GRASPING PERCEPTION WITH WEBER'S LAW

KRIS L. CORMIER
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KRIS L. CORMIER

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Dr. C.L.R. Gonzalez Supervisor	Associate Professor	Ph.D.
Dr. R. Gibb Thesis Examination Committee Member	Associate Professor	Ph.D.
Dr. S. Pellis Thesis Examination Committee Member	Professor	Ph.D.
Dr. A. Luczak Chair, Thesis Examination Committee	Associate Professor	Ph.D.

Dedication

To Sean, my favorite person in the world.

Abstract

Previous studies have shown that information processing in the visual modality can be parsed into two distinct but interrelated streams: an action stream which engages a dorsal pathway and processes absolute metrics from an egocentric frame of reference; and a perception stream which engages a ventral pathway and processes relative metrics from an allocentric frame of reference. When presented with identical stimuli, each stream engenders different kinematics. The kinematics of action- and perception- driven behaviors have been found to respectively violate and adhere to Weber's law of human perception. This thesis investigates how the action and perception streams in *haptics* relate with Weber's law in grasping and pantomime tasks. Blindfolded participants were given objects to haptically manipulate with one hand and then used the same hand to grasp the object or pantomime the object's size. Grasp and pantomime behaviors were found to violate and adhere to Weber's law, respectively.

Acknowledgements

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Chapter 1. Introduction and Literature Review

Overview

We are aware of the physical world surrounding us. We use our senses as interfaces to understand and interact with the environment. Each sensory modality processes different aspects of a given stimuli (what we sense) and produces different mental representations from these experiences. For example, the visual modality processes light via the eye, while the somatosensory modality processes the sense of touch through various stimuli, externally and within the body, such as temperature, pressure, pain, and haptics, via the skin. Put together, our sensory modalities provide us with a holistic view of our environment and allow us to interact appropriately with our world as we experience it.

We experience numerous stimuli daily through our multiple sensory modalities. Each sensory modality functions as its own nervous system with specific receptors, neural pathways, and primary processing area(s) in the brain. Sensory information is processed at many neural levels. The lower-levels begin at the sensory receptors whereas higher-levels of neural processing are more complex, often involving more than one brain area to interpret and integrate lower-level information. Higher-levels of processing necessarily involve components of memory. For example, consider the following scenario: visual information about an object is received through the eye, sent to the primary visual cortex (V1) in the occipital lobe, where it is processed and integrated through the ventral and dorsal visual pathways for recognition and, or interaction with the object**.** For the visual modality, low-level processing entails how the retina transduces light and how features of the object are extracted from retinal stimulation. Higher-levels process how the features are used to recognize objects, produce mental representations and, in turn, can elicit behaviors to interact with said object.

Mental representations are products of higher level processing that involve different information processing streams in a given modality. Functional pathways, such as the action and perception pathways for vision or haptics, do not produce the same mental representations despite their simultaneous experience of a given stimuli. In other words, if you are shown an object, your mental representations for action on the object are not the same as those you have for perception of the object. The action and perception streams both engender their own separate and different mental representations based on their function. The action pathway involves absolute metrics allowing us to accurately interact with our physical environment. The mental representation for perception involves relative metrics – an element of our subjective experience and of our memory processes. This allows us to remember object identity and placement relative to other things in the world.

Vision for action and perception has been studied extensively through respective grasping and pantomime tasks in visuomotor studies. Grasping tasks draw out action-stream behaviors because they rely on constantly updated and immediately available information to perform the behavior. Pantomiming tasks, on the other hand, have contentiously been used as a perceptual (and in some cases an action) measure because the behavior produced in pantomime tasks is executed based on relative information and available through memory. The fundamental difference in the way object size is computed for action and for perception in visuomotor tasks can be observed through the kinematics of grasp and pantomime behaviors for the same object stimulus (for example, the length or width of an object). Psychophysical principles of human perception, such as Weber's Law, provide a consistent and reliable way to measure and compare human action-stream and perception-stream behaviors.

My thesis is that there is a fundamental difference in the way information for a stimulus is computed for action and for perception in the *haptic* modality, a topic seldom investigated. My thesis examines the following two research questions: first, do the underlying psychophysical principles of human perception (Weber's Law) make pantomime behaviour action- or perception- stream driven? Second, how do the kinematics (behavioral metrics) of action and perception streams for *haptic* processing relate with Weber's Law of human perception and differ from each other in grasping and pantomiming tasks? To answer my first research question, I investigate *action* by looking at the kinematics of grasping behavior and *perception* by looking at the kinematics of pantomimed grasping behavior. To answer my second research question, I investigate whether haptic grasping and haptic pantomime behaviors are driven by perception or action streams of haptic information processing according to Weber's law of psychophysics. Specifically, I investigate whether haptics-for-action and haptics-for-perception violate or adhere to Weber's law of human perception.

The organization of this thesis begins with a description of the cortical organization and system models for visual and somatosensory information processes. I then focus on the action and perception dichotomy and how mental representations (elusive as they may be) can be measured through the field of psychophysics, specifically through Weber's law. This brings me to the crux, my thesis, which will be presented along with the methods and results of my experiments, followed by a discussion and future directions.

The Visual System

The visual system is possibly one of the most studied and well understood sensory modalities that we use daily. This is not surprising as a large percentage of our brains are involved in processing visual information directly or indirectly (Allman & Kass, 1975; Felleman & Van Essen, 1991; Sheth, Sharma, Rao, & Sur, 1996). It is responsible for synthesizing visual information with other modalities to coordinate and produce meaningful and appropriate behavior in our everyday lives (Kolb, Whishaw, & Teskey, 2014). The visual system is exteroceptive and allows us to perceive, understand, interpret and interact with our environment (Kolb & Whishaw, 2009).

Cortical organization & neuroanatomy

Many cortical and subcortical areas are activated and involved in vision processing. The eye receives sensory input in the form of light patterns (Livingstone & Hubel, 1988). The light is converged onto the retina where photoreceptors (vision's sensory receptor) transduce the stimulus to electrical impulses through to the optic nerve (Hendry & Hsiao, 2014). From here, the optic nerve forms two distinct projections to the brain via the thalamus: the geniculostriate and the tectopulvinar pathways (DeYoe & Van Essen, 1988; Goodale & Milner, 1992; Livingstone & Hubel, 1988; Schiller, Logothetis, & Charles, 1990). Both pathways decussate at the optic chiasm before terminating in different areas of the visual cortex. The geniculostriate pathway projects from the lateral geniculate nucleus (LGN) of the thalamus to Brodmann's areas 17, 18, and 19 of the striate cortex (primary visual cortex, V1). This pathway also includes projections from the striate cortex (V1) to areas 20 and 21 of the secondary visual cortex (V2) (Figure 1, Figure 2). The geniculostriate pathway enables the perception of color, form, and pattern recognition and conscious visual function (Kolb & Whishaw, 2009; Livingstone & Hubel, 1988). The second, phylogenetically older channel, is the tectopulvinar pathway (Goodale, 1983; Schneider, 1967; Trevarthen, 1968). Here, visual information travels from the retina to the superior colliculus in the tectum, is then relayed to the lateral posterior pulvinar, and finally projects to areas 20 and 21 of V2 (Kolb & Whishaw, 2009). This pathway is responsible for detecting, locating, and orienting to visual stimuli (Kolb & Whishaw, 2009).

