accurate perceptions, but the localization task surprisingly produced a distorted perception of the hand. The localization task however, would encompass both "on-line" processing (from the sensory information available during the task), as well as "off-line" processing (from the perceptual judgments of hand size), whereas the body image task requires only "off-line" processing (from the stored knowledge gained from experience with the hands). Therefore it is possible that the different tasks (body image and localization task) used different mechanisms of body perception yielding differences in the accuracy of hand representation. Taken together, these studies (Linkenauger's and Longo's) suggest that anatomically accurate body perception depends on how it is measured and on what mechanisms (body image vs body schema) it is based upon. A follow-up study by Longo and Haggard provides further evidence for this (Longo & Haggard, 2012b). In this study, participants completed the body image and localization tasks as before, but added a "metric" measure of body image as well as the template-matching task used in earlier studies (Longo & Haggard, 2012b). This metric measure asked participants to indicate whether the participants thought that a line was shorter or longer than individual parts (each individual finger, and the distances between each knuckle pairing) of the participants' hands. Interestingly, the

underestimation of finger lengths found in the localization task was also seen in the metric measure of body image (but not in the template matching). This result suggests that the metric methods of the localization task are partially responsible for the distortions found in Longo and Haggard (2010). Longo and Haggard argue that the localization task is isolating a body model that is concerned with information about the metric properties of the hand. The metric properties of the hand must be informed by stored knowledge of the hand (as no signals provide this information) and are then combined with postural information (from the proprioceptive signals) to form body schema. Potentially, body image and body schema are different in their accuracy of body perception.

However, since body image and body schema are both types of body perception and both studies involve aspects of both body image and body schema, the conflicting results of these two studies are somewhat confusing, as hand perception cannot be both anatomically accurate (Linkenaguer et al, 2009) and inaccurate (Longo & Haggard, 2010). Perhaps the differing underlying mechanisms of body schema and body image caused the differences observed between the two studies. Another possibility is that the differences between the two studies methods may be influencing the results. Thus, further analyses on how we perceive our hands (hand perception), and the situations in which this distortion (overestimation of hand width and underestimation of finger length) does and does not occur are warranted.

Chapter 3. Theory, Hypotheses, and Predictions

3.1 Theory, Hypotheses, and Predictions

Theory: The two studies included in this thesis are rooted in the theory that body perception (including the perception of our hands) matches anatomical dimensions.

The hypothesis and predictions are listed below.

Hypothesis 1: Hand perception resembles its anatomical dimensions when perceived holistically rather than in pieces.

Prediction 1: Including a reference point when estimating hand size will increase the likelihood of forming a holistic perception, and therefore it will more closely resemble its anatomical dimensions.

Hypothesis 2: Part of the previously described distortion of hand perception is as a result of visual and haptic information interfering with one another.

Prediction 2: If vision and haptic information interfere with one another, estimates of hand size will match anatomical dimensions when only vision or haptic feedback is available

Chapter 4. Experiment 1: A Kinematic Examination of Hand Perception*

*(A version of this document was submitted to Psychological Research)

4.1 Abstract

Previous research has found that the perception of our hands is inaccurate. This distorted perception has several constant characteristics including an overestimation of hand width and an underestimation of finger length. In the current study we further investigate this phenomenon by exploring the boundaries of hand perception. Participants placed one hand underneath a tabletop so it was occluded from view. Using their free hand, participants were instructed to point to the location where they believed the tips and bases of each of their fingers were. These ten landmarks were recorded using a motion capture system. One group of participants pointed to the landmarks in a random order (as done in previous studies) while another group pointed to them in a systematic fashion (from the tip of the thumb sequentially through to the little finger). Furthermore, to explore if having a frame of reference facilitates hand perception, some participants initiated each of their estimations directly from the previous landmark while others initiated them from a home spot located outside the span of the hand. Results showed that the participants who pointed in the systematic order made numerous accurate judgments of hand size and were overall more precise than participants who pointed in a random order. Including a frame of reference however, had no effect on the judgments. The results also showed asymmetries in hand perception. These findings are discussed in relation to different possible internal body representations and hemispheric asymmetries in body perception.

4.2 Introduction

Body perception is defined as a constantly updated sensorimotor and remembered metric representation of the body that functions to register where the body is in space, and how the individual parts of the body come together (Dijkerman & de Haan, 2007; Haggard et al., 2006; Keizer et al., 2013). Body perception is important because we often use our bodies as a metric to guide our actions. For example, estimating whether an object is within arm's reach or determining whether the body can fit through a small space is impossible without an anatomically accurate perception of arm length or shoulder width (Keizer et al., 2013; Warren & Whang, 1987). Some studies have shown that when participants are asked to estimate the length of their own bodies, these estimates match the anatomical size of the body (Bolognini et al., 2012; Guardia et al., 2010; Sposito et al., 2012; Sposito et al., 2010). Furthermore, the perception of body length has been shown to be more accurate than the perception of extrapersonal objects. For example, in a task where participants estimate the length of their own forearms or a similarly sized cylindrical model, participants are better at estimating their limbs compared to the cylinder (Sposito et al., 2010).

The hand is our main source of contact with the environment (Napier, 1980). Surprisingly, the internal perception of our hands has been shown to be distorted (Longo & Haggard, 2010). In that study, participants were asked to judge the location of the knuckles (the Metacarpophalangeal joints (mp joints)) and tips of each of their fingers while their hands rested underneath a tabletop so participants had no vision of their hand. The results showed a consistently distorted perception of the hand: an overestimation of hand width (measured as the distance between knuckle pairings) and an underestimation of finger length (measured as the

distance between knuckle and fingertip). The authors concluded that such distortion is evidence of a body model that is not cognizant of its own metric properties.

The finding of misperceived hand size is puzzling for at least two reasons. First, other studies have shown anatomically accurate estimates of body parts (Sposito et al., 2012) or body size (Warren & Whang, 1987; Wing & Fraser, 1983); and second, one would expect more accurate estimates of body parts that are in constant interaction with the world. After all, it is through our hands that we grasp, manipulate, and identify objects hundreds of times a day. If the internal stored model of our own hands does not match its anatomical size, how are we able to make accurate and consistent grasping movements?

One possibility is that the visuomotor system utilizes a holistic image of the hand rather than isolated landmarks when reaching to grasp an object. Research into the perception of human faces for example, has shown that we do not process faces as a group of individual facial features but as an integrated perceptual whole (Richler & Gauthier, 2014). In the Longo and Haggard (2010) study, participants were asked to point to the ten locations on their hand in a random order (e.g. from the tip of the index finger, to the base of the ring finger, to the base of the thumb etc.). Participants were also instructed to return to a home spot (outside the span of the hand) between each trial. It is possible that this “fragmented” methodology prevented participants from creating a holistic perception of their hand yielding the much distorted map. In the present study we introduce a systematic methodology and a reference point in order to increase the likelihood of forming a holistic perception of the hand to further examine its internal perception.

Participants were asked to point to the ten landmarks of their hands in either the random fashion (random order; e.g. Longo & Haggard, 2010), or in an ordered configuration (systematic order). Participants with the systematic order pointed at their fingertips and knuckles in sequence (i.e. starting at the thumb [digit 1] and continuing sequentially until they pointed to the little finger [digit 5]). Because previous research has shown more accurate body perception when given a single joint as a reference point (Neri, 2009), within each order, half of the participants pointed in a continuous pattern. That is, participants did not return to a home spot, instead they used their previous point on their hand as a landmark for their next estimation. The other half of the participants pointed in an interrupted sequence in which they were required to return to a home spot (outside the span of the hand) after each trial (Longo & Haggard, 2010). We hypothesized more anatomically accurate hand maps in the systematic group and when participants pointed using a continuous pattern.

4.3 Methods

Participants

Forty-eight university students (37 females) participated in exchange for course credit. Handedness was evaluated using modified Edinburgh (Oldfield, 1971) and Waterloo (Brown, Roy, Rohr, & Bryden, 2006) handedness questionnaires. Forty-six participants identified as right-handed and two as left-handed. All participants gave written consent prior to participating.

Materials

An Optotrak Certus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of an infrared emitting diode that was attached to the end of a stylus. The location of the diode was recorded for 1s at 100 Hz for each trial.

Procedure

Participants sat in front of a Plexiglas desk (86.5 X 41.0 cm) with a wooden shelf placed 12 cm below the Plexiglas. Participants were asked to place their right or left-hand (counterbalanced among participants) palm up underneath the Plexiglas and in contact with it (See Fig. 6). The forearm was supported by a thin pillow. Initially half of the participants placed their hand palm down against the wooden shelf (10mm below the Plexiglas; see Fig.6). However, our primary analysis found that the results did not depend on hand orientation so we continued testing only in the palm up condition. After the participant was comfortable, a black tablecloth was placed over the Plexiglas, which occluded vision of the hand. Trials without vision of the hand are subsequently referred to as estimation trials. Participants kept their target hands in a fixed position. They were then instructed to point with the stylus in their free hands to where they believed the tip (the edge of their finger nail) and the base (the knuckle (mp joint)) of each of their digits were. The tablecloth was removed after the estimation trials and participants were instructed to point to their visible landmarks. These were referred to as the real-hand trials.

The experimental design was a 2 X 2 X 2 mixed design. The factors were Order (systematic, random), and Pattern (continuous, interrupted), and there were 12 participants in each of the four groups (systematic-continuous, systematic-interrupted, random-continuous, random-interrupted). Participants with the systematic order pointed at their fingertips in

sequence, from digit 1 (thumb) to digit 5, then to their bases with the same order (half of the participants pointed to their fingertips first and the other half to their bases). Participants with the random order followed Longo and Haggard’s design, in which they randomly pointed to the ten locations on their hand. Participants with the continuous pattern pointed to a target location and then moved to the next target location. Participants with the interrupted pattern returned to a “home spot” that was situated directly above the participant’s fixed forearm [as per Longo and Haggard, 2010]. In all cases, the experimenter verbally instructed the participant where to point on each trial.

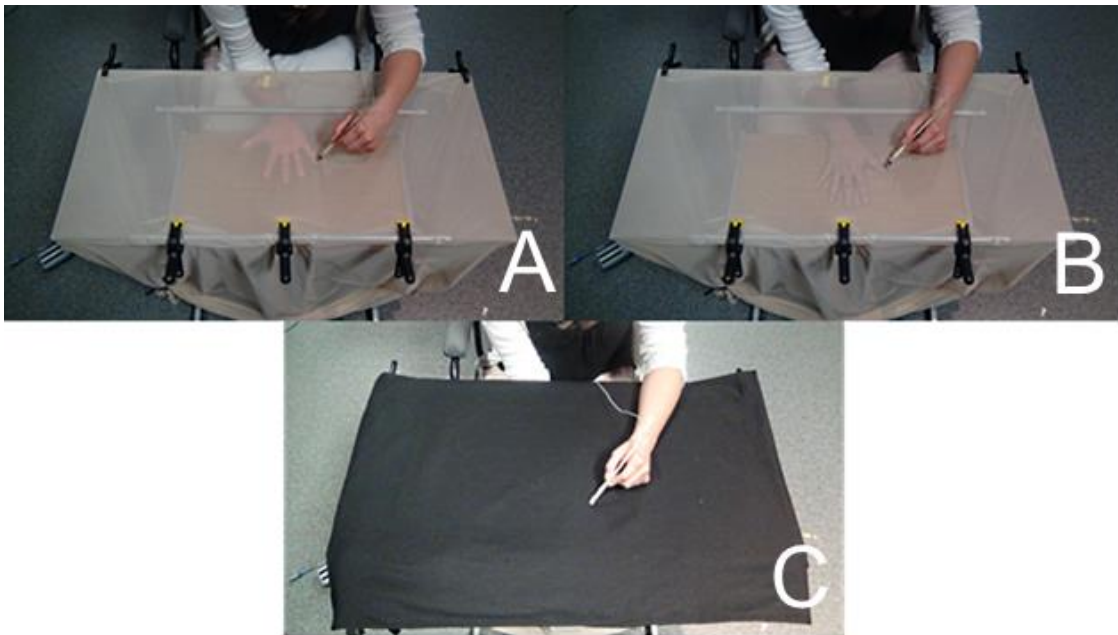


Figure 6: Schematic of the experimental setup. Picture A demonstrates the Palm Up condition. Picture B demonstrates the Palm Down condition. Picture C demonstrates the without vision part of the experiment.