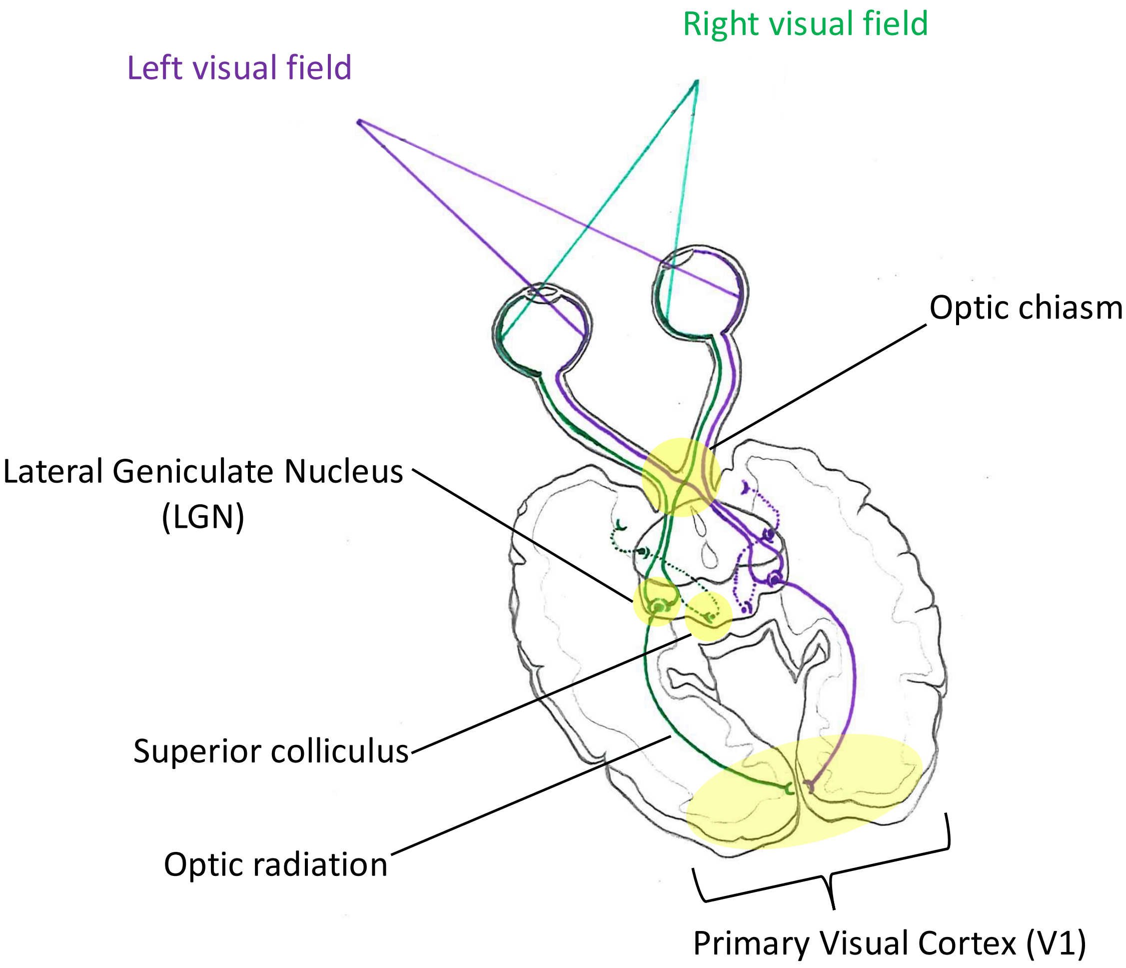

Figure 1 – A horizontal cross section of the brain and the pathways that traffic visual information to the striate cortex. From the retina, photoreceptors transduce stimuli information into electrical energy. These electrical impulses follow the optic nerve, decussate at the optic chiasm, and synapse at the lateral geniculate nucleus (LGN) in the thalamus, and the superior colliculus (tectum in the midbrain). From the LGN, visual information is projected to areas of the primary visual cortex (V1) via optic radiation.

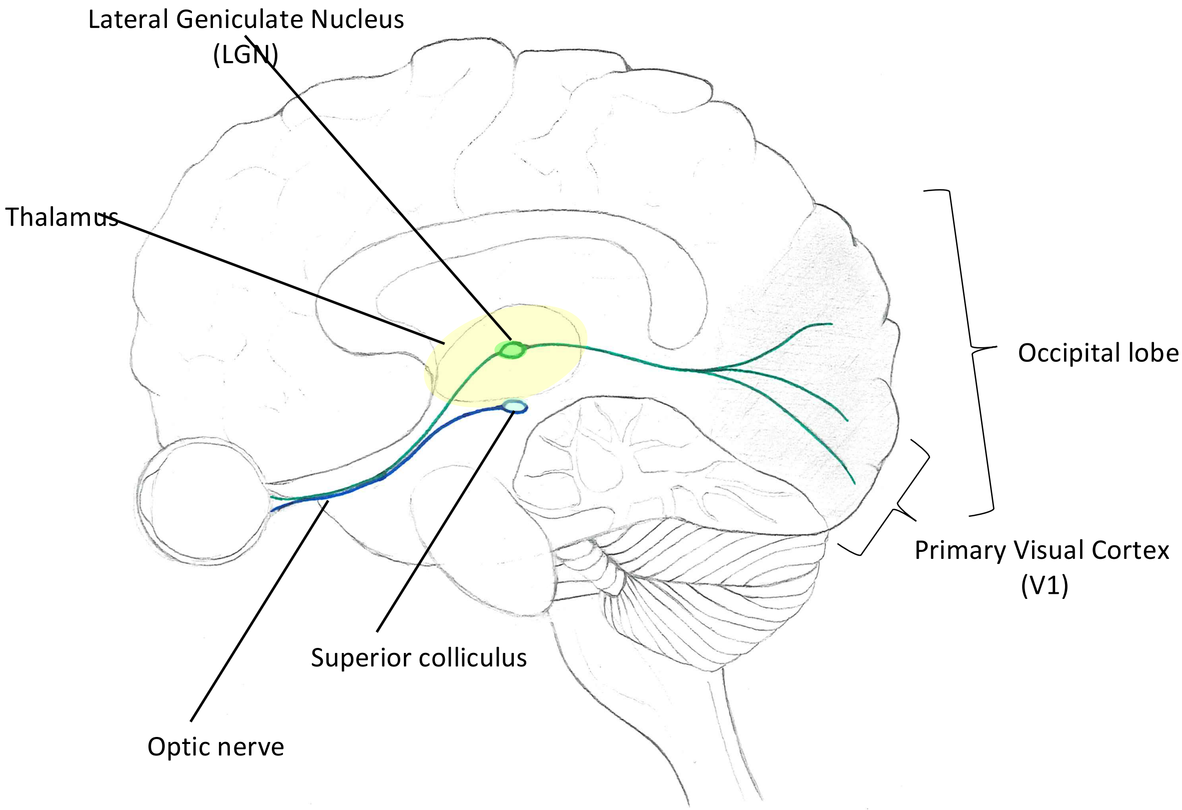

Figure 2 – A medial-sagittal cross section of the brain and the lateral geniculate and the tectopulvinar pathways from the retina to V1 and V2, respectively. The geniculostriate pathway (green) projects from the lateral geniculate nucleus (LGN) of the thalamus (in the diencephalon) to Brodmann's areas 17, 18, and 19 of the striate cortex (primary visual cortex, V1). This pathway also includes projections to areas 20 and 21 of the secondary visual cortex (V2). The tectopulvinar pathway (blue) projects from the superior colliculus in the tectum (part of the midbrain), to the lateral posterior pulvinar (in the thalamus), to Brodmann's areas 20 and 21 of V2.

Early attempts to research visual information processing relied on lesion studies in animals such as hamsters, frogs, monkeys, and primates (Goodale, 1983; Held, 1970; Ingle, 1973; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Trevarthen, 1968). Typically, animals were trained to perform specific visual tasks and were retested following a manipulation (ablation or lesion). If the animal could not perform the task after the manipulation, then the area treated was considered essential for that particular behavior (Schneider, 1967). This type of research served to build a foundation on how the sensory systems operate. Below is brief historical description of the studies that generated the concept of two functionally distinct visual pathways.

Schneider and two distinct brain areas of visual processing

In 1967, Schneider published influential research on brain lesions in the golden hamster (Schneider, 1967). He found that spatial localization and visual discrimination could be dissociated by means of ablation of different brain areas. Hamsters were unable to discriminate visual patterns after ablation of the visual cortex, however they retained the visual ability to localize an object in space (spatial localization). When the superior colliculus was ablated, Schneider reported opposite effects from those observed after visual cortex lesions; hamsters showed poor spatial localization (they could not properly orient themselves to the position of a visual stimulus), but they demonstrated unimpaired pattern discrimination abilities. His findings suggested that the superior colliculus (an evolutionarily older subcortical visual component) in animals allowed for object localization whereas the visual cortex (a newer cortical system) allowed for object identification. This meant that different visual information would travel to different cortical and subcortical areas for processing. Schneider's findings gave rise to the notion that visual information was processed for two very distinct purposes in different brain areas (Schneider, 1967, 1969).

Ungerleider & Mishkin's two cortical visual streams in primates

Ungerleider and Mishkin's research resulted in an intellectual breakthrough in the neurophysiological study of the primate visual system (Mishkin & Ungerleider, 1982). Their research conclusions demonstrated two cortical pathways with different specializations for visual processing. The specializations were for 'object' vision and 'spatial' vision (Mishkin, Ungerleider, & Macko, 1983). These findings were significant for two reasons: First, because primates are more closely related to humans than hamsters (or frogs), they provided a closer model approximation for which to study the human visual system (Goodale, 1983; Goodale, 1996; Schneider, 1967; Trevarthen, 1968). Second, their discovery of the two pathways was localized to the cortex. They defined object vision (and identification) as the 'what' pathway travelling from V1 to the inferior temporal lobes (Mishkin & Ungerleider, 1982). This pathway specialized in processing of color, form, and object identification. Spatial vision, also known as the 'where' pathway, was for object localization and included the occipital (V1) and posterior parietal cortex (PPC) (Mishkin & Ungerleider, 1982). Ungerleider and Mishkin's influential contribution to visual science was a model for visual information processing in which they proposed separate ventral ('what') and dorsal ('where') streams (Mishkin & Ungerleider, 1982; Mishkin et al., 1983).

Milner & Goodale's neuropsychological case studies

Milner and Goodale continued the investigation of the two cortical visual systems but this time in humans. In studying neurological patients, they found that lesions to temporal or parietal areas led to impairments in visual recognition of objects or in guided action and that these behaviours were dissociable. Patient DF suffered from lesions to her lateral occipital cortex and temporal lobe damage which caused visual form agnosia (Milner & Goodale, 1995). This type of damage has been shown to impair the perception of objects while preserving the ability to perform actions towards them (Goodale, Milner, Jakobson, & Carey, 1991; Sedda & Scarpina, 2012). DF could not recognize or perceive the dimensions of objects without using her hands. However, she could navigate about her daily life and appropriately interact with her environment. DF could correctly shape her hands and scale her grip to the dimensions of an object about to be picked-up, despite her inability to identify the object. For example, she would grasp a block by correctly opening her fingers but was unable to discriminate its dimension (Goodale et al., 1994; Goodale et al., 1991; Milner et al., 1991). The brain damage associated with DF's functional and behavioral deficits was a fundamental area in visual processing for recognition and identification of objects: the ventral visual stream. Although DF's brain damage was quite diffuse, her primary visual cortex and parietal cortex remained largely intact. The sparing of these structures allowed her to interact with her environment appropriately. This indicated that vision was still utilized for this purpose: vision for action.

A condition that produces opposite behaviour to that of DF's is known as optic ataxia. Patients with optic ataxia have suffered lesions to the superior regions of the posterior parietal cortex (PPC) (Culham & Valyear, 2006). These patients are able to recognize and identify objects using vision (perception) but cannot appropriately interact with them (they often have difficulties in reaching and grasping visually-presented objects) (Goodale, 2011; Goodale & Milner, 1992; Perenin & Vighetto, 1988). For example, optic ataxic patient AT, could judge the size of an object perceptually but was impaired in his behavior when asked to grasp it (Jeannerod & Rossetti, 1993). Patient AT's behavior strikes a stark contrast to DF's behavior in similar goal-oriented tasks. This is a classic exemplification of double dissociation where two related mental processes are localized in two different parts of the brain. Although both processes (vision for action, vision for perception) pertain to the use of vision, the brain structures that control them (ventral and dorsal streams) work independently. Visuomotor tasks, such as grasping an object, require both the action and perception streams of vision to process and produce the behavior. When the ventral stream is damaged, DF can still navigate her environment and shape her hands appropriately to interact with objects (dorsal stream) but is unable to identify or recognize any of it without first touching it. On the other hand, when the dorsal stream is damaged, as is the case with AT, he can identify and recognize all manner of environmental stimuli (objects), but is unable to appropriately interact (shape his hands or orient his body) with the objects in his environment. Together, these cases demonstrate that different types of behavior are driven by different visual processing pathways (Milner & Goodale, 2008).

Milner and Goodale found that when performing a goal-directed task, such as grasping, with respect to a visual stimulus, the visual processing involved requires the activation of the dorsal visual stream (Goodale & Milner, 1992). The function of the dorsal stream is to provide spatial localization of objects and to compute more complex features of the environment from an egocentric perspective, such as the position of an object in relation to the author's hand, including the programming and online control of motor behaviors (Thaler & Goodale, 2011). The dorsal stream processes object features such as relative shape and orientation (unconsciously), but is used to perform movement or behavior in space (Goodale, 2011; Goodale & Milner, 1992; Sedda & Scarpina, 2012). Producing goal-oriented movement requires constant online updating of information because objects and subjects are constantly changing. In other words, movements need to be planned according to the dynamic world with which we interact daily (Cohen, Cross, Tunik, Grafton, & Culham, 2009; Striemer, Yukovsky, & Goodale, 2010).

More recently, neuroimaging studies have confirmed the division of labour between the two visual streams (Culham et al., 2003; Culham & Valyear, 2006; James, Culham, Humphrey, Milner, & Goodale, 2003). For example, Culham and colleagues used fMRI to investigate what areas (dorsal or ventral) would be activated when participants performed a grasp or a reach behavior (Culham et al., 2003). They found there was more activation in many areas involving the dorsal stream, including the anterior intraparietal sulcus (aIPS), for grasping behaviors. In contrast, when participants were asked to compare pictures of intact objects to scrambled images (in a matching "1-back" task), they found higher activation in the ventral stream areas, including the lateral occipital complex (LOC).

The Perception-Action frame of reference (PAM)

One of the most significant contributions to the study of the visual system is Milner and Goodale's suggestion that the visual system should be studied from the perspective of its behavioral purposes rather than cortical anatomy. They proposed a neurological dissociation between perceiving objects and acting upon them. They advanced the notion that the concept of vision for perception and vision for action was a more "useful" organizing principle on which to base the study of the visual system (Goodale & Milner, 1992; Goodale & Milner, 2006). This came to be known as the Perception-Action Model (PAM).

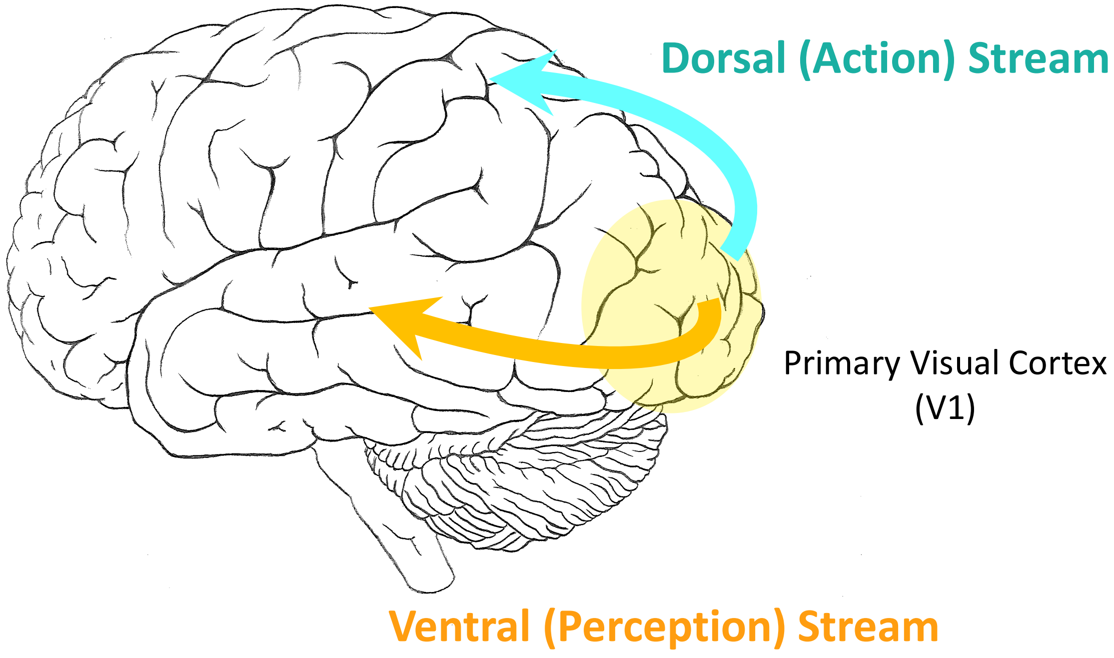

Figure 3 – Goodale and Milner's Perception-Action Model (PAM) showing the dorsal and ventral visual streams of information processing. Visual information diverges into two processing streams from the occipital areas (V1): the dorsal, vision-for-action stream (blue) and the ventral, vision-for-perception stream (orange).

Although the PAM identifies two distinct visual systems that produce different behaviours, these systems necessarily work together. As Goodale and Milner have held, the streams are "not hermetically-sealed" but rather complement each other to produce purposeful behavior (Goodale, 2011). Nevertheless, each stream utilizes vision differently to produce their own mental representation. This will be further discussed when introducing Weber's law. The PAM has been useful as a model to study other sensory systems, most notably the auditory (Kaas & Hackett, 2000) and somatosensory (Caselli, 1993; Chan & Newell, 2008; Dijkerman & De Haan, 2007; Lederman & Klatzky, 2009; Reed, Klatzky, & Halgren, 2005) modalities. Because my thesis deals with haptics, the somatosensory system is reviewed next.

The Somatosensory System

To interact with our environment, vision does not suffice; manipulation of objects necessitates haptic processing. While the eyes *see* the world around us, the somatosensory system *feels* it. Generally, we understand the somatosensory system as the sense of touch and proprioception – body awareness of where body parts are located in space – collectively referred to as haptics (Grunwald, 2008; Keysers, Kaas, & Gazzola, 2010; Lederman & Klatzky, 2009; Stone & Gonzalez, 2015). The somatosensory system follows a hierarchical structure, similar to that of all other senses, which includes receptors in the periphery, neural relays from the periphery to the brain, a primary processing area in the cortex, and representations within the cortex (Sedda & Scarpina, 2012). Sensory receptors are specialized cells that receive and transduce sensory stimuli to the neural pathways in the form of electrical impulses known as action potentials. Different receptors respond to specific external stimuli. For example, photoreceptors (in the retina) respond to light stimuli but not to tactile physical stimuli whereas mechanoreceptors (in the skin) respond to tactile physical stimuli but not to light stimuli. In other words, we acquire specific sensory information through specific receptors. As previously discussed in vision, light is the stimuli that activate the photoreceptors of the retina. In haptics, touch and proprioception each have their own types of receptors, mechanoreceptors and proprioceptors, to transduce different mechanical information.

The submodality of touch responds to external stimulus information of fine touch and pressure through five different cutaneous (embedded in the skin) mechanoreceptors: 1) Meissner's corpuscles respond to touch; 2) Pacinian corpuscles respond to flutter; 3) Merkel's disks respond to steady and constant skin indentation; 4) Ruffini endings respond to vibration; and 5) hair receptors respond to flutter or steady skin indentation. Meissener's corpuscles, Pacinian corpuscles and Ruffini endings are all rapid response receptors (100 – 1000 Hz), while Merkel's and hair receptors are both slow response (0.3 – 100Hz) (Purves et al., 2012).

The submodality of proprioception provides detailed and continuous online information about the position of body parts relative to each other and in space. Proprioception relies on three different types of proprioceptors found between joints and muscles and respond to movement stretching: 1) muscle spindles respond to muscle stretch; 2) Golgi tendon organs respond to tendon stretch; and 3) joint receptors respond to joint movement. All three of these are rapid response (100 - 1000 Hz) receptors.

The haptic modality, like that of vision, serves an exteroceptive function in sensing stimuli from the environment acting upon us (response to stimuli produced by an external agent – i.e., when being touched). However, haptics is the only sensory system that is also interoceptive. Interoception informs us about the position and movement of our bodies and allows us to discriminate what is being done to us from what we are authoring.