Analyses

Each participant completed 200 trials. There were 50 estimation trials (5 to each of the 10 locations on the hand) and 50 real-hand trials and this was repeated for each hand. We conducted two analyses on the data. The first (estimation vs. real-hand) was conducted to investigate whether the perceived hand (width and finger length) was different from the real one. A series of paired-samples t-tests were conducted on the raw values (expressed in mm) of the perceived versus real hand dimensions (Longo & Haggard, 2010).

The second analysis (effects of Order, Pattern, and Hand) was a 2 X 2 X 2 mixed design ANOVA that included Order (systematic, random), Pattern (continuous, interrupted), and Hand (left, right) as factors. Order and Pattern were between participants factors and Hand was the within participant measure. For the analyses we normalized the data by expressing the estimated values as a percentage of the real-hand values $[(\text{perceived hand}/\text{real hand}) * 100]$. For instance if the perceived distance between the tip of digits 1 and 2 was 120mm and the real distance was 111 mm, the normalized value would be 109%, a 9% overestimation. We made this transformation to account for individual differences in hand size¹. Reported values are means and standard error of the means.

The two analyses were repeated for four dependent variables: hand width, finger length, thumb length, and opposition. Hand width was determined by the great span, which was defined as the sum of the distances between the tips of each digit, including the thumb (see Figure 7). Finger length was calculated by averaging the distance from the tip to the base of each digit for

¹ We also conducted a repeated measures ANOVA using the standard deviation of the five repetitions to each landmark to assess if hand differences were related to the hand employed to point to the landmarks. No significant differences were found between the right and left hands.

all five digits, including the thumb. Two measures were used to investigate the perception of the thumb: length, the distance from the tip to the base of digit 1; and opposition, the distance between digits 1 and 2. We introduced the great span and opposition measures as they are of particular relevance with respect to power- (using the whole hand) and pincer-grasps (using the index finger and thumb).

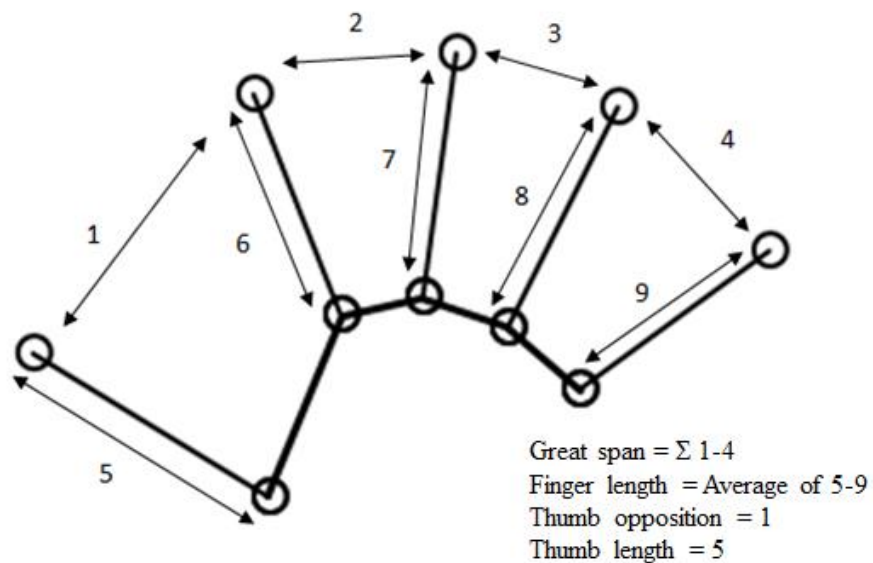


Figure 7: Representation of the measures used to analyze hand size.

Data processing:

All Trials were visually analyzed and extreme outliers were removed from subsequent analysis (<1% of the trials).

4.4 Results

Analyses included all participants but they were also conducted without the two left-handed individuals to ensure that their inclusion did not have an effect on the results. Results from every measure were similar with and without the left handers so we opted to include them.

Hand width

Estimation vs Real Hand

Participants with the systematic order accurately estimated the width of their hands as the real and estimated values were not significantly different from each other, $p > .1$. In the random order however, there was a significant overestimation of the left and right hands [left hand estimated $210.65\text{mm} \pm 6.32$, left hand real $193.51\text{mm} \pm 4.22$, right hand estimated $211.23\text{mm} \pm 8.11$, right hand real $185.36\text{mm} \pm 4.13$; $t(23) = -2.58$, $p = .02$, $t(23) = -2.95$, $p < .01$].

Effects of Order, Pattern, and Hand

There was a main effect of order, $F(1,44) = 10.7$, $p < .01$, $\eta^2 = .196$. Participants with the random order overestimated hand width more than the participants with the systematic order ($12.4 \pm 3.3\%$ versus $-2.98 \pm 3.3\%$ respectively). An effect of hand approached significance $F(1,44) = 3$, $p = .09$, $\eta^2 = .064$, where the right hand ($6.9 \pm 2.9\%$) was overestimated more than the left hand ($2.5 \pm 2.4\%$). There were no other significant main effects or interactions.

Finger length

Estimation vs Real Hand

When participants pointed using the systematic order, finger lengths for the right hand were accurate [$p > .1$], but estimates for the left hand were significantly underestimated, [left hand estimated $48.9\text{mm} \pm 2.1$, left hand real $56.2\text{mm} \pm 0.9$, $t(23) = 3.9$, $p < .01$]. Participants in the random order however, underestimated the length of their fingers in both hands, [left hand estimated $46.8\text{mm} \pm 1.7$, left hand real $56.7\text{mm} \pm 2.2$, $t(23) = 3.3$, $p < .01$; right hand estimated $44.6\text{mm} \pm 1.3$, right hand real $54.2\text{mm} \pm 0.7$, $t(23) = 7.3$, $p < .01$].

Effects of Order, Pattern, and Hand

There was a main effect of order, [$F(1,44) = 6.4$, $p = .02$, $\eta^2 = .127$]. Participants assigned to the random order underestimated finger length ($-16.6 \pm 2.6\%$) more than those assigned in the systematic order ($-7.3 \pm 2.6\%$). The order by hand interaction was also significant [$F(1,44) = 4.7$, $p = .04$, partial $\eta^2 = .135$]. Follow up t-tests showed that in the systematic group, finger length on the left hand was underestimated when compared to the right $t(23) = -2.4$, $p = .02$. The same was not the case in the random group $t(23) = 0.5$, $p = 0.6$, which underestimated finger length of their hands to the same extent (see Figure 8).

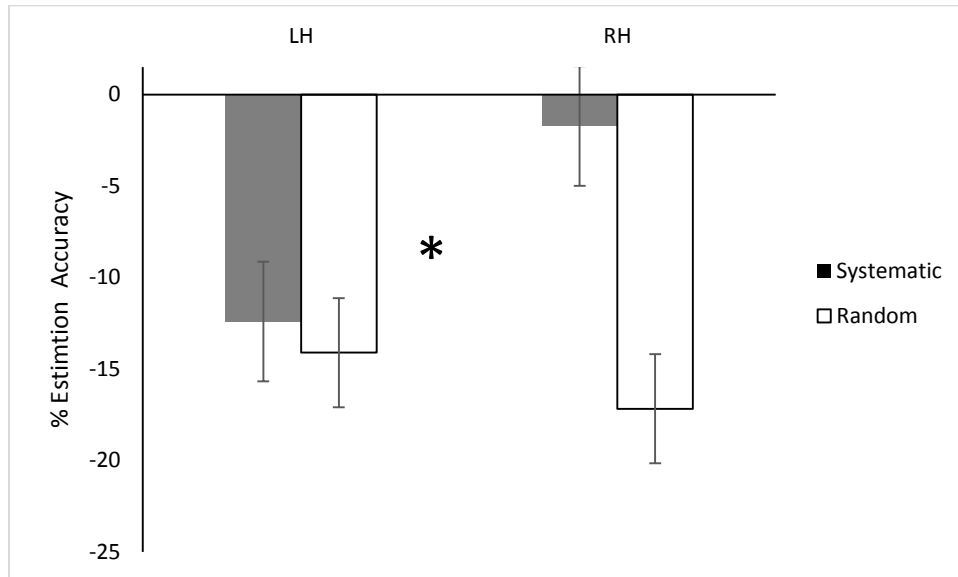


Figure 8: Results of the Finger length Order X Hand interaction. The grey bars represent the systematic group’s estimates and the white bars represent the random group’s estimations. There was a significant interaction between the right hand of the systematic and random group, where the random group underestimated their finger lengths significantly more than the systematic group. The error bars represent the standard error of the mean.

Thumb Length

Estimation vs Real Hand

No main effects were found.

Effects of Order, Pattern, and Hand

There was a significant main effect of hand, $F(1,44)=4.2$, $p=.05$, $\eta^2=.087$, where length of the left thumb ($-8.9\pm 4.1\%$) was underestimated more than of the right thumb ($1.6\pm 4.1\%$).

Thumb Opposition

Estimation vs Real Hand

Opposition in both hands and both orders was underestimated [systematic order left hand: $t(23)=-5.7$, $p<.01$; right hand: $t(23)=-8$, $p<.01$; random order left hand: $t(23)=-2.4$, $p=.02$; right hand: $t(23)=-2.9$, $p<.01$].

Effects of Order, Pattern, and Hand

There was a significant main effect of order, $F(1,44)=5.6$, $p=.02$, $\eta^2=.113$.

Participants assigned to the systematic order underestimated ($-23.9\pm 3.6\%$) the distance between digits 1 and 2 more than those participants assigned to the random order ($-11.8\pm 3.6\%$). No other main effects or interactions were found.

4.5 Discussion

In the present study, participants placed one hand underneath a tabletop and pointed at the location where they thought their knuckles and fingertips were located. One group of participants pointed at these landmarks in a systematic fashion (Digit 1, 2, 3...), while the other group indicated the location of the landmarks in a random order. Half of the participants pointed in a continuous pattern (moved directly from one landmark to the next), the other half pointed in an interrupted pattern, returning the stylus to a home spot between trials. Hand maps were constructed from coordinates acquired with a 3D motion capture system. The effects of order (systematic, random), pattern (continuous, interrupted), and hand (left, right) were investigated for hand span, digit length, thumb length, and thumb opposition. The results showed several

significant differences for order and hand, but not for pattern (see Table 1). These results are discussed below.

Table 1 – List of distortion seen by order and pattern. A ↑ indicates a significant overestimation, a ↓ indicates a significant underestimation, and a — indicates no change.

Systematic order					Random order				
	Continuous		Interrupted			Continuous		Interrupted	
	LH	RH	LH	RH		LH	RH	LH	RH
Width	—	—	—	—	Width	—	↑	↑	↑
Finger Length	↓	—	↓	—	Finger Length	↓	↓	↓	↓
Thumb Length	—	—	—	—	Thumb Length	—	—	—	—
Thumb Opposition	↓	↓	↓	↓	Thumb Opposition	—	↓	↓	—

Longo and Haggard (2010) reported a distorted body model of the hands. They described the distortion as an overestimation of hand width and an underestimation of finger length. The results from the random-interrupted group replicate those found by Longo and Haggard; participants overestimated the width of their hands but underestimated the length of their fingers (see Table 1). When participants pointed to the landmarks of their hands in a systematic order however, hand perception was less distorted. Sequential pointing allowed for many accurate estimations of hand size, particularly in terms of width. Surprisingly, there were no differences

between those participants who completed the task in a continuous pattern and those who used an interrupted pattern. This result suggests that the more accurate estimates made by participants in the systematic group was not because they used a reference point within the hand to make their estimates, otherwise those in the continuous group would have been more accurate. We offer three (non-mutually exclusive) possible explanations to account for the greater accuracy found in the systematic group.