Cortical organization & neuroanatomy

Haptic stimuli are received and transduced to sensory information in the form of action potentials by receptors in the periphery (skin and joints). The information acquired from haptic stimuli travels along three successive afferent neurons leading to the primary somatosensory processing cortex (SI) located in the postcentral gyrus of the anterior parietal cortex (APC); Brodmann's areas 3a, 3b, 1, and 2 of the parietal lobe (Figure 4**Error! Reference source not found.**). Primary afferents extend from the receptor, through the dorsal root ganglion, then enter and ascend the dorsal white matter of the spinal cord. Primary afferent neurons synapse with secondary afferents in the medulla (in the brainstem). Secondary afferents decussate in the medulla and form a new tract, the medial lemniscus, and ascend to synapse with tertiary afferents in the ventral posterior lateral nucleus (VPLn) of the thalamus (Jones & Powell, 1973; Mai & Paxinos, 2011; Martin & Jessell, 1991; Mountcastle, 1984; Nelson, 2001; Purves et al., 2012). From the VPLn, tertiary afferents project to four distinct subregions of SI (Brodmann's areas 3a, 3b, 1, and 2), as well as Brodmann's area 4 in the primary motor cortex (Purves et al., 2012) (Figure 4). The path followed by the three aforementioned afferents to relay sensory information (delineated above) is known as the dorsal column-medial lemniscal pathway (Purves et al., 2012). All areas of SI project to the secondary somatosensory cortex (SII), to Brodmann's areas 5 and 7 in the superior parietal lobule (which project to motor and premotor cortical areas) and to Brodmann's area 4 in the adjacent primary motor cortex (Figure 5). From SI, haptic information is projected into two main pathways. One pathway projects from the SI to the PPC and has been found to involve action-related processing (action stream), whereas the second stream projects from the SI to the posterior insula via SII and is involved with processing perception and memory (perception stream) (Dijkerman & De Haan, 2007; Lederman & Klatzky, 2009; Purves et al., 2012).

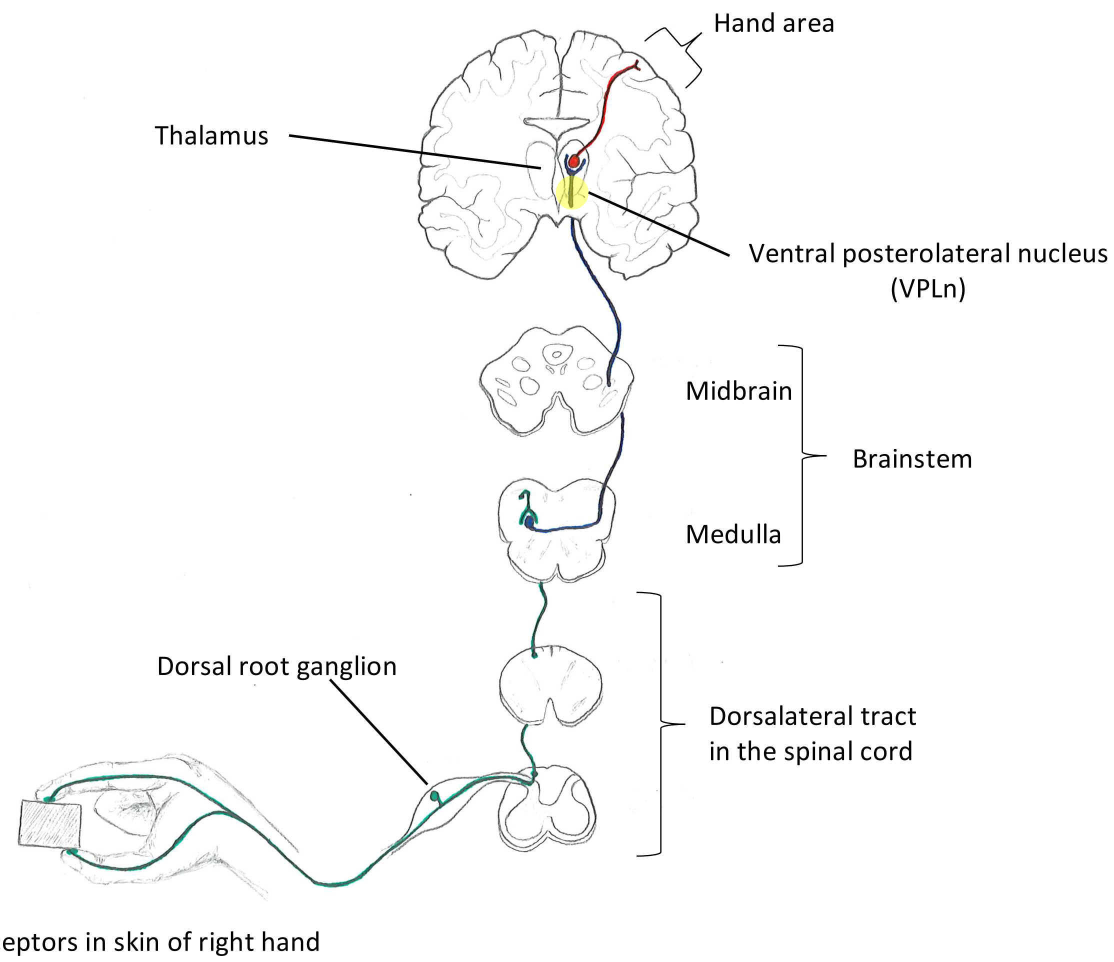

Figure 4 – The dorsal column-medial lemniscal pathway. Mechanical energy (stimuli) from the sensory receptors of the right hand are transduced into electrical impulses. These impulses travel through primary afferents (green), ascend the dorsal white matter of the spinal cord, and synapse with secondary afferents (blue) in the medulla. Secondary afferents decussate in the medulla, form the medial lemniscus, and ascend to synapse with tertiary afferents (red) in the ventral posterior lateral nucleus (VPLn) of the thalamus. Tertiary afferents project to the specific subregion of SI (Brodmann's areas 3a, 3b, 1, and 2), as well as Brodmann's area 4 in the primary motor cortex for the receptor type – all of which are in the left (contralateral) hemisphere to the right hand.

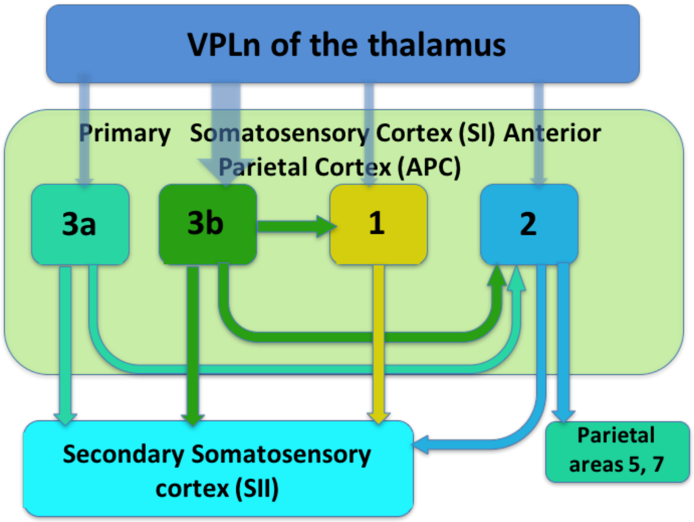

Figure 5 – Line diagram for somatosensory stimuli input to corticocortical connections.

The somatosensory cortex and sensory representations

Different mechanoreceptors are associated with different but corresponding cortical targets in SI (Johansson & Vallbo, 1983). This was first elucidated by Wilder Penfield when he stimulated the cortex in conscious epileptic patients (Schott, 1993). The patients reported where on the body they felt the sensations while different areas of the sensory cortex were stimulated. Penfield created a topographical map representing the direct association between the sensory cortex and the sensation of the body surface (location being stimulated) (Penfield, 1953) (Figure 6). This somatotopic map, known colloquially as the homunculus, features disproportionately-sized body parts onto SI. In other words, somatotopic maps do not represent the human body in its actual proportions. The disproportional representations are, in large part, due to the varying densities of the mechanoreceptors in the periphery of one body part compared to another. The density distribution of mechanoreceptors determines the sensitivity of a particular sensory system for a given event or stimuli. In other words, receptor density provides a measure of sensitivity where more receptors populating an area provide greater sensitivity of that area. For example, body parts such as our hands, lips, and tongue have greater mechanoreceptor densities than do those of our trunk and legs; meaning that we are more sensitive to a given stimuli in our hands, lips, and tongue relative to other body surfaces. Evolutionarily, it makes sense to have a greater density of mechanoreceptors in these areas compared to other areas as human survival is highly dependent on hand and mouth manipulation (Kolb & Whishaw, 2009).

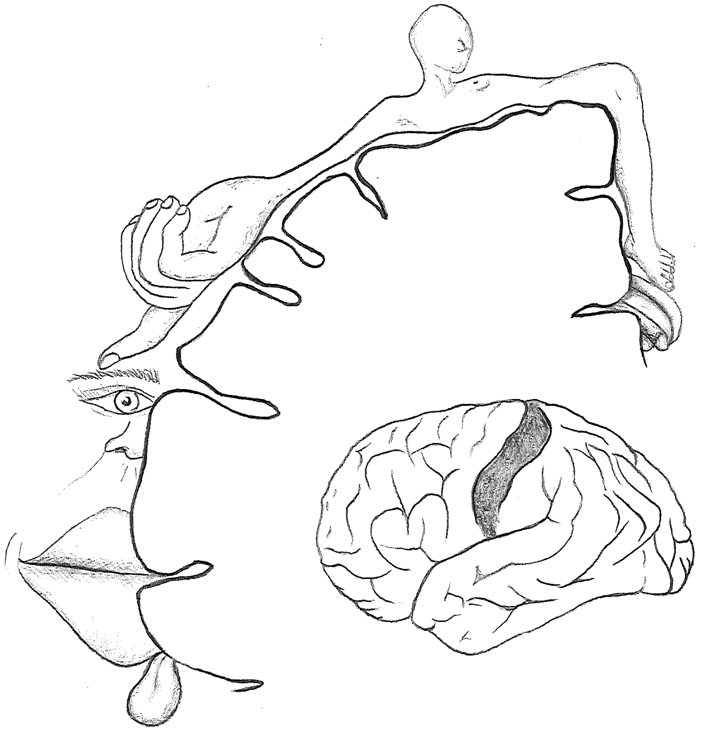

Figure 6 – Author's representation of Penfeild's interpretation of the primary somatorsensory cortex (SI) (shaded area of the brain) and the associated areas representing body parts sensitive to sensory stimulation, i.e., the human homunculus. Note: this depiction is Penfeild's interpretation of the SI. Other interpretations have suggested a different (i.e., upside down) orientation of the face not reflected here. Penfeild's is the most common representation of the SI. The differences between representations are irrelevant to this thesis.

Many studies have confirmed the existence of somatotopic maps in animals and in humans (Purves et al., 2012). In fact, Mountcastle (1957, 1975), among others, found that SI presents with multiple somatosensory maps rather than only the one that Penfield originally mapped and showed that each of the Brodmann's areas (3a, 3b, 1, and 2) contain separate and complete representations of the body; each have their own different homunculi (Kaas et al., 1990; Kaas, Nelson, Sur, Lin, & Merzenich, 1979; Mountcastle, 1957, 1975; Nicolelis & Fanselow, 2002; Nicolelis & Ribeiro, 2002; Woolsey, Erickson, & Gilson, 1979). These mapping studies show that distinct areas of SI are dominated not only by responses to receptor density but also to the *type* of body mechanoreceptor. Essentially, each receptor is associated with a different but corresponding cortical target in SI. Each of Brodmann's four areas in SI is managed by different response properties corresponding to one type of body receptor. For example, neurons in area 3a represent the position and movement of muscles, and respond mostly to stimulation of proprioceptors.

Two pathways for haptic representation

Similar to what has been found for vision information processing, haptic information follows specific trajectories given the type of haptic information (tactile or spatial) it encodes. In touching an object, all haptic information about the object is projected from SI to SII, the PPC, and the insula. The PPC is involved with action-related processing whereas the insula has been linked with recognition, memory, and perception-related processes. This is to say that from SI, haptic information about how to manipulate the object is projected to the PPC. This produces an egocentric frame of reference (with relation to oneself – i.e., body schema). Haptic information from SI to the insula (via SII) is concerned with perception and memory of the object and allows for identification of the object relative to other things surrounding it. This represents allocentric processes (with relation to context – i.e., body image). Body schema and body image are two distinct body representations (Anema et al., 2009; Dijkerman & De Haan, 2007; Gallagher, 2005; J Paillard, 1999; Jacques Paillard, Michel, & Stelmach, 1983). Body image is defined as a representation necessary for the recognition of one's own body as an object (e.g., size, configuration of parts). Body schema, on the other hand, is a representation responsible for the programming and guidance of direct actions towards our own body. Body image and body representation are analogous to the "what" and "how" of our conscious perceptual judgments and unconscious sensorimotor guidance, respectively. This has been evidenced in double dissociation studies between disorders of perceptual detection and sensorimotor guidance (Anema et al., 2009; Dijkerman & De Haan, 2007; Gallagher, 2005; J Paillard, 1999).

Like with vision, haptic studies have shown dissociable pathways for action and perception for haptic processing however, less is known about these two haptic pathways. Below is a summary of evidence from behavioral, neuropsychological, and neuroimaging studies.

Behavioral Evidence

Westwood and Goodale (2003) suggested that a similar dissociation to that of the visual system mediating object perception and object-directed action also exists for haptics (Westwood & Goodale, 2003). They assessed the effect of a haptic version of the visual size-contrast illusion (Hu & Goodale, 2000). The size contrast illusion is an experiment designed to measure the effects of relative and absolute object size processing in grasping and estimation tasks. Participants are presented with two 3-D objects of different sizes and are asked to grasp or estimate (pantomime) the size of one of the two, known as the target object. For every trial, the target object is always the same whereas the accompanying object is either larger or smaller than the target object. In the haptic version, participants were presented with two separate displays, one for each hand. The display for the left hand consisted of two objects, a flanker and a target, fixed on a board so the objects could be manipulated and explored without disturbing the display. The right-hand display was a single fixed object that matched the target object in the left-hand display. Participants used their left hand to feel the objects and used their right hand to grasp or estimate (pantomime) the matching sized object. The illusion works by causing a distortion in the perceived size of the target object by making it appear larger when paired with a small object or smaller when paired with a large object. They measured the maximum (or peak) grip aperture (MGA) and the grip aperture (GA) during the action (grasping) and perception (pantomime) responses, respectively. The MGA is the maximum distance between the thumb and index finger in flight to grasping an object. The GA is the stable distance between the index finger and thumb to show the perceived size of an object dimension. They found that grasping movements were not influenced by the size-contrast illusion meaning that action behaviors are only concerned with the size of the target object (absolute metrics). Perceptual estimations, on the other hand, reflected a size-contrast illusion which indicates that pantomiming uses relative metrics of objects rather than absolute ones. Because the participants relied only on haptic feedback this is evidence supporting a dissociation between perception and action for somatosensory processing. This finding is consistent with those found in visual studies and suggest that a dissociation between action and perception may be reflected across sensory modalities.

Dissociation studies, as demonstrated in the vision experiments of neurological patients, have proven to be very useful as they are non-invasive approaches to determine which cortical areas manage or control different functions and functional behaviors. Another behavioral example of dissociating action from perception in the somatosensory system is Chan and Newell’s 2008 study. Chan and Newell (2008) modified Tresch’s (1993) selective interference paradigm to conduct a double dissociation study to examine the behavioral effects of haptic information processing for shape recognition and localization of object features (spatial location) (Chan & Newell, 2008; Tresch et al., 1993). The interference tasks they employed were all matching tasks involving texture processing for the “what” interference task (recognition), or rotation matching for the "where" interference task. Blindfolded participants were first presented with stimuli (Lego models) fixed on a plate that participants had freedom to explore haptically i.e., using only a hand with which to feel and receive stimuli information. They were also instructed to recall the shape or the orientation of the stimulus as they would be required to compare it with another stimulus later in the experiment. Participants were then presented with an interference task. In one case participants had to discriminate the roughness of different strips of sand paper (texture) or the placement (orientation) of those strips (spatial). Finally, participants were presented with a test condition in which they were presented with the same or a new Lego model as the one presented originally. They found that texture processing interfered with shape recognition and orientation interfered with spatial localization. Importantly, texture processing did not interfere with spatial localization nor did orientation interfere with shape recognition. This study clearly supports the proposal of two separate streams for haptic processing, one that deals with shape and the other with space.

Neurological Evidence

A handful of studies have shown selective deficits in tactile object recognition or during exploratory hand movements supporting a dissociation between tactile agnosia and tactile apraxia. Tactile agnosia is the inability to recognize an object through exploratory hand movements. Tactile apraxia is an impairment in hand use when manipulating an object in the absence of paresis (Ferdinand Binkofski & Buxbaum, 2013; F Binkofski, Kunesch, Classen, Seitz, & Freund, 2001; Danckert & Rossetti, 2005). These two neurological deficits are the behavioral correspondents of a selective lesion in one of the two somatosensory streams (Dijkerman & De Haan, 2007). When the target of the action is an external object, tactile agnosia is a specific deficit of the perception stream, given that only tactile object recognition is impaired (Dijkerman & De Haan, 2007). Conversely, tactile apraxia directly refers to an action stream deficit because hand movements for object exploration are impaired even when finger movements without an object are spared. This dissociation between tactile agnosia and tactile apraxia nicely parallels the distinction between visual agnosia and optic ataxia that concur with the formulation of the action and perception streams in the visual domain (Danckert & Rossetti, 2005; Dijkerman & De Haan, 2007).

Anema and colleagues (2009) demonstrated a double dissociation of the somatic system processing streams in two stroke patients both with intact tactile detection. They used two tactile localization tasks. In both cases a stimulus (touch) was presented to the dorsum of the hand. Patients had to use their other hand to touch the spot where they had been stimulated or they had to indicate the location of the stimulus on a line drawing of a hand. Patient KE showed body schema related impairments. He could not identify the position of where he had been touched on his own hand but could identify the stimuli location on a line drawing of a hand. In contrast, patient JO, exhibited the reverse pattern; she could not identify the position of where she had been touched on a line drawing of a hand but was able to point accurately towards the actual position on her hand itself. These cases demonstrate a clear dissociation: that different types of behavior are driven by different haptic processing pathways. In their study (between disorders of perceptual detection and sensorimotor guidance), Anema and colleagues (2009) highlight the importance of the two distinct body representations (body schema and body image) as they are thought to be involved with conscious perceptual judgements and unconscious sensorimotor guidance (Anema et al., 2009).

Other studies report similar findings in neurological patients (Aglioti, Smania, Manfredi, & Berlucchi, 1996; Jacques Paillard et al., 1983; Pause, Kunesch, Binkofski, & Freund, 1989; Rode, Rossetti, & Boisson, 2001; Rossetti, Desmurget, & Prablanc, 1995; Volpe, LeDoux, & Gazzaniga, 1979) and all demonstrate cases of clear dissociation that provide further support for separate processing streams for body image and body scheme. These studies demonstrate that the execution of a motor action toward a spatially defined target does not necessarily depend on conscious awareness of that target (as is the case in the visual system), which again, supports the idea of two separate pathways for action and conscious haptic perception.