First, it has been argued that body perception utilizes a stored body model, as well as a model that uses online sensory information for constant updating (de Vignemont, Ehrsson, & Haggard, 2005). It is possible that participants in the systematic group had access to *both* perceptions; the stored model plus the continuously updating one that in this case used visual information from the previous landmark to update the perception of the hand. Second, a “neighbouring effect” could also explain the more anatomically accurate estimates made by the systematic group. A recent study examining toe perception found more accurate identification between neighbouring toes (Cicmil, Meyer, & Stein, 2015). For example, identification of digit 2 (toe 2) was more accurate following stimulation of digit 1 but not digit 4. This result suggests that in a body localization task, moving sequentially through body parts (as it was done in the systematic group) could enhance their perception. Third, it is also possible that participants who completed the task in the systematic order had access to a more “holistic” perception of their hand. Research has shown that when learning about spatial layouts, two independent representations can be formed (Saulton, Dodds, Bulthoff, & de la Rosa, 2015; Shelton & McNamara, 2004). One of these representations is analytical and relies on the relationship *between* individual landmarks (i.e. distance), while the other relies on a holistic image accessed

by memory. Importantly, research has found that human faces and body parts are processed holistically and not only analytically (Farah, Wilson, Drain, & Tanaka, 1998; Reed, Stone, Bozova, & Tanaka, 2003; Seitz, 2002; Tanaka & Farah, 1993). So it is possible that the group that pointed to the landmarks systematically was accessing a holistic representation of the hand that facilitated its perception. This possibility offers an explanation as to how we are able to effectively grasp objects even with a distorted body model of the hand; when we grasp an object we are likely accessing a holistic perception of the hand and not relying on where individual landmarks are located in space. Previous research has suggested that grasping involves the independent programming of the index finger and thumb (Smeets & Brenner, 2001). The current findings would suggest, however, that a holistic perception of the hand would yield more accurate grasping movements. This speculation warrants further research.

Another finding of the current investigation is that hand perception is different across hands. We found that when compared to their left hand, participants overestimated the width of their right hands to a greater extent. In addition, underestimation of finger length was greater for the left hand than for the right hand. Because the width of the right hand was overestimated and finger length of the left hand underestimated the result was an overall larger perception of the right hand (see Figure 9). Previous research has found similar results (Linkenauger et al., 2009). In that study participants were asked to indicate on a tape measure the perceived width and length of their left and right hands. The results showed that the right hand was overestimated when compared to the left hand. The same study also found that participants perceived their right hands as being capable of grasping larger objects than their left hands (Linkenauger et al., 2009). It is possible that because right-handers prefer to use their dominant hands for a multitude of actions

including grasping, object manipulation, and tool use (Corey, Hurley, & Foundas, 2001; Gonzalez & Goodale, 2009; Janssen & Steenbergen, 2011; Porac, Coren, Steiger, & Duncan, 1980; Steenhuis, Bryden, Schwartz, & Lawson, 1990; Stone & Gonzalez, 2014) they may perceive their right hand as being more capable of performing actions. This, in turn, would lead to a smaller perception of the left hand as it affords fewer possibilities than the right hand. Current studies in the lab aim at addressing this possibility.

In their paper Longo and Haggard (2010) argue that the misrepresentation of the hands shares similar characteristics with that of the homunculus such as an accentuation of the mediolateral over the proximodistal axis. A larger perception of the right hand could also be explained in terms of homuncular representation. It has been shown that in right-handers, the cortical somatosensory representation of the hand is larger for the right than for the left hand (Buchner, Kauert, & Radermacher, 1995; Soros et al., 1999). If the homunculus provides a cortical map of the hand and the somatosensory representation of the right hand is larger than of the left, this would explain why we found hand differences. Future studies are needed to characterize the conditions in which such asymmetries in hand perception arise.

One last finding worth noting is regarding the estimates of thumb length and opposition. The thumb was the only digit for which length was estimated accurately in *every* condition and in both hands, suggesting a more reliable perception of this digit. It has been argued that the evolution of the thumb allowed for upright posture, tool making, and tool use, all of which led to an enlarged brain (Napier, 1980; Susman, 1988). Mapping studies of the primary somatosensory cortex (S1) using electrophysiological methods showed that the area for the thumb is larger than the area representing the other digits (Penfield & Boldrey, 1937; Sutherling et al., 1992). A recent

neuroimaging study used 7T fMRI to precisely map the cortical representation of single digits in human S1 (Martuzzi, van der Zwaag, Farthouat, Gruetter, & Blanke, 2014). For the study, participants laid inside the scanner while each one of their fingers was stimulated by touch. The results showed that the thumb has a much larger cortical representation than the representation of the other fingers. The authors discuss that because such magnification has not been shown in non-human primates, the enlargement is likely reflective of the increased tactile function in humans due to thumb opposition and precision grip. Perhaps because of its evolutionary relevance and greater somatosensory cortical representation, the perceptual estimates of the thumb were not underestimated as was the case for the other digits. With respect to thumb opposition, our results showed an underestimation of the distance between thumb and index finger for both hands in both orders. Previous research has shown that the perception of the thumb is that of being nearer to the index finger (Margolis & Longo, 2015), which aligns with the current findings. Margolis & Longo argue that this is caused by the thumb being orientated “side-on” (when all the fingers are spread out) whereas the rest of the fingers are orientated “front-on.” So it is possible that participants tried to align the thumb more like a finger and thus its perception would be that of being closer to the index finger (see Figure 9). Another possibility is that the perception of the distance between thumb and index finger also follows the somatosensory map of S1. Puzzling, the distance between adjacent digits has been shown to only be different between dyads D1-D2 and D4-D5 (Martuzzi et al., 2014). In other words, somatotopically, the distance between thumb and index finger is not different from the distance between index finger and middle finger or middle finger and ring finger. This might explain why we found the distance between D1 and D2 to be underestimated.

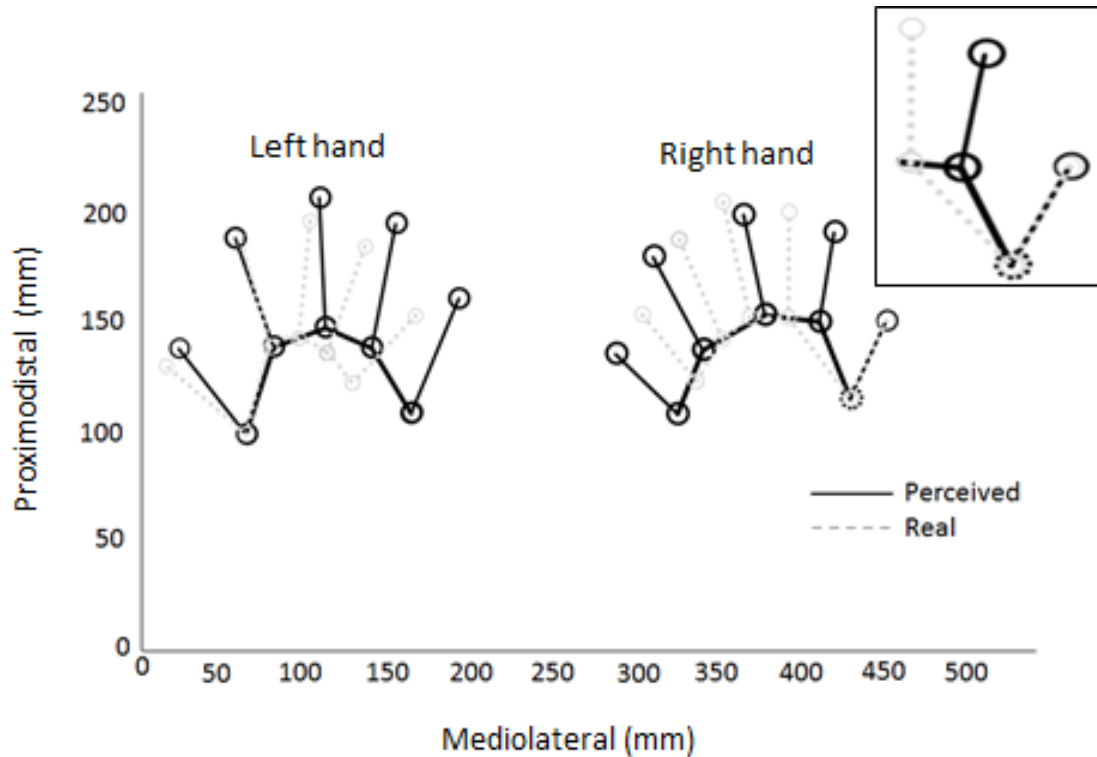


Figure 9: Schematic of the distortion seen in both hands. The close up (framed) focuses on how “side on” perception of the thumb compares to the “front on” perception of the rest of the digits. The perception of the right hand was overall larger than the perception of the left hand.

In conclusion, the current study confirms the notion that the perception of the human hand is inaccurate (when compared to its corresponding anatomical size), but demonstrates that when pointing to each finger in succession, the magnitude of the distortion substantially decreases. In the case of the width of the hands, the distortion was eliminated completely. The study also found that the right hand is perceived as being larger than the left, and that the only digit not underestimated was the thumb, which was accurately perceived. Taken together, these results suggest that the perception of our hand is dynamic, and that it seems to resemble the somatotopic representation in S1.

Compliance with Ethical Standards

Funding: This study was funded by a discovery grant awarded to Claudia LR Gonzalez from the Natural Sciences and Engineering Research Council of Canada.

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent: Informed consent was obtained from all individual participants included in the study.

Chapter 5. Experiment 2: The Visual and Haptic Contributions to Hand Perception

5.1 Abstract

The present study examined the contributions of vision and haptics separately and combined to the perception of our hands. Based on previous studies we hypothesized that perception would more closely resemble the anatomical size when hand estimates were produced under a single sensory modality. To this end participants pointed to their concealed hand in one of three groups: Vision+Haptics, Vision-only, or Haptics-only. Participants in the Vision+Haptics group had vision (non-informative) of the experimental set up and of the pointing hand (but no vision of the hand being estimated). They also experienced haptic feedback as the palm of the hand was in contact with the undersurface of a tabletop where the estimations were made. Participants in the Haptics-only group completed the task with the hand underneath the tabletop (as in the Vision+Haptics group) but did so while wearing a blindfold (no vision). In the Vision-only group instead of placing the hand to be estimated underneath the tabletop, they placed it behind their backs. Participants in this group were asked to imagine (no tactile feedback) as if the hand was under the table when making their estimations. All participants estimated the position of ten landmarks on the hand; the fingertip and the metacarpophalangeal joint of each digit. Hand maps were constructed by using a 3D motion capture system. Supporting our hypothesis, participants in the Haptics-only group produced the most anatomically accurate hand maps. Contrary to our hypothesis the maps were most distorted in the Vision-only group. We discuss the possibility that vision interferes with somatosensory processing.

5.2 Introduction

A perception of body size that matches its anatomical dimensions is necessary in order to interact efficiently with our surroundings. This is because we use our bodies as a guide to perform actions in our environment. For example, tasks such as reaching out to grab a glass of water, stepping over an obstacle, or reaching to a high shelf would be impossible without an accurate perception of the length of ones arms and legs. Body representation is defined as representations of body dimensions stored in the brain (Dijkerman & de Haan, 2007; Gallagher, 2005; Haggard & Wolpert, 2005; Paillard, 1999; Serino & Haggard, 2010). Body perception refers to the individual's account for this neural representation. Body perception can be measured by both explicit and implicit methods. Explicit body perception tasks refer to tasks in which participants must actively assess their own body size. Whereas, implicit tasks are concerned with how participants view a landmark on their body. Many studies on body perception have shown that it matches the anatomical size (Bolognini et al., 2012; Guardia et al., 2010; Sposito et al., 2012; Sposito et al., 2010). However, most of these studies use explicit methods to investigate if the perception of the body is anatomically accurate. For example, a study investigating perceived reaching capabilities asked participants to instruct the experimenter to raise or lower an object, until it was at what the participant believed to be her/his maximum reaching height. The results showed that participants were consistently within 90% of their actual max capacity (Wagman et al., 2013). Similarly another study found that participants were able to accurately identify the size of their bodies as well as of body parts (Hennighausen, Enkelmann, Wewetzer, & Remschmidt, 1999). In this study, participants had to assess photographs of their

bodies and indicate if the photo reflected their accurate body size. They also assessed individually the size of their lower leg, thigh, chest, and head. Other research using implicit methods however, has shown inaccurate perception of body parts, specifically of the hands (Longo & Haggard, 2010). In this study, participants were asked to identify ten locations on their hands (the tips and Metacarpophalangeal joints (mp joints) of each finger) when they had no vision of their hands. The results showed a distorted hand, that was significantly wider than the participant's real hand, and the finger lengths were significantly shorter. These findings have been replicated numerous times (Longo, 2014; Longo & Haggard, 2012a, 2012b; Longo, Long, & Haggard, 2012; Saulton et al., 2015). Interestingly, this study employed an implicit testing technique as the task required the participants to identify a location in space. This result is puzzling as it is with our hands that we primarily interact with our environment in a (usually) efficient and accurate manner.