Neuroimaging Evidence

Many neuroimaging studies support the pathways for somatosensory processing. Grounding their research in the distinction between spatial and object vision (Mishkin et al., 1983), Reed, Klatzky and Halgren (Reed et al., 2005) investigated whether a “what” vs “where” or “how” dissociation exists for somatosensory processing in humans. They compared cortical activation between tactile object recognition (TOR) and tactile object localization (LOC) tasks. Participants were required to recognize or localize one of six common objects while in an MRI scanner. The six objects were each glued in one of six possible positions on a board which fit under the participant’s hand. Participants were given tasks that required object localization while ignoring the object identity (tactile object localization task, LOC), or object recognition while ignoring its location (tactile object recognition task, TOR). For the LOC task, participants had to localize an object in one of the six numbered locations while ignoring the identity of the object. To do this, the participant performed a hand-movement sequence which entailed moving his right hand along the surface of the board to find the object, grasp it, and release it. When he recognized the specific object location (1-6), he would indicate it by gesturing with his index finger of the left hand. For the TOR task, participants had to recognize an object while ignoring the location in which it was found. Participants would use a hand-movement sequence to move their right hand across the board until they found the target and raised the index finger of their left hand to indicate recognition of the object. The results showed differential activation patterns between the two tasks. TOR activated the frontal and bilateral inferior parietal and left prefrontal regions that have been shown to be involved in tactile feature integration and naming (Bonda, Petrides, & Evans, 1996; Caselli, 1991, 1993). LOC on the other hand, activated bilateral superior parietal areas which we know are involved in spatial processing (Caselli, 1993; Rossetti et al., 1995). Their findings confirm separate processing streams for recognition and localization of somatosensory information. Again, this distinction (between object and spatial processing streams) appears to follow an organizational principle in the brain across modalities.

The Somatosensory Processing frame of reference (SPM)

Dijkerman and de Haan approached the somatosensory system the same way Milner and Goodale did for the visual system. They shifted their research perspective to reflect the functional relevance (in terms of behavioral purposes) of the somatosensory system rather than examining the details of the stimuli characteristics itself (cortical anatomical functions) (Dijkerman & De Haan, 2007). In light of the extensive behavioral, neuropsychological and neuroimaging research evidence, Dijkerman and de Haan (2007) suggested two dissociable pathways for haptic information processing: a ventral and a dorsal pathway. The ventral pathway extends from the SI via SII to the posterior insula (figure 7). This pathway supports tactile perceptions and perceptual judgements by comparing the *relative* properties of an object with its context (other objects) or by accessing stored representations (memory) from previous tactile experiences (allocentric frame of reference). The dorsal pathway projects from the APC and the SII to the PPC (fig. 7). The dorsal pathway mediates actions. At higher levels of processing, the dorsal pathway (contrasts ventral) mediates actions independent of top-down knowledge via *absolute* comparisons between the object and the body (egocentric frame of reference) (Dijkerman & De Haan, 2007). Dijkerman and de Haan advanced that the concept of haptic perception and haptic action were more useful organizing principles on which to base the study of the somatosensory processing system (Dijkerman & De Haan, 2007; Goodale & Milner, 1992; Goodale & Milner, 2006). Their proposed model is known as the Somatosensory Processing Model (SPM) (Fig. 8). The SPM posits that tactile actions and perceptions are mediated via functionally and anatomically distinct cortical pathways and exemplified through respective egocentric and allocentric frames of reference (Dijkerman & De Haan, 2007).

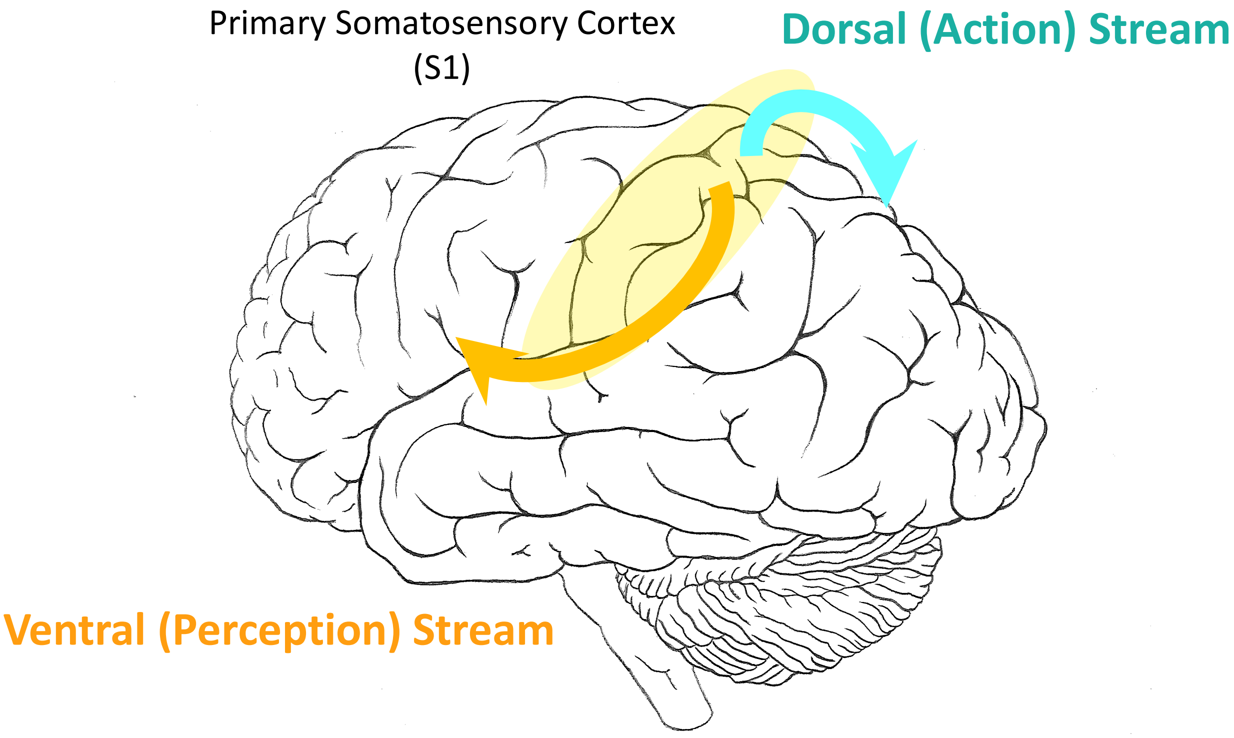

Figure 7 – The haptic ventral and dorsal pathways project from the VPLn of the thalamus where they diverge in their respective streams. As per Dijkerman and de Haan’s proposed SPM, the dorsal, haptics-for-action, stream (blue) projects to the PPC via the SI and SII. The ventral, haptics-for-perception, stream (orange) projects to the posterior insula from the SI, via the SII.

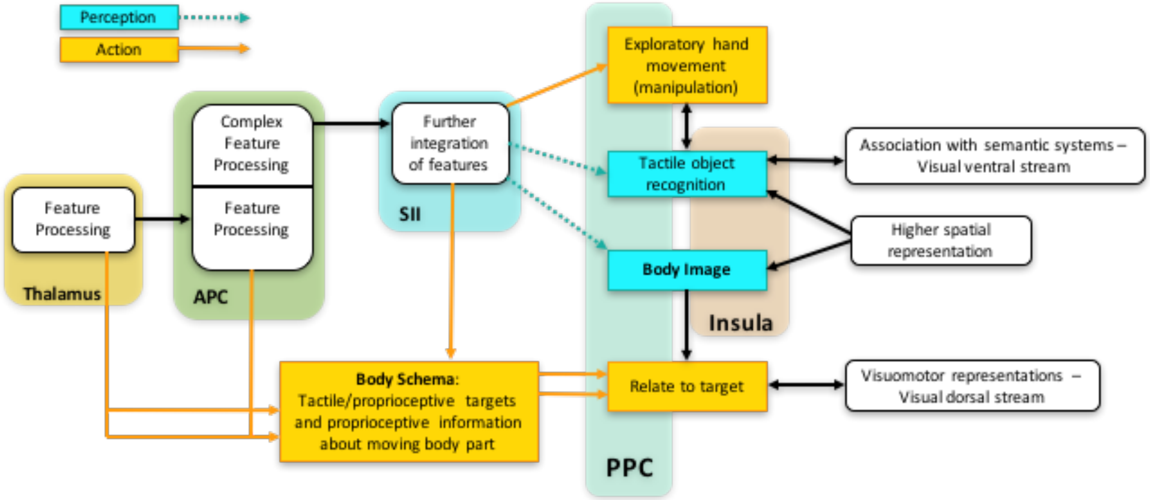

Figure 8 – The Somatosensory Processing Model (SPM). Adapted from Dijkerman and de Haan (Dijkerman & De Haan, 2007).

Although the SPM identifies two distinct haptic systems that produce different behaviours, these systems necessarily work together. Despite distinct functions of the two haptic pathways, the SPM's haptic processing streams are not as independent as the visual processing streams in PAM set forth by Milner and Goodale (Dijkerman & De Haan, 2007). Nonetheless, each stream applies haptic information differently to produce its particular mental representation. These mental representations inform behaviors produced and will be further discussed next in terms of psychophysics and Weber's law.