One interpretation is that the hand displays these distortions of body perception because it is reflecting underlying tactile receptive field geometry (Longo & Haggard, 2011). In this study, two tactile stimuli were presented on the back of a participant's hand. Participants then judged which of the pairs of stimuli felt further apart. One of the stimuli was presented along the hand and the other was presented across the hand. Across the hand stimuli were constantly perceived as being larger than along the hand stimuli. The authors argue that the reason why the dorsal side of the hand is constantly overestimated is because the tactile receptive fields are anisotropic. In other words the tactile receptive fields on the hairy side of the hand are oval shaped and this leads to the distortions of hand perception.

A different possibility as to why the perception of the hands was shown to be distorted is because during testing, visual information modified somatosensory processing, specifically

haptic information. Haptic feedback refers to both tactile information from the skin receptors, and proprioceptive information from the receptors in the joints, ligaments and muscles (Grunwald, 2008; Keysers, Kaas, & Gazzola, 2010; Lederman & Klatzky, 1990). For example, in the aforementioned study by Longo and Haggard (2010), participants were asked to point on a table to where they believed their mp joints and fingertips were while their hand rested underneath a tabletop. So participants had haptic information of the hand they were estimating but no vision of this hand. They however, had vision of the tabletop and of their free hand executing the pointing movements. This visual information, although not informative with respect to the hand being estimated, could have influenced the results. Previous research has shown that vision interferes with tactile perception. For example, in one study, participants were asked to indicate when they felt a pulse delivered to the left index finger. The results showed that there were significantly more false alarms (the participant reported a pulse when there was not one) when participants had vision of their hands, suggesting that vision interferes with tactile perception (Mirams, Poliakoff, Brown, & Lloyd, 2010). In a different study, it was examined if objects that resemble the shape of the human hand also displayed distortions of perception like the hand (Saulton, Longo, Wong, Bühlhoff, & de la Rosa, 2016). Participants were asked to estimate the size and shape of their own hand, a rubber hand, and a rake (using similar methods as that of Longo & Haggard (2010)).

When estimating their own hand participants had vision and haptic feedback. However, the visual information that was available to the participant only included the experimental set-up and the hand with which they used to point to each landmark, as the hand underneath was occluded from view. Therefore, participants received no visual information about their hidden hand(s), encouraging them to rely only on haptic feedback to estimate its shape and size. However, for

estimating the rubber hand and rake, no visual *or* haptic feedback was available to the participants. Surprisingly, the characteristic distortion was present to the same magnitude in both the rake and the rubber hand, which were significantly less distorted than to the hand. This result suggests that a participant's perception of an object can be distorted similarly to the distortion seen in hand perception. The distortion in the perception of the object however, is significantly smaller in magnitude than the distortion in the perception of the hand. An additional study also found this same result (Saulton et al., 2015). The authors suggest that the differences in distortion magnitude between the hands and the objects may be as a result of participants having visual information (non-informative) and haptic/somatosensory information about their hands, whereas they did not have haptic information about the objects. This suggests that haptic information may be driving the distortions seen in previous studies. A second possibility is that the increased magnitude of distortion seen in the hand could be as a result of the two sensory modalities (vision and haptics) interfering with one another.

Previous research has found that when participants were blindfolded they performed significantly better at localizing the landmarks on their hands than when they had vision (i.e. non-informative) of the hand (Longo, 2014). The author argued that this result could be due to hand perception being plastic. That is, the differences between blindfolded and non-blindfolded conditions could be the result of immediate vision inducing rapid changes in hand perception, or of blindfolding causing a short-term change in hand perception through inhibition of the somatosensory cortex (Longo, 2014). A different possibility is that when participants only had haptic information they performed better as they did not have visual information competing and interfering with the perception of the hand. If vision and haptics are interfering with one another

(Mirams et al., 2010), then testing each of these sensory modalities separately should produce more anatomically accurate hand estimates.

The purpose of the present study was to conduct a comprehensive examination of the role that vision and haptics play on the perception of the human hand. To investigate how different sources of sensory information shape hand perception, we designed a task wherein participants were recruited and assigned to one of three groups: (1) Vision+Haptics, (2) Vision-only, and (3) Haptics-only. The participants in each of the three groups were required to point to where they believed ten different landmarks on their hands were located, while their hands were hidden from their view. The Vision+Haptics group completed the task while seated in front of a Plexiglas desk with one hand placed palm up against the undersurface of the Plexiglas (and haptic feedback available). The Plexiglas was covered by a black tablecloth to prevent vision of the hand being estimated (only non-informative visual information was available). The participants in the Vision-only group were instructed to imagine as if their hands were placed underneath the tabletop, but instead they placed their hand behind their backs (no tactile feedback). Participants in the Haptics-only group completed the task just like the Vision+Haptics group but they wore a blindfold to prevent non-informative visual information from playing a role in the estimations. We hypothesized that the Vision+Haptics group should yield results similar to those by Longo and Haggard (2010), whereas the Vision-only and the Haptics-only groups would have better accuracy in the perception of their hands, as they would not have conflicting sources of sensory information to rely on when making the judgements.

5.3 Methods

Participants

Fifty-one right-handed university students (45 females) participated in the study in exchange for course credit. Handedness was evaluated using modified versions of the Edinburgh (Oldfield, 1971) and Waterloo (Brown, Roy, Rohr, & Bryden, 2006) handedness questionnaires. All participants gave written consent prior to participating.

Materials

An Optotrak Certrus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of an infrared emitting diode that was attached to the end of a stylus. The location of the diode was recorded for 1000ms at 100 Hz for each trial.

Procedure

Participants were divided into three equal groups: Vision+Haptics group, Vision-only group, and the Haptics-only group (17 participants per group). The Vision+Haptics group placed their hands palm up underneath a Plexiglas desk (86.5 X 41.0 cm) with a wooden shelf placed 12 cm below the Plexiglas (see Figure 10). Their forearm was supported by a thin pillow. The table was then covered by a black tablecloth, occluding vision of the participant's hand (the estimation trials). The participant was then asked to locate (in a random order) ten different locations (the Metacarpophalangeal joints and tips of each of the five fingers) on their hands using a wooden stylus that contacted the top of the plexiglass table (directly above where the hand was located). After each trial, the participant returned the stylus to a home spot that was located directly above

the participant's forearm. After the participant completed the estimation trials, they repeated the task but with full vision of their hands (the real trials). The real trials were conducted so that an actual measure of the participant's hands could be used to compare the estimation trials to. The task was then repeated again using the other hand. Starting hand was counterbalanced across the participants. The Vision-only group completed the same task but in order to eliminate tactile feedback about the hand, participants were instructed to imagine like their hands were placed palm up underneath the glass table, but instead were instructed to place their hands behind their back. The Haptics-only group completed the same task but instead of having a black tablecloth occlude the hand, participants in this group completed the estimation trials while wearing a blindfold (no vision). The Haptics-only group completed the same procedures as the other two groups.



Figure 10. Setup of the experiment for the real condition, and then the estimation conditions for each of the three groups (Vision+Haptics, Vision-only, Haptics-only). Picture A is the setup of the real condition for each of the three groups. Picture B is the estimation trial setup of the Vision+Haptics group. Picture C is the setup of the Vision-only group's estimation trials. Picture D is the setup of the Haptics-only group estimation trials.

Participants completed a total of 200 trials; 50 estimation trials and 50 real trials per hand. In both conditions (estimation and real trials) participants pointed to each of the 10 locations on the hand 5 times (for a total of 50 trials per condition). Two main analyses were conducted on the data. The first analysis consisted of a series of a priori comparisons between the real and estimated hand dimensions (analysis 1). These raw values were obtained by taking the distance between each average landmark location for each measure used in the analyses. These a priori comparisons were modeled after the analysis used by Longo and Haggard (2010). The second analysis (investigating the effects of Group and Hand) consisted of a 3 X 2 mixed design ANOVA that included Group (Vision+Haptics, Vision-only, Haptics-only) as a between factor and Hand (left, right) as a within factor (analysis 2). For this analysis the data were normalized by expressing the estimated values as a percentage of the real hand values (estimated hand-real hand) / (real hand*100). This normalization was done in order to account for individual hand size differences.

The two analyses were repeated for five dependent variables: great span, little span, finger length, thumb length, and opposition (see Figure 11). The great span was defined as the summed distance between digit 1 and digit 5. The little span was defined as the summed distance between the tip of digit 2 and the tip of digit 5. Finger length was calculated by averaging the distance between the tip and metacarpophalangeal joint (mp joint) for each of the five digits. Thumb length was determined as being the distance from the tip of digit 1 to the mp joint of digit 1. Thumb opposition was determined as the distance between the tip of digit 1 to the tip of digit 2. We included the two analyses of width as the great span includes the thumb (which is the distance that would be used to perform a power grasp), whereas the little span is what is

traditionally used in this research (Longo & Haggard, 2010). We also included an in-depth analysis on measures about the thumb (length and distance to the index finger) as thumb opposition is what makes a pincer grasp.

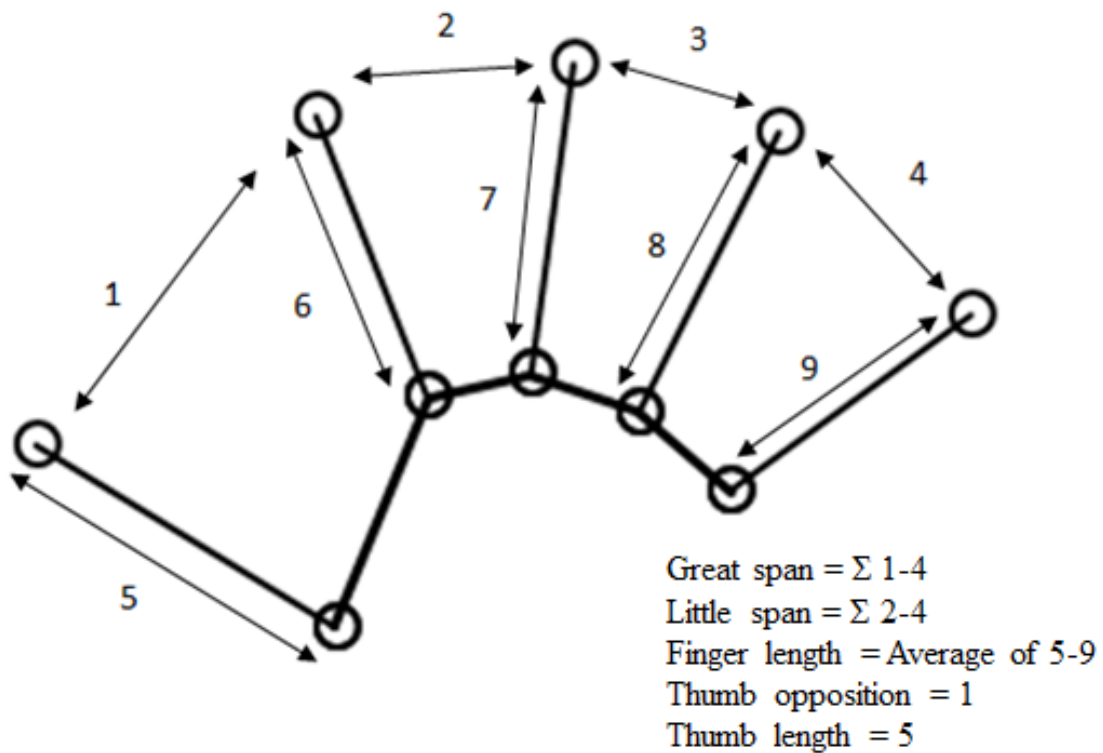


Figure 11. A representation of the measures used in the experiment.

Data processing:

All trials were visually inspected, and extreme outliers were removed from the analysis (<1% of all trials). Visual inspection involved determining whether the trials were greater than 5 cm from any of the other landmarks for the same location.

5.4 Results

Table 2 summarizes the findings. Below *only significant results* are described. Reported values are means and standard error of the means.

Analysis One

Vision+Haptics

Hand Width: Great Span: Width of the great span was overestimated in both hands [Left hand $t(16)= 2.6, p=.02$; Estimated hand $220.8\text{mm}\pm 7.5$, Real hand $197.3\text{mm}\pm 5.2$; Right hand $t(16)=2.7, p=.02$; Estimated hand $221.1\text{mm}\pm 8.6$, Real hand $191.6\text{mm}\pm 4.9$].

Hand Width: Little Span: Width of the little span was overestimated in both hands [Left hand $t(16)= 3.7, p<.01$]; Estimated hand $125.6\text{mm}\pm 13.0$, Real hand $102.4\text{mm}\pm 8.1$; Right hand $t(16)=4.8, p<.01$; Estimated hand $152.2\text{mm}\pm 6.7$, Real hand $110.9\text{mm}\pm 4.5$].

Finger Length: Participants underestimated the length of their fingers in both hands [Left hand: $t(16) = -2.7, p = .02$; Estimated hand $47.6\text{mm} \pm 1.9$, Real hand $58.6\text{mm} \pm 3.0$; Right hand: $t(16) = -4.4, p < .01$; Estimated hand $46.9\text{mm} \pm 1.8$, Real hand $55.6\text{mm} \pm 0.8$].

Vision-only

Hand Width: Little Span: Width of the little span was overestimated for the left hand [$t(16) = 2.8, p = .01$ Estimated hand $147.5 \text{ mm} \pm 9.6$, Real hand $119.3\text{mm} \pm 3.9$].

Finger Length: Participants underestimated the length of their fingers in both hands [Left hand: $t(16) = -5.8, p < .01$ Estimated hand $40.7\text{mm} \pm 1.7$ Real hand $52.2\text{mm} \pm 1.6$; Right hand: $t(16) = -6.2, p < .01$ Estimated hand $42.1\text{mm} \pm 1.15$, Real hand $53.4\text{mm} \pm 1.1$].

Thumb Opposition: This measure was significantly underestimated for both the right and left hands [Left hand: $t(16) = -4.3, p = .01$ Estimated hand $51.5\text{mm} \pm 4.7$, Real hand $74.3\text{mm} \pm 2.6$; Right hand: $t(16) = -4.9, p < .01$ Estimated hand $55.9\text{mm} \pm 4.0$, Real = $78.1\text{mm} \pm 2.8$].

Thumb Length: The thumb length estimates were marginally underestimated. This underestimation was approaching significance in both hands [Left hand: $t(16) = -2.085, p = .053$ Estimated hand $43.3\text{mm} \pm 3.4$ Real hand $50.4\text{mm} \pm 2.77$; Right hand: $t(16) = -2.068, p = .055$ Estimated hand $40.71\text{mm} \pm 3.11$ Real = $47.91\text{mm} \pm 1.48$].

Haptics-only

Hand Width: Great Span: Width of the great span was overestimated for the right hand only

[t(16)=2.7, p=.02 Estimated hand 208.3mm±7.4, Real hand 186.5mm±4.6].

Hand Width: Little Span: Width of little span was also significantly overestimated for the right

hand only [t(16)=2.4, p=.03 Estimated hand 138.2mm±7.0, Real hand 116.2mm±6.5].

Table 2 - List of distortion seen by group. A ↑ indicates a significant overestimation, a ↓ indicates a significant underestimation, and a — indicates no change. Arrows in grey represent measures that were approaching significance.

	Vision + Haptics		Vision-only		Haptics-only	
	LH	RH	LH	RH	LH	RH
Great Span	↑	↑	—	—	—	↑
Little span	↑	↑	↑	—	—	↑
Finger Length	↓	↓	↓	↓	—	—
Thumb Opposition	—	—	↓	↓	—	—
Thumb Length	—	—	↓	↓	—	—

Analysis Two

Group Comparisons

Hand Width: Great Span: The hand X group interaction approached significance

[$F(2,48)=2.909, p=.06$]. Follow-up paired samples t-tests revealed that participants in the Haptics-only group approached significance in overestimating their right hands ($12.24\% \pm 4.4$) compared to their left hands ($3.05\% \pm 5.67$) $p=.06$. No differences were found between the hands for the participants in the Vision+Haptics and Vision-only groups in estimating the width of the great span.

Hand Width: Little Span: There was a main effect of hand [$F(1, 48)=5.068, p=.03$ partial $\eta^2=.095$], indicating that participants overestimated the width of their right hands ($27.57\% \pm 5.56$) more than their left hands ($17.63\% \pm 4.57$). There was also a hand X group interaction [$F(2,48)=5.401, p<.01$ partial $\eta^2=.184$] (see figure 12). Follow-up paired samples t-tests revealed that the participants in the Vision+Haptics group overestimated the width of their right hands ($43.67\% \pm 12.23$) more than their left hands ($18.39\% \pm 6.38$; $t(17)=-3.07, p<.01$). The Haptics-only group showed a trend in this same direction (right hand = $23.15\% \pm 8.1$, left hand = $9.05\% \pm 7.4$); $t(17)=-1.96, p=.07$. There was no difference between the hands in the Vision-only group ($p=.221$).

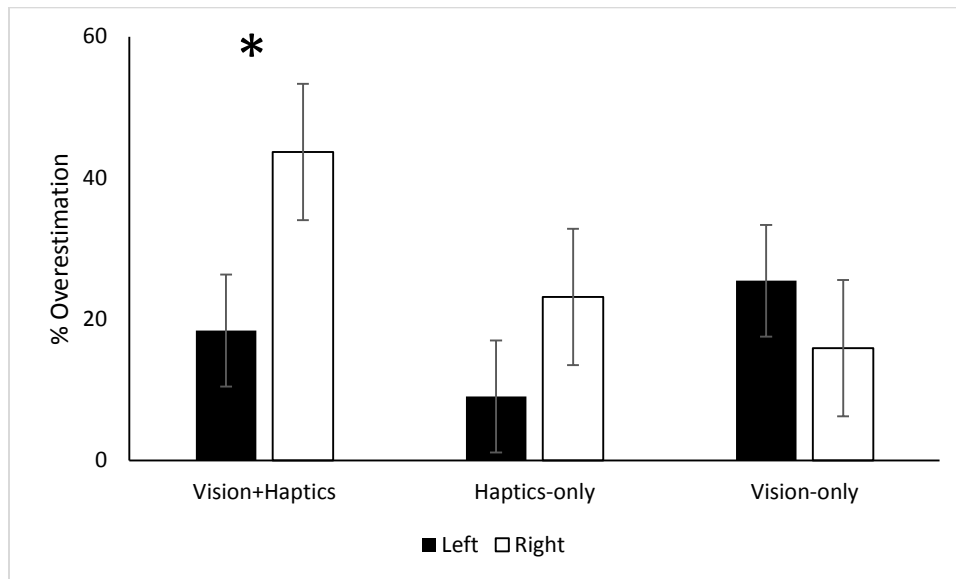


Figure 12. Results of the hand X group interaction for the Little Span. The black bars represent the left hand and the white bars represent the right hand. Note the significant difference between the left and the right hand in the Vision + Haptics group, but not for the other groups. Error bars represent standard error of the mean.

Finger Length: There was a main effect of group [$F(2,48)=6.6$, $p<.01$ partial $\eta^2=.215$]. Follow-up pairwise comparisons revealed that the participants in the Vision+Haptics group underestimated the length of their fingers more than participants in the Haptics-only group ($-15.7\% \pm 3.5$ vs. $-3.6\% \pm 3.5$; $p<.01$). Participants in the Vision-only group underestimated their finger length significantly more than participants in the Haptics-only group ($-21.1\% \pm 3.5$; $p<.01$). However, there was no significant difference between the Vision+Haptics when compared to the Vision group ($-15.7\% \pm 3.5$ vs. $-21.1\% \pm 3.5$ $p=.81$) or to the Haptics Group ($p=.06$).

Thumb Opposition: There was a main effect of group [$F(2,48)=6.4$, $p<.01$, partial $\eta^2=.211$].

Follow-up pairwise comparisons revealed that participants in the Vision-only group ($-28.5\% \pm 5.2$)

underestimated thumb opposition significantly more ($p < .04$ for all comparisons) than the participants in the Vision + Haptics group ($-6.9\% \pm 5.2$) and the Haptics-only group ($-7.9\% \pm 5.2$).

Thumb Length: No significant main effects or interactions were found.

5.5 Discussion

The present study aimed to examine the contributions of vision and haptics separately and in conjunction to the perception of our hands. To this end, participants were asked to point-to-indicate certain parts of their unseen hands in one of three groups: Vision+Haptics, Vision-only, or Haptics-only. Participants in the Vision+Haptics group had vision (non-informative) of the experimental set up and of the pointing hand (but no vision of the hand being estimated). They also experienced haptic feedback as the palm of the hand was in contact with the undersurface of the tabletop where the estimations were made. Participants in the Vision-only group placed their hand behind their backs (instead of under the table). They were asked to imagine (no tactile feedback) as if the hand was under the table when making their estimations. In this way, participants had vision of the experimental set-up (but not tactile feedback at the visually attended location). Participants in the Haptics-only group completed the task with the hand underneath the tabletop (as in the Vision+Haptics group) but did so while wearing a blindfold (no vision). Participants in all groups were asked to estimate the position of ten landmarks on the hand: the fingertip and the mp joint of each digit. Hand maps were constructed by using a 3D motion capture system. Effects of group (Vision+Haptics, Vision-only, and Haptics-only), and

hand (left, right) were investigated for hand width (great span and little span), finger length, thumb opposition, and thumb length.

For participants in the Vision+Haptics group both the left and right hands were significantly overestimated in terms of hand width, and significantly underestimated with regards to finger length (see Table 2). The findings of the Vision+Haptics group replicate numerous studies (Longo, 2014; Longo & Haggard, 2012a, 2012b; Longo et al., 2012; Saulton et al., 2015) including that of Longo and Haggard (2010) and the results of experiment 1. Similarly, to Longo and Haggard (2010) who found that the thumb was the least distorted digit, we found no significant differences between real and perceived thumb opposition and thumb length for this group. Participants in the Haptics-only group did not replicate these results, or those of Longo (2014). As it can be appreciated in Table 2, except for a slight overestimation of width in the right hand, all other estimations were accurate. This result is consistent with our hypothesis that at least part of the distortion seen in previous studies is the result of visual and haptic information competing with one another. Our prediction that participants in the Haptics-only group would produce more anatomically accurate perceptions than those participants in the Vision+Haptics group was therefore supported. The findings are also consistent with a previous report showing a decrease in the magnitude of hand distortion when participants had no vision compared to when they had vision and haptic feedback (Longo, 2014). It is clear therefore, that non-informative vision interferes with perceptual judgements of hand size. Contrary to our hypothesis however, participants in the Vision-only group produced the most distorted hand maps. This group underestimated: finger length, thumb opposition and thumb length of both hands, and overestimated hand width (little span) of the left hand. Since the Haptics-only group had more

accurate judgments than the Vision+Haptics group, but the Vision-only group was the least accurate group, the results cannot be fully explained by interfering sensory modalities (otherwise the Vision-only group would have been more accurate than the Vision+Haptics group). The results suggest that the visual perception of the hand is distorted, while the haptic perception of the hand matches its anatomical size. Therefore, it is through haptic feedback that this observed distortion is reduced. As humans primarily rely on visual information to guide our volitional movements, this could explain why the Vision and the Vision+Haptics groups shared a similar magnitude of distortion. This suggests that the observed distortion in hand perception is not as a result of two different sensory modalities interfering with one another, but that instead, visual information interferes with accurate perception of the hands.

Previous research, has also found that visual information interferes with somatosensory processing. Non-informative vision has been associated with higher false alarms in a somatic detection task (Mirams et al., 2010), altering touch perception (Longo & Sadibolova, 2013), reducing information about stimulus intensity (Beck, Làdavas, & Haggard, 2016), and decreasing body perception (Longo, 2014). For example, Longo (2014) found that when participants were wearing a blindfold, they had significantly less distorted perception of their hands than when they had vision during the task. Our results were very similar, as we found that participants in our Haptics-only group had more accurate hand perceptions than those in the Vision+Haptics and Vision-only groups. It has been suggested that remembered visual information is more variable than proprioceptive information (Bellan et al., 2015). This study had participants watch a video of their hand moving, but actually moved the participants hand in the opposite direction. Participants were asked to indicate with an arrow which direction their hand had moved. The

results showed that participants became significantly faster at identifying the direction their hand was moving over the course of testing. The authors suggest that this can be explained by visual memory being more variable than updated proprioceptive information. Perhaps this is why in our study, the groups with vision produced larger distortions of hand perception. Additionally, when visual information is removed, haptic information becomes relied upon, and since haptic information has been shown to be less variable (Bellan et al, 2015), perhaps this leads to the smaller distortions in the Haptics-only group.