Chapter 2. Psychophysics

Psychophysics, perception, and Weber's law

Psychophysics is a methodological approach applied to study perceptual systems. This approach enables quantitative examination of the relationship between physical stimuli and a perceptual system. Sensation is the activity of receptors, associated afferent pathways, and engagement with primary cortical areas. Perception, on the other hand, is the subjective experience of the sensation of a transduced stimulus. A subjective experience, perception, is the product of higher order, cognitive processes involving memory and consciousness. Perception, as the subjective experience of a stimuli, is in and of itself, immeasurable. For example, how is the *perception* of star brilliance measured? The classical psychophysical method of adjustment provides a method for testing perception of stimulus detection and difference detection. This is accomplished by allowing the perceiving agent to control the level of the applied stimulus until a detectable difference is perceived. This test is repeated several times to produce average responses for given stimuli intensities. The standard deviation for a particular stimulus intensity can thus be calculated to provide information about the variability of a particular percept. This method necessarily involves the agent to control the intensity of the variable stimulus by indicating that a variable is distinctly greater or less than the first one perceived. In visuomotor experiments this method is often used in which participants reproduce the stimulus such that it matches the standard in a given dimension, for example, the length of a line on a screen.

Ernst Heinrich Weber developed a principle that demonstrated we cannot subjectively detect the change between two stimulus intensities unless they differ by a minimum (or threshold) difference – the just noticeable difference (JND). In other words, there must be a certain amount of change (a just noticeable difference, JND) in stimulus *intensity* in order to *perceive* a different experience of the stimulus. Weber was thus able to quantify the subjective perception of change in a given stimulus (Ganel, Chajut, & Algom, 2008; Stern & Johnson, 2010). For example, it is possible to measure the brightness of two stars as well as the difference in the brightness between these stars in terms of a rate or intensity of brightness. A subjective experience between two stars yields a perception that one star appears brighter than the other. The perceived experience of brightness is plotted in relation to the stimulus intensity to demonstrate a linear relationship between perception and stimuli intensity. The relation between the *perception* of an experience (that of stimulus intensity *change*) and the actual stimulus intensity difference act in constant proportion and as such, create a positive linear relationship – where the *perception* of a brighter star corresponds to a greater difference in the actual stimulus intensity change. In other words, the subjective, just noticeable difference (JND), for a stimulus relates linearly and in direct proportion to the intensity of a stimulus. Weber's basic psychophysical principle was mathematically refined and formalized by Fechner as Weber's law. This can be understood mathematically as:

$$\mathrm{JND} = \mathrm{KI}$$

Where K is the constant proportion of the stimulus intensity and I is the stimulus intensity.

Weber's law has quantified perceptions of weight, sound, and vision and its principles hold true except in the most extreme kinds of stimulations (i.e., ceilings). Nonetheless, people's sensitivity to change on a given physical continuum is relative rather than absolute when measured in physical units (Marks & Algom, 1998). Weber's law is a historically important psychological law as it is one of the first and still the most widely tested and confirmed formal principle in modern psychological science that characterizes human perception for all sensory dimensions (Baird & Noma, 1978; Stevens, 1975).

Weber's law in relation to vision and tactile haptics

Ganel and colleagues (Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, & Algom, 2008) investigated the different modes of visual organization for perception and for action (PAM) with respect to Weber's law (Ganel, Chajut, & Algom, 2008). They investigated the possibility that visual control of action is subject to the same universal psychophysical function through a series of psychophysical visuomotor experiments. Ganel and colleagues compared the sensitivity for changes in object size for visually-guided action and visually-guided perception using the study of object size resolution.

Because Weber's law measures perceptual sensitivity to stimulus change, Ganel and colleagues rationalized that the behavioral outputs of vision-for-action and vision-for-perception tasks of grasping and pantomiming, respectively, could be quantified according to Weber's law (Ganel, Chajut, & Algom, 2008). They predicted that vision-for-action behavior (grasping) should show no adherence to Weber's law, while vision-for-perception behavior (pantomiming) should follow Weber's law. According to the PAM, vision-for-action and vision-for-perception should function as distinct processing streams. It stands to reason that given an action task, i.e., grasping, the vision-for-action stream should be activated and produce a mental representation in line with vision-for-action. The elicited behavior should then reflect the mental representation created; that of an action task – grasping. Given a perception task, such as pantomiming, the vision-for-perception stream should be activated and produce respective behavior reflecting this perception. Ganel and colleagues suggested that while grasping behavior requires the online and absolute metrics provided by action-stream processing, pantomime behavior recruits the relative metrics of the perception-stream (Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, et al., 2008). Therefore, pantomiming behavior is not considered an action-stream-based behavior.

In this study, a classical method of adjustment was used to calculate the JNDs which involved measuring participants' MGAs while they performed action tasks (grasping) or grip apertures (GAs) while they performed perceptual tasks (pantomiming) of differently sized objects. JNDs were defined by the variance, or standard deviations, of the MGAs and GAs for a particular object size. In other words, the JNDs reflect how consistently grasping or pantomiming is reproduced over several trials for differently sized objects. Grasping behavior should not exhibit much variance meaning that the JNDs should be stable for all sizes because action-stream processes are constantly updating the absolute measures available. Pantomime behavior, on the other hand, should show variance increasing with object size such that JNDs should show a positive linear relationship because of the relative metrics of allocentric and memory processing involved. This is based on the classic psychophysical method of adjustment in which participants reproduce the standard stimulus such that their behavior (grasp or pantomime) matches the standard stimulus.

Ganel and colleagues found that both behavioral tasks produced appropriate size scaling to objects meaning that MGA and GA scaling increased as object size increased (Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, et al., 2008). When looking at the JNDs for each behavior, they found that the action (grasp) task did not adhere to Weber's law while the perception task (pantomime) did. The standard deviations for MGAs stayed the same for visually-guided actions (grasping) despite the increasing size of object length, demonstrating a violation of Weber's law. For visually-guided perceptions (pantomiming), the standard deviations for GAs increased with the increasing size of object length exemplifying an adherence to Weber's law. Simply put, visually-guided actions did not adhere to Weber's law whereas visually-guided-perceptions adhered to Weber's law. These findings reflect a fundamental difference in the way that object size is computed for action and for perception in visually-guided behavior (Ganel et al., 2008).

Ganel and colleagues then conducted a follow-up experiment to rule out possible ceiling effects for the produced MGAs and GAs. A ceiling effect in this context is the point at which the behavior for differently sized objects no longer affect the MGA or the GA. The MGAs of grasping behaviors were compared for the same participants under the same experimental conditions but this time a memory component was added to the task. Real-time behavior was contrasted with a delayed, memory-based behavior in which the object was occluded for five seconds after the participant saw it. Memory-based grasping (without vision) is regarded as a standard perceptual condition where, ``performance has been shown to be driven by perceptual representations and which can be fully dissociated from real-time grasping`` (Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, et al., 2008; Goodale, Westwood, & Milner, 2004). In other words, an action (dorsally-driven) task, such as grasping becomes perceptually driven when a memory component is added to the task. The experimental results showed that the MGAs in the memory-delayed grasping task were larger overall than those for real-time grasping. This confirmed that the pantomimed results were not due to a ceiling effect. The results also showed that the JNDs for memory-delayed grasping increased with object size whereas those in real-time grasping did not which demonstrated that memory-guided grasping adheres to Weber's law. In other words, memory-guided grasps were just like pantomimed behaviors; perceptually driven. Ganel and colleagues` findings are consistent with previous neuropsychological and behavioral data (Ganel, Chajut, Tanzer, et al., 2008; Goodale et al., 1991) and demonstrate qualitative differences between visuomotor control and visual perception.

Recently, Davarpanah Jazi and Heath (2014) examined the allocentric principles of Weber's law in tactile action and perception (Davarpanah Jazi & Heath, 2014). They compared the JNDs produced in four different behavioral tasks of differently sized objects: a grasping task, two pantomiming tasks, and a method of adjustment task. In all tasks, participants used their right hand to match the size of a block placed on their left palm. Participants were not allowed to manipulate object. In the grasping task, participants grasped the object placed on their left palm. For one of the pantomime conditions, participants were provided with terminal tactile feedback (grasping) of the object after they completed the pantomime to provide a similar experience as in the grasping condition. For the other pantomime condition, participants were not provided with terminal tactile feedback. Finally, the method of adjustment task required participants to match the size of an object they felt by pressing a computer key that adjusted the size of a line until the perceived width of a line appearing on the screen matched the width they felt on the left hand. They found that the JNDs for grasping did not follow Weber's law whereas the JNDs for pantomiming and the method of adjustment task increased as a function of increasing object size and therefore adhered to Weber's law. These findings support the SPM's founding principles that action and perception behaviors are mediated via respective egocentric and allocentric frames of reference (Davarpanah Jazi & Heath, 2014; Dijkerman & De Haan, 2007).

In another experiment, Davarpanah Jazi, Hosang and Heath (2015; 2015) examined the effects of memory delay and the haptic feedback of a target object on tactile perceptions and actions. Participants used their right hand to pantomime (perception task) the matching size of a block that was placed on their left palm. The task was performed in each of four conditions: with or without haptic terminal feedback and with or without a delay (memory-guided) condition. They found that pantomime behaviors adhered to Weber's law regardless of the memory and haptic feedback manipulations used. As such, pantomime behaviors reflect a perceptual task mediated via an immutable and relative percept of object size. On the other hand, they found that the JNDs for grasping violated Weber's law, during immediate grasping and during memory-guided but only when sensory feedback was provided. Memory-guided grasps without sensory feedback adhered to Weber's law. This suggests that tactile feedback supports the absolute calibration between tactile defined object and the required motor output and without this feedback the action is rendered perceptual.

Chapter 3. Theory and Experiments

Theory

According to the SPM, there are different mental representations for the haptic-action and haptic-perception streams of information processing. The different mental representations of haptics-for-action and haptics-for-perception produce corresponding behaviors vis-à-vis egocentric and allocentric frames of reference. Behaviors that demonstrate an adherence to the principles Weber’s law are informed by the haptic-perception stream of somatosensory information processing.