Another possible explanation for the very different results seen between the Vision-only and Haptics-only is that we give different amount of weight to each of these senses depending on what we are doing with our hands. For example, if we reach out to grasp a cup without a handle, we would rely on haptic feedback to decipher if the cup was hot or cold. Alternatively, differences between the groups could be as a result of these two sensory modalities having different representations of space. It has been suggested that visual information is more accurate in estimates of lateral space whereas haptic information is more accurate in estimates of depth (Van Beers, Sittig, & van der Gon, 1998; Van Beers, Sittig, & van Der Gon, 1999). For example, in one study participants had to match the position of a target with or without vision (Van Beers et al., 1998). The results showed that in the visual condition participants were more accurate at estimating the horizontal position of the target, and in the proprioceptive condition they were more accurate at estimating the vertical position. Interestingly, in the present study we found that participants in the Vision-only group underestimated finger length whereas participants in the Haptics-only group significantly overestimated hand width. These different directions of

distortion (vertical finger length vs horizontal hand width) align with previous studies (as in Van Beers et al, 1998; 1999) and suggest that vision and haptics have distinct spatial representations.

A different possibility is that during haptically-guided tasks participant's errors tend to be overestimations (regardless of spatial orientation), whereas in visually-guided tasks, the errors that are made are underestimations. For example, a previous study investigating proprioceptive- and visually-guided target matching found overestimation errors in the haptic matching and underestimations in the vision matching (Goble & Brown, 2008). The study asked participants to either match an elbow position (haptics) or to point to the location in which a target had appeared (visual). For the proprioceptive task, participants overestimated the distance between where the position was and where they perceived it to be. For the visual task, participants underestimated the target position. The authors argue that this supports the view of different spatial representations for different sensory modalities. Thus, potentially, hand perception that relies on haptic feedback overestimates width and hand perception that relies on visual feedback underestimates length as a result of these differing spatial representations.

Another finding of the present study concerns hand differences. Participants in the Vision+Haptics and in the Haptics-only group overestimated their right hands as being wider than their left hands. Moreover, participants in the Haptics-only groups accurately perceived their left hands for all measures. This result could suggest a left hand advantage for haptic processing. Previous studies have found that the left arm may in fact, be more specialized for haptically-driven actions (Colley, 1984; Goble, Lewis, & Brown, 2006). For example, elbow-matching tasks have been shown to be more accurate in the left arm than in the right (Goble & Brown, 2007, 2008). Other research has also suggested a right hemisphere left hand specialization for haptic

processing (Butler et al., 2004; Cormier & Tremblay, 2013; Fontenot & Benton, 1971; Franco & Sperry, 1977; Harada et al., 2004; Kumar, 1977; Loayza, Fernández-Seara, Aznárez-Sanado, & Pastor, 2011) For example, studies from our lab have found an increase in left-hand use for grasping when vision is occluded and an increase in right-hand use when haptic feedback is minimized (Stone & Gonzalez, 2014). Both of these studies support the suggestion of a left hand right hemisphere specialization for haptic processing. The asymmetries in hand perception seen in the Vision+Haptics group (right hand significantly more overestimated than the left for both spans) were also found in a previous study from our lab (experiment 1) and others (Linkenauger et al., 2009). For example, a study found that participants estimate their right hands as being more capable of grasping objects than their left hands (Linkenauger et al., 2009). Participants in that study were asked to estimate if they were able to grasp different sized blocks that were presented in front of them. The results indicated that with their right hands the participants overestimated their grasping abilities, suggesting that they viewed their right hands as more capable than they actually were. The overestimation of the right hand found in the present study could be a result of the right hand being viewed as more capable. Finally, it is also possible to explain the bigger representation of the right hand with neuroimaging studies that have found that right-handers have larger cortical areas for the right hand when compared to the left (Buchner et al., 1995; Soros et al., 1999).

One last consideration regarding the results from the Vision-only group is that perhaps their estimations were erroneous because visual and haptic information conflicted with each other. Although we removed tactile feedback to the hand by preventing participants from touching the undersurface of the tabletop, participants in the Vision-only group still received

proprioceptive information. This proprioceptive information was non-informative, as the hand was behind the participant's back, therefore, this information might have interfered with visual information (like non-informative visual information interfered with haptic processing). Future research will aim to investigate this possibility.

To conclude, the present study examined the role of vision and haptics separately and in conjunction to hand perception. The study found that when participants completed the task using haptic information (i.e. without vision), the perception of the hand was significantly more accurate than when participants completed the task with both haptic and visual information or with visual information only. These results suggest that visual but not haptic feedback interferes with the metric perception of the hand.

Compliance with Ethical Standards

Funding: This study was funded by a discovery grant awarded to Claudia LR Gonzalez from the Natural Sciences and Engineering Research Council of Canada.

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent: Informed consent was obtained from all individual participants included in the study.

Chapter 6. General Discussion

6.1 General Discussion

Previous research investigating the accuracy of hand perception has yielded two different results. In one study where participants were tasked with locating 10 different landmarks on their hand (localization task), the results showed a distorted perception (Longo & Haggard, 2010). This distortion had several notable characteristics, including an overestimation of hand width and an underestimation of finger length. A different study, however, found that when participants were asked to indicate to the experimenter the length and width of their hands, participants were remarkably accurate (Linkenauger et al., 2009). The purpose of this thesis was to further explore the conditions in which hand perception is distorted. As Longo & Haggard's methods produced distorted perceptions, and Linkenauger et al did not (the perception of the hands matched the anatomical size), the methods used in this thesis were adapted from Longo and Haggard. The thesis was based off of two hypotheses: 1) hand perception resembles its anatomical dimensions when perceived holistically rather than in pieces; and 2) part of the previously described distortion of hand perception is as a result of visual and haptic information interfering with one another.

To test these hypotheses two experiments were designed that asked participants to localize ten different landmarks on their hands (i.e. localization task). The first experiment investigated if a holistic perception of the hand produced estimates that match its anatomical size. This was tested by having participants point in a systematic pattern (in a linear path from the tip of the thumb to the base of the little) or in a random pattern (to any of the ten locations after the first point). Additionally, half of the participants pointed in an interrupted order (they would return their stylus to a neutral home spot between each point), and the other half in a continuous

order (they initiated each point from the previous point location). In the second experiment the roles that visual and haptic information play in the perception of our hands was investigated. This was examined by manipulating the sensory modalities available to the participants as they completed the localization task. In the first study, it was predicted that the participants who completed the task in a systematic pattern and in a continuous order would produce accurate hand maps. This is because they could rely on previous estimates to inform them of where the next landmark was located. This would also allow for participants to focus on an outline of their hands. Creating an outline of the hand would allow participants to think holistically about the size and shape of their hands rather than just localizing a single landmark in space. In the second study, it was predicted that the participants who completed the task with only one sensory modality available would produce more accurate hand maps than those who completed the task with multiple sensory modalities available. This is based off of previous research that has found that when participants complete a localization task without vision, perception improves (Longo, 2014) and other studies that have shown that vision interferes with tactile perception (Mirams et al., 2010). In the current studies, it was predicted that when participants completed the localization task with only one sensory modality (either vision or haptics), perception would improve.

The following sections will discuss the effects that these manipulations had on specific measures of hand perception, and how the results relate to a perception of body size that matches its anatomical structure (the theory that this thesis is based). The final section will focus on limitations of the studies and future directions.

6.2 Hand differences

One finding that was present in both experiment 1 and experiment 2 was the difference in perception between the hands. In both of these experiments the right hand was more overestimated when compared to the left hand. This finding suggests that the right hand is represented as being larger than the left hand. This is supported by a previous study showing that the right hand is perceived larger than the left hand (Linkenauger et al., 2009). Linkenauger asked participants to indicate on a measuring tape how long and how wide they perceived their hands to be (Linkenauger et al., 2009). Participants estimated their right hands as being larger than their left hands. This result, together with the findings in this thesis, indicate that there are asymmetries in hand perception. The reason for this asymmetry is unknown but it could be nested at the cortical level. A neuroimaging study showed that right handers have larger cortical areas for their right hands than their left hands (Soros et al., 1999). This suggests that hand perception may be reflecting characteristics of the homunculus. Another potential explanation as to why these asymmetries exist is that the right hand may provide more opportunities for action in our environment. In one study participants had to estimate if they could grasp different sized objects with either their left or right hands (Linkenauger et al., 2009). Participants estimated that they could grasp larger objects with their right than with their left hands. This suggests that the right hand is perceived as more capable than the left hand, and provides support for the idea that participants estimate their right hands as being larger than their left hands because they view their right hands as affording them more possibilities for action.

The manual asymmetries found in this thesis together with Linkenauger's findings, differ from results that of Longo & Haggard (2010) who found no differences between the perceptions

of the two hands. This discrepancy may be due to methodological differences. For example, both experiment 1 and experiment 2 used motion capture technology to track the position of where participants were pointing, whereas, Longo & Haggard took still photographs of these locations. There were other differences in methodology. For example, in the present studies hand width was measured by the great span, which was defined as the summed distance between the tips of each of the five digits (including the thumb), whereas Longo & Haggard used the distance between the bases of the index finger to the little finger. We included the measure of the thumb into our measure of width because without the thumb, manipulating the environment with our hands would be very difficult. If asymmetries in the perception of our hands exist because we perceive our right hand as being more capable than our left hand, then it makes sense that these asymmetries would be muted to non-existent in a measure that did not allow for maximal manipulation of the environment. It is also possible that measuring the fingertips allowed for more variability (i.e. each fingertip can move a further distance than each knuckle), while knuckles only have a limited amount of mobility. Finally, it is also possible that additional sensory information was provided through the muscles that allow for adduction and abduction of the fingers.

6.3 Characteristic distortion

In both experiment 1 and experiment 2, our results showed the characteristic distortion found by Longo and Haggard (2010), with significant overestimation of hand width and underestimation of finger length. This shows that even with the modifications to the methods (using motion capture technology instead of still photographs) and analysis (a measure of width that

included the thumb and that was taken from the tips of the fingers) the results remained relatively similar. This finding indicates a robust distortion in hand perception through the localization method. However, several of the modifications to this method that were implemented in this thesis improved perception of the hand (albeit none produced a completely accurate map). These modifications will be discussed in the following section.

While the experiments in this thesis produced similar results to those of Longo and Haggard, the magnitude of the hand distortion was significantly smaller in both experiments. One possible reason for this difference in magnitude is that in both experiment 1 and 2, participants estimated the palmar side of their hands, and Longo and Haggard had them estimate the dorsal side. An additional study by Longo & Haggard however, found that the distortion was present in both sides but the dorsal side exhibited a significantly larger distortion (Longo & Haggard, 2012a).

The characteristics of the distortion have been shown to be present in a variety of conditions when different sensory modalities are available, such as when visual and haptic information are available (Longo & Haggard, 2010), when only haptic information was available (Longo, 2014), and with no haptic feedback from the pointing hand (Longo et al., 2012). In Longo et al, (2012) the researchers tested a 38 year old amputated woman on the same task as in the original report (Longo & Haggard, 2010). As she could not point with her amputated hand, the researchers were verbally instructed by the participant as to the location of each landmark (no haptic feedback of the pointing hand). She also completed a map of her phantom hand, by pointing to the locations (with her intact hand) as they would appear if her hand was there. Future research is needed in this area, but preliminary results showed the distortion occurring with the same characteristics and with the

same magnitude regardless of if the participant had haptic feedback from their pointing hand or not, and in both the phantom and intact hands.

6.4 Group differences

In both experiments 1 and 2, the distorted characteristics of hand perception were replicated, however one group within each experiment performed better than the others. In experiment 1, participants in the systematic groups performed significantly more accurately than the participants in the random groups. In experiment 2 participants in the Haptics group produced almost completely accurate perceptions of their hands. This suggests that under certain conditions hand perception can be substantially improved. Perhaps, completing the task in a systematic pattern and with no visual feedback would produce a perception of the hand that matches the anatomical structure.

In experiment 1, our systematic group displayed a relatively accurate perception. Only finger length of the left hand and thumb opposition were underestimated. The methods in the systematic group may have allowed participants to use a holistic strategy as each estimation was of neighbouring digits. The participants who pointed in a random pattern, however, had no relative information on which to base their next estimate and presumably focused on individual landmarks' location. If this were the case, it would indicate that a holistic perception yields more accurate estimates of hand size. Two types of representations are formed when learning a spatial layout; one that is analytical (relies on distances), and one that is holistic (Shelton & McNamara, 2004). Previous research has shown that body parts (most notably the face) are processed holistically rather than analytically (Farah et al., 1998; Reed et al., 2003; Seitz, 2002; Tanaka &

Farah, 1993). Therefore, it is possible that the hands are processed holistically (like the face), and that participants in the systematic pattern accessed this holistic representation, which resulted in perception that more closely matched the anatomical size of the hand. Thus, it is likely that when we use our hands to interact with the environment we are relying on a holistic perception of the size of our hands. This offers a possible solution as to how we can interact with our environments if we have a distorted perception of our hands. If the perception of the hand is processed holistically and this perception is accurate, we may not need to have an accurate perception of individual landmarks.

In experiment 2 the Haptics-only group produced significantly more accurate measures of hand perception than either of the other two groups. This result is similar to that of Longo (2014) who found that the magnitude of distortion was significantly smaller when participants had no visual information. Since the visual group displayed the greatest magnitude of distortion, it can be assumed that visual information interferes with somatosensory processing. Previous studies, have found that non informative visual information is associated with higher false alarms in a somatic detection task (Mirams et al., 2010), altered touch perception (Longo & Sadibolova, 2013), and reduced information about stimulus intensity (Beck et al., 2016). For example, one study asked participants to decipher between differing intensities of a stimulus delivered to their hands, both when they could see them and when they could not (Beck et al, 2016). They found that participants were worse at estimating the intensity of tactile stimulus when they had vision of their hands compared to when they did not. This is evidence that visual information can interfere with another sensory modality, in this case nociceptive (pain) information. The results from the Haptics-only group in this thesis differed from the results of Longo (2014) however. In the

Haptics-only group every measure besides one was accurately estimated, whereas Longo found every measure to be distorted (albeit to a lesser degree than those participants who had visual and haptic feedback). This discrepancy is likely due to the differences in methodology (e.g. measuring hand width from the tips of each of the five digits) between the two studies. Since our experiment produced a magnitude of distortion less than that of Longo (2014), when participants were estimating with haptic information alone this decrease in distortion (in our experiment) likely allowed for participants to have an accurate perception.

6.5 Thumb measures

In this thesis the thumb exhibited the most anatomically accurate perception. In both experiments thumb length was accurately perceived in almost every single group (with the vision-only group in experiment 2 being the only group that underestimated thumb length). The accurate perception of thumb length could be reflecting the evolutionary importance of the thumb, as it allowed for developments that led to an enlarged brain (Napier, 1980). Through the development of the flexor pollicis longus muscle (that allows the thumb to flex), precision grasping and stone tool making became possible (Napier, 1962; Susman, 1988). These changes allowed for tool use, food to be cooked, and the ability to walk upright. Moreover, the thumb has a larger cortical area than any of the other digits (Penfield & Boldrey, 1937; Sutherling et al., 1992). One study discusses the possibility that since no other non-human primate exhibits larger cortical areas for the thumb, it is possible that this reflects the increased tactile functions that humans have due to thumb opposition (Martuzzi et al., 2014). Perhaps the larger cortical representation as well as the evolutionary importance of the thumb led to accurate estimates of

thumb length (which did not occur in any of the other digits). Additionally, thumb musculature differs from the rest of the digits. The thumb is independently controlled, whereas the musculature of the other digits is connected (Lang & Schieber, 2004). It is possible that the dedicated musculature that allows for thumb opposability increases the amount of sensory feedback of this digit. Together, all these features may have influenced perception of thumb length to render it accurate.

Interestingly, thumb opposition did not follow the stereotypical characteristics of hand distortion. This measure was the only measure of width that was underestimated in some of the groups. In all groups of experiment 1 and in the Vision group in experiment 2 thumb opposition was underestimated, the Vision+Haptics group and the Haptics-only group (experiment 2) showed accurate thumb opposition. One possible explanation as to why underestimation occurs is that the representation of the distance between the digit pairings does not follow an anatomical layout. A previous study asked participants to lay in an MRI scanner while each of their 5 digits was stimulated. It was found that the distance between the thumb and index finger was represented as being the same as two other digit pairings. In particular, thumb opposition was only shown to be represented as larger than D4-D5, so thumb opposition is represented no differently than the distance between D2-D3 or D3 -D4 (Martuzzi et al., 2014). In other words, it appears that the distance between the thumb and index finger is somatopically represented as being no different than the distance between two of the other three digit pairings (between the index and middle finger, and the middle and ring finger). If the representation of the distance between thumb and index finger is not different than the representation of the other digits' pairings, this could explain the underestimation of perceived thumb opposition. Another

possibility is that thumb opposition was underestimated because every digit, except for the thumb, is visually located “front-on” and the thumb is visually located “side-on” (Margolis & Longo, 2015). Front-on refers to how when the hand is placed up against the plexiglass table top, the four fingers are all located at the front of the hand and facing forward, and side-on refers to how the thumb is located to the side of the hand. Haptically (through proprioceptive and cutaneous signals) there is information that the thumb is located “side-on”, and this could allow for participants to estimate that their thumb is located in a different anatomical set-up than the other four digits. This could explain why in the Haptics-only and Vision+Haptics groups there was no significant underestimation, as haptically there is information about where the thumb is actually located. However, if participants used a visual strategy (the other groups) when completing this task, and they chose to employ the same strategy when estimating the thumb it would result in a localization just like any of the other digits (front-on), and this would have led to the underestimation of this distance. For participants to correctly identify the location of the thumb they would need to consider the thumb as being situated in a very different position to the rest of their fingers, and perhaps they did not want to overestimate this distance and so they were conservative in their estimates. In the previous research by Margolis and Longo (2015), participants were asked to locate on a silhouette image of the hand where the knuckles were located. The authors argue that the reason why the thumb was estimated as being closer to the index finger is that participants did not want to estimate it too close to the edge of the silhouetted image. Perhaps, similar conservative estimates were experienced in this thesis. However, when pointing in a haptically-guided task the cutaneous and proprioceptive signals would help identify that the thumb is located side-on.

6.6 Theory

While certain groups experienced more accurate perception, all of the groups showed a certain degree of hand distortion. So, even when participants have a relevant reference point on the hand, they follow a systematic order, or have no competing sensory information, there are still areas that display a distorted perception. This thesis was based on the theory that hand perception matches anatomical structure, however none of our groups produced a perception of hand size that was completely accurate across all measures. The theory is based on numerous studies that have found anatomically accurate perceptions of the body (Bolognini et al., 2012; Guardia et al., 2010; Sposito et al., 2012; Sposito et al., 2010).

Two possibilities exist as to why the hand did not render completely accurate perceptions. First, it is possible that the distortions reflect a misconception of anatomical knowledge, rather than distorted perceptions. Further work by Margolis and Longo (2015) has found that people estimate their knuckles as being located more distally on their hand than what is anatomically correct (Margolis & Longo, 2015). This indicates that distortions seen in previous studies on hand perception (including the ones in this thesis) may be as a result of a distorted knowledge of body structures rather than self-body perceptions. Perhaps we do not know the anatomical structure of our joints and so when completing a localization task the perception becomes distorted. This may reflect why underestimations of finger length still occur in the groups that follow a systematic pattern in experiment 1. The results of Margolis and Longo (2015) suggest that the underestimation of finger length is likely due to the knuckles being perceived further up the hand, and not that the tips are located further down the finger. Also, these results may indicate that we actually do know the length of our fingers, but we are just unaware of where our knuckles

are located. If participants did not know where their knuckles were located, this could explain why they were accurate at identifying pictures of their hands but were inaccurate at localizing the landmarks (Longo & Haggard, 2010). If we are aware of the size of our fingers but are unaware of where our knuckles are located on our hands, then accurately perceiving finger size could provide further support that body perception of the hand relies on the image of the hand as a whole and not on individual landmarks.

Secondly, it is possible that identifying only the tips and knuckles of each of the five fingers does not actually provide a holistic perception of the hand. For example, the conflicting results between being able to visually identify the size of our hands (Linkenauger et al., 2009) and being unable to identify locations on the hand accurately (experiment 1, experiment 2, Longo & Haggard, 2010), could be as a result of one testing the entire hand (Linkenauger et al., 2009), and the other studies testing only the distance encompassing the fingers. For instance, Longo and Haggard (2010) compared the conscious body image and the internal perception of the hands (through a localization task) using two different measuring techniques. The body image task utilized a picture of the entire hand, whereas the localization task was only concerned with identifying landmarks on the fingers. The results showed that when participants were asked to identify their own hands from a set of photographs (body image), they were able to complete this task accurately. However, when they were asked to complete the localization task (internal perception), hand width was grossly overestimated and finger length underestimated. One explanation by the authors is that body image is more accurate and coherent than the internal perception produced by the localization task (Longo, 2015b). However, it is also possible that the results from these two tests were different because participants were shown the complete image

of the hand (from wrist to the tip of their fingers) for the body image test, yet for the localization task they were only identifying landmarks on their fingers (the knuckles and tips of each finger). Perhaps if participants were shown pictures from the knuckles to the edge of their fingers the results would be similar. Since there are differences between the definitions of conscious body image of the hand and the internal perception of the hand, this could also explain why these differing results occur. The conscious body image of the hand refers to the remembered metrics, which are established through memory and experience. This differs from the internal perception of the hand, as this refers to a perception of the hand that is constantly updating through somatosensory information and underlies position sense.

Our Vision+Haptic group, surprisingly had the same magnitude of distortion as the Vision-only group, but our Haptic-only group had the most accurate estimations. So if people do not understand where landmarks are located on their hands because of anatomical misconceptions (as in Margolis & Longo, 2015), then when vision is removed their estimates of those locations will rely on haptic information and thus produce more accurate estimations. Previous studies have found that when estimating distances haptically, the errors made tend to be overestimations (Goble & Brown, 2008). This result aligns with research that has found that visual estimates are more accurate in the lateral dimension of space, whereas haptic information is more accurate in the depth dimension (Van Beers et al., 1998; Van Beers et al., 1999). In experiment 2, the errors found in the Haptic-only group were in the width dimension. Perhaps the errors occurred in this dimension because the lateral spatial representation is not as accurately processed by haptic information (Van Beers et al., 1998; Van Beers et al., 1999).

Lastly, the nature of the task used in the present thesis may have influenced the results. Previous research has found that at least part of the distortion observed when estimating hand size is as a result of the metric nature of the task (Longo & Haggard, 2012b). Hand posture seems to affect the magnitude to which hand perception is distorted. In their original report, Longo and Haggard (2010) found the characteristic distortion (overestimation of hand width and underestimations of finger lengths) regardless of hand posture (with or without 90° rotation of the arm). However, a different study found that the distortions were larger for the normal rather than the rotated position (Saulton et al., 2016). The authors suggest that a viewer-centric bias may be influencing the observed distortions. Thus, potentially the overestimation of hand width and underestimation of finger length could be explained by the position of the hand during testing. Interestingly, the distorted characteristics of hand perception have also been found on non-corporeal objects (Saulton et al., 2015; Saulton et al., 2016). Therefore, it is possible that body perception and hand perception are accurate but the methods of testing caused the distortions seen in the present thesis. As neither study in this thesis found that hand perception matches its anatomical structure, the theory in which this thesis was based needs to be reviewed more carefully. Additional research is needed to either accept or refute the idea that hand perception reflects its anatomical structure.

In conclusion, the studies conducted in the present thesis make three contributions to the modest (but growing) body of literature on the internal perception of the hand. These contributions are: 1) that sequential landmark identification improves hand perception; 2) that vision interferes with the perception of the hand; and 3) that we perceive our right and left hands differently.

6.7 Limitations and future directions

Over the course of running and analyzing these experiments, a few limitations have come to light. The following section (summarized in 4 themes) will focus on changes that I would make to the experimental setup and design to address some of those caveats. I have also identified future directions of this research.

6.7.1 The accurate measure of the thumb

Firstly, although we tested two systematic patterns in experiment 1, trial order always started at the tip of the thumb and progressed across the hand to the little finger. Also, participants ran through the systematic pattern five times (for a total of 50 trials), starting at the thumb each of those five times. Since the most accurate measures were of the thumb, it is possible that initiating each condition (estimations or real measures for either hand) from the thumb, helped to produce the more accurate perception seen in this group. In addition, participants in the random pattern started from any of the ten landmarks and progressed through 50 random trials for each of the four conditions, and these orders were individualized per participant. In order to examine the possibility that starting the estimations from the landmarks on the thumb allowed for more accurate estimations of total hand size, we would need to test an additional group in the systematic order. This group would have participants either start by pointing to the little finger and working across the hand to the thumb, or starting from a random digit and working anatomically across the hand. Additionally, it would also be interesting to see if the initiation site had an effect on the random order. To test this, a group of participants would complete the task in a random order but they would initiate each condition from the thumb.

Secondly, previous studies have found that when grasping an object visual information guides the thumb (but not any of the other digits) just prior to contact (Melmoth & Grant, 2012). Allowing participants to directly view their thumbs would potentially produce accurate results in the localization task. Thus, it would be interesting to design an experiment that allowed for participants to see their thumb at all times while the rest of their hand is occluded. If this method produced more accurate estimates than the systematic method, it would suggest that accurate perception relies on knowledge of where the thumb is and not necessarily the perception of the hand as a whole.

6.7.2 Holistic perception

One of the main differences, between Linkenauger (2009) and Longo's (2010) experimental designs was that each had a different definition of hand length. In Linkenauger et al (2009), the measurement used for hand length was the distance between the tip of the middle finger and the middle of the crease in the wrist (encompassing the entire hand). Longo, however, defined hand length as the distance between the tip of the middle finger and the mp joint of the middle finger (middle finger length), even for his overall analysis of hand shape (the shape index). If hand perception relies on a holistic perception, then one could predict that participants would be able to accurately estimate hand length when it includes the entire length of the hand (from fingertip to wrist), rather than only a portion of the hand (from fingertip to mp joint). In both of our experiments, we only measured finger length and not hand length, and so we cannot make any conclusions about the length of the hand or the shape of the hand. Therefore, it would be interesting to complete the localization task with a measure of hand length. This could be

achieved by having a landmark located at the crease in the wrist and then have participants localize this landmark in addition to the other ten landmarks. In our systematic group there was still underestimation of finger length in the left hand, and this could potentially be the result of finger length being tested in a non-holistic way. By adding a measure that encompasses the entire hand length, the underestimation may be reduced. If hand length is accurately estimated, then it could provide additional support for a holistic accurate perception of the hands.

6.7.3 Sensory Modalities

In our second experiment, we investigated the influence of vision and haptics on hand perception. There are however, more underlying questions about the sensory modalities involved in hand perception that have yet to be investigated. The following are my proposed follow-ups to study 2: complete the task with no haptic information, with no tactile information, and with a mismatch between tactile and proprioceptive information.

In our analyses of the influence of different sensory modalities we found that non-informative vision interferes with somatosensory processing, but haptic information does not. One possibility as to why the Vision-only group showed a magnitude of distortion similar to the Vision+Haptic group is that humans primarily rely on vision to interact with our environments, and so participants ignored all haptic information even when using this information would be informative. A different possibility is that the results from our Vision-only group were influenced by incorrect haptic information. As participants in this group placed their hands behind their back they were still receiving proprioceptive information about that hand, even though it was non-informative for the task. Perhaps this non-informative proprioceptive feedback influenced the

results in the same way that non-informative visual information influenced the results of the Vision+Haptics group. In order to test this prediction an additional study would need to be conducted in which both proprioceptive and tactile information is completely unavailable to the participants. Previous research into the field of body image has used a pressure-cuff to temporarily cut off sensory information to the arm (Bruttini, Esposti, Bolzoni, & Cavallari, 2014; Gandevia, Smith, Crawford, Proske, & Taylor, 2006; Gross & Melzack, 1978). So if participants completed the task while wearing a pressure-cuff, this would allow for participants to be tested without haptic feedback. If non-informative haptic information did influence the results in our vision-only group, then it is still possible that our hypothesis that haptic and visual information interfere with one another to partially cause this distorted body perception is correct.

The participants in the Haptic-only group had both tactile and proprioceptive information, and so it is hard to decipher if their contribution is equal to the more accurate perception of hand size. Thus, another logical extension of the present work would be to test tactile and proprioceptive feedback separately. Then we could isolate if the improved hand perception in the Haptics-only group is being driven by either proprioceptive or tactile information, or if both sensory modalities contribute to a perception of the hands that matches the anatomical structure. One possible way to test for this would be to have the participants use an anesthetic cream (EMLA © cream), so that tactile feedback is reduced and only proprioceptive information is available. If the results of this group are similar to those of experiment 2, then it is likely that participants are relying mostly on proprioceptive information to make their estimates of hand size and shape. Alternatively to using anesthetic cream, tactile feedback could be reduced using a thick and textured pair of gloves (see Stone and Gonzalez, 2015). An experiment could be

conducted using the protocol from this thesis (have the participants blindfolded and ask them to estimate where ten landmarks are located on their hands) and having participants wear a glove on the hand that they are pointing to. The results of this group could help disentangle which modality of the Haptics-only group (tactile or proprioception) is contributing to the increased accuracy in the perception of the hands.

As it is very difficult to eliminate proprioceptive information without eliminating tactile information, another possibility would be to create a discrepancy between proprioceptive and tactile information. One way to accomplish this would be to have participants complete a rubber hand illusion task prior to examining the perception of the hand. This would allow for accurate tactile information but incorrect proprioceptive information. The illusion would make participants perceive that their hand was located in a different position (incorrect proprioceptive information), then both the rubber hand and the real hand would be occluded from view and participants would complete the localization task. If the results remain consistent with the characteristics of the distortion, then tactile information is contributing to the distorted perceptions of the hands, whereas accurate proprioceptive information is not necessary to produce these distortions. This would indicate that the results from the Vision-only group are due to visual information interfering with somatosensory processing and not incorrect proprioceptive information.

One likely possibility as to why participants in the Haptics-only group of experiment 2 experienced more accurate estimates is that, when blindfolded, participants focused their attention on the haptic information they were receiving. To further test this possibility, an experiment could be designed in which added haptic feedback is available to the participant. If

haptics was responsible for providing the best sensory feedback, perhaps adding more of it would in fact make hand perception accurate. In order to test this, we could manipulate the experiment so that participants would tap their finger as they estimate where they perceive the location of their finger to be. Tapping a finger against the plexiglass would increase haptic feedback as it would increase proprioceptive signals (when the finger is moving), and would provide active cutaneous feedback (from repeatedly coming into contact with the tabletop). This could be completed both with vision (i.e. Vision+Haptics group) to test if increased proprioception improves hand perception (even when vision is available), and with no vision (i.e. Haptics-only group) to investigate if a perception that fully matches its anatomical structure is possible. If the added movement of the finger improves the accuracy of hand perception, it would support the suggestion that perception is improved with added haptic feedback.

Another possible experiment to assess the effects of added haptic feedback would be to test participants in the localization task while they are gripping an object. By gripping an object in their hand, (rather than just passively having the palm in contact with the surface of a table) participants would have enhanced haptic feedback. They would have constant haptic feedback because they would be required to hold the object for the duration of the experiment without having it slip out of their hands, which may increase proprioceptive and tactile attention.

6.7.4 Methodology

In the second experiment, the experimental protocol for the Haptics-only group differed from the other two groups. In the Haptics-only group, participants wore a blindfold to assure that they had no vision of the experimental setup and thus no tablecloth was covering the table. It is

possible (although unlikely) that there was different feedback from the table when the tablecloth was present than when it was not. It is worth noting, however, that regardless of condition a thin sheet of nylon, covered the table so even in the haptic condition there was material covering the table, reducing the potential for different feedback in the Haptics-only group. We conducted a preliminary analysis examining if different amounts of sensory feedback from the pointing hand influenced the perception of our hands, and found that the amount of sensory feedback from the pointing hand did not influence the results. We had participants point with their finger or with a stylus and found no significant differences between these two different groups. This result indicates that the potential for differing feedback influencing the results and causing the more accurate perception found in the haptic-only group is slim.

Lastly, in order for us to have a baseline measure of the participant's real hand size to compare their estimations to, we included a real hand measure. Our measure of the real hand's dimensions was calculated by having participants point to the target locations when they could see their hands (i.e. identical to the estimation conditions). Although this procedure increased methodological rigour, a number of issues could have arisen. For example, it is possible that from one hand to the other, participants slightly varied their responses of where each landmark was, or they could have moved their hand slightly through testing, or opened one hand wider than the other. These factors could have caused an individual participant to report one hand as being of different size than the other. To account for the expected variability in the estimation trials, the average of the five trials to each landmark was used to calculate each of the measures. However, the variability should be minimal when we can see our hands and can accurately identify the landmarks (real trials). Although we also took the average of the five points for the real trials, any

difference between the hands in these trials is harder to account for. Perhaps a better baseline control would be to take a photograph of each of the participants' hands and measure the real distances from that photo, or to physically measure the participants' hands after the testing is completed. This would assure an anatomically accurate measure of hand size to use when comparing the estimations of hand size.

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Appendix 1

Handedness questionnaire

Waterloo / Edinburgh 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

23. Is there any reason (e.g. injury) why you have changed your hand preference for any of the above activities?

YES (Explain) NO

24. Have you ever been given special training or encouragement to use a particular hand for certain activities?

YES (Explain) NO

25. Do you consider yourself:

Right-handed Left-handed Ambidextrous (both hands)

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

If yes, who _____

27. Did you ever change handedness? Yes or No

If yes, please explain _____

28. Is there any activity not on this list that you do consistently with your "non-dominant" hand? If so, please explain:

Appendix 2

Letter of information and consent form

INFORMATION AND CONSENT FORM

Adult Optotrak

Department of Kinesiology
The University of Lethbridge

Study Title: Hand perception with and without vision

Investigators:

Dr. Claudia L.R. Gonzalez, 403-329-2147. Email: claudia.gonzalez@uleth.ca
Lara Coelho, email: lara.coelho@uleth.ca

Dear Participant,

You are being invited to participate in a single-session research study on visuomotor integration. In particular, we are interested in your perceptions of your hands both when you have vision and when you do not. Although there will be no direct benefits for your participation in this particular study, you will be providing the researchers with valuable information. If you wish to receive a copy of the results from this study, you may contact the principal investigator at the telephone number given above.

Several steps will be taken to protect your anonymity and identity. Your name and any personal information will be kept confidential. Names will be translated into number codes and all data collected, will be labelled with the number codes rather than your name. This information will be kept in the researcher's locked office at the University of Lethbridge. Research assistants and transcriptionists will be asked to sign a confidentiality agreement. If you choose to participate and then change your mind, you may withdraw from the study at any time for any reason. If you do this, you will have the choice of having the information contributed removed from the study and destroyed, or allowing the information contributed until the time of withdrawal to be included in the study, and that no more information or data will be collected from you from that point on. Again, there will be no consequences to any decisions you make.

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. Again, your personal information, including your name, will be kept confidential and not be distributed in any way. All research materials and data, if not destroyed because of incomplete participation, will be kept for five years followed by destruction.

The procedures and risks for the study are explained below:

1. You will be required to point at the base and tips of each of your fingers. You will complete this task with both hands twice (once when you can see your hands, and once when you cannot).

2. The points will be measured and recorded using OPTOTRAK system, which measures the position of your hand in space using infrared light emitting diodes. This device does not pose any known physical or psychological risks to you.

3. There are no significant physical or psychological risks associated with your participation in this study. The data in this study will be used for research purposes only, and your confidentiality is assured.

The study takes approximately 30 minutes to complete, and you will receive 1% bonus mark for your participation (even if you decide to withdraw from the study).

Consent of Participant

I have read and understood the information presented above about the procedures and risks involved in this study and have received satisfactory answers to my questions related to this study. I understand that if I have any questions or concerns resulting from my participation in this study, I may contact the Office of Research Services, University of Lethbridge (Phone 403-329-2747 or email: research.services@uleth.ca). I am aware that I may withdraw from the study at any time, and in doing so, **I will still receive the 1% bonus mark.** With full knowledge of all foregoing I agree, of my own free will, to participate in this study.

Print Name

Signature of Participant

Date

Email