Thesis

There is a fundamental difference in the way that object size is computed for action and for perception in the haptic modality.

Question

How do haptics-for-action and haptics-for-perception relate with Weber's law in grasping and pantomime tasks that are purely *haptic* (no vision available)?

Hypotheses & Predictions

Hypothesis I

Mental representations of haptics-for-action and haptics-for-perception streams involve different mechanisms or neural streams which can be studied by observing and measuring the kinematics of haptically-guided-action (grasping) and haptically-guided-perception (pantomiming) behaviors in object size resolution tasks. These mental representations should produce corresponding behaviors that are different from each other (i.e., a mental representation for action will draw from the action stream (online processing) and produce an action behavior; a mental representation for perception will draw from the perception stream (memory component) and produce a perception behavior). These behaviors can be kinematically measured through MGAs (grasping) and GAs (pantomiming). The standard deviations of the MGAs and GAs produce JNDs which can then serve to compare different behaviors against the principles of Weber's psychophysics law of human perception as JNDs.

Prediction I

If the mental representations for haptic action and perception streams produce behaviors corresponding to object size sensitivity, then they will be identifiable through the kinematic variables of maximum grip aperture (MGA) during grasping and grip aperture (GA) during pantomiming. In other words, the behavior should demonstrate corresponding MGAs and GAs with the presented stimuli such that they (MGAs/GAs) increase with increasing object size.

Prediction II

If there is a difference between the processing streams of haptic action and perception for object size sensitivity, then these differences will be identifiable through the kinematic variable of the just noticeable differences (JNDs) – measured by the standard deviation of MGAs/GAs – as per Weber's law. In other words, if the mental representation is an action function, then the JNDs for the behavior will show a violation to Weber's law. However, if the mental representation is a perceptual function, then the JNDs will show an adherence to Weber's law.

Hypothesis II

Mental representations of haptics-for-action and haptics-for-perception should be contingent upon a memory component and produce corresponding behaviors that are similar to each other i.e., more in line with perceptual mental representation JNDs, and as measured kinematically against the principles of Weber's law. Haptics-for-action behaviors that are memory-guided utilize perceptual processes thus rendering the JNDs more like a haptics-for-perception behavior.

Prediction

If memory-guided behaviors (grasping or pantomiming) are perception-stream tasks, the kinematic behaviors (JNDs) for any memory-guided task should adhere to Weber's Law of human perception.

Hypothesis III

In line with the PAM and the SPM, mental representations of action and perception processing streams should be engendered through similar patterns of behavior across sensory modalities given the same stimuli.

Prediction

If the same stimulus is presented in vision and haptic conditions for a task, then both modalities should engender the same kinematic pattern violating (action) or adhering to (perception) Weber's law. In other words, if a stimulus is presented in vision and haptic conditions for an action (grasping) task, then both modalities will demonstrate the same kinematic pattern of their JNDs violating Weber's law. However, if the same stimulus is presented for a perception (pantomiming) task, then both modalities will demonstrate the same kinematic pattern of their JNDs adhering to Weber's law.

Experiments

To test these hypotheses, I conducted two experiments in which I calculated the JNDs from the measured MGAs and GAs in all groups. Experiment one (1) tested the vision modality and Experiment two (2) tested the haptic modality. Both experiments featured the same stimuli (differently sized wooden squares: 20mm, 30mm, 40mm, 50mm), tasks (grasping or pantomiming), and temporal (immediate or delayed) conditions. Each experiment involved separate left-hand and right-hand blocks for the unimanual execution of a task behavior (grasping or pantomiming) a presented stimulus. A grasping task was used to draw out the action-stream behavior because action tasks rely on constantly updated and immediately available information to perform the behavior. A pantomiming task, on the other hand, was used to draw out perception-stream behavior: behavior that is executed based on information from memory and relative metrics.

To test my first hypothesis, that mental representations can be studied by observing behaviors in object size resolution, and that these mental representations produce different behaviors respectively from each other, I measured the MGAs and GAs, and JNDs of differently sized objects. The MGAs and GAs should show scaling for object size both for grasping (action) and pantomime (perception) tasks. Moreover, both tasks should demonstrate different patterns of JNDs and violation or adherence to Weber's law. The grasping (action) task should show a violation of Weber's law and the pantomiming (perception) task should show an adherence to Weber's law. In other words, the grasping task JNDs should show a flat line in terms of variance (standard deviations) of object scaling whereas the pantomime task JNDs should show an increasing linear relationship with increasing object size.

To test my second hypothesis, that mental representations are contingent on memory processes and thus produce behaviors similar to perception behaviors, I measured the JNDs during memory conditions of grasping and pantomiming and compared the JNDs between the immediately and the delay-memory performed tasks of grasping and pantomiming. Both tasks should show different patterns of JNDs. The immediate grasp (action) task should be the only task that shows violation of Weber's law whereas the immediate pantomime (perception), and delayed grasp and pantomime tasks (from memory) should all show an adherence to Weber's law. In other words, the grasping task JNDs should show a flat line in terms of variance (standard deviations) of object scaling whereas the pantomime task JNDs should show an increasing linear relationship with increasing object size.

To test my third hypothesis, that mental representations of action and perception processing streams should be engendered through similar patterns of behavior across sensory modalities given the same stimuli in terms of object-size resolution, I compared the JNDs of the four visual conditions to four haptic conditions using the same stimuli. All grasping (action) tasks and all pantomime and delay-memory tasks should demonstrate respective JND patterns that violate and adhere to Weber's law regardless of modality.

Data collection and extraction

Participant behavior (grasping or pantomiming) was tracked using an Optotrak Certus motion capture camera and infrared emitting diodes (iREDs) that were affixed to participants' index, thumb, and wrist (figure 9). Kinematic data were recorded and collected at a frequency of 400Hz during a three second window in which participants were prompted to elicit a behavior (grasp or pantomime) for every trial. The Optotrak coordinate system was calibrated prior to every new participant in all conditions. I used a Matlab program to control and semi-automate the data recording, collection, calculations, and experimental procedure of both experiments.

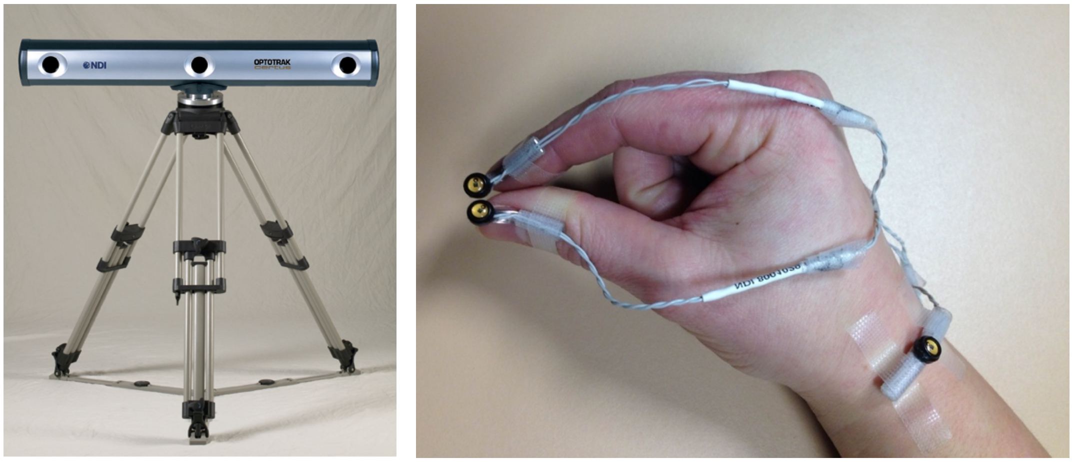

Figure 9 – The left panel shows the Optotrak Certus motion capture camera used to track participants' index, thumb, and wrist movements in three dimensions. The right panel shows the IRED placement on participant's index, thumb and wrist.

For both the grasping and pantomiming conditions, data were derived from the x, y, and z coordinates of the index and thumb iREDs. The distance between the index finger and thumb for each trial was calculated using Pythagorean's theorem (in the Matlab code). To analyze grasp behaviors, the maximum grip apertures (MGAs) of the in-flight distance between the index and thumb were extracted. I used a Matlab code to calculate the maximum distance (mm) between the index and thumb after movement onset in each trial. Movement onset was defined as the wrist velocity reaching greater than (>) 50m/s in the three second collection/recording window. To analyze pantomime behaviors, the grip apertures (GAs) of the stable state position between the index and thumb were extracted. I used a Matlab code to calculate the distance (mm) between the index and thumb vectors once they reached a steady state after the movement onset.

Analyses

Kinematic parameters were determined through Pythagorean's theorem and the kinematic calculations were performed using Matlab v2016/17. The statistical analyses were computed using SPSS v24. For all groups in both experiments, I conducted repeated measures ANOVAs with hand and object size as the within subject variables, and modality (vision or haptic), task (grasp or pantomime), and temporality (immediate or delay) were the between subject variables.

Setup, materials and general procedure

Participants in Experiment 1 (vision) wore PLATO Liquid Crystal goggles to control for visual exposure of the object stimuli. PLATO Liquid Crystal goggles are engineered to provide translucent or opaque lenses for a given condition. For Experiment 2 (haptic), in order to produce a purely haptic testing condition, participants were blindfolded and no vision was available to them for the duration of the haptic experiment.

A table was positioned in front of two Optotrak motion capture cameras. On the table, a crosshair and 'home' position were measured and marked out from the same edge of the table (figure 10). The crosshair was measured and marked 190 mm from the edge of the table. This crosshair was to ensure a) consistent and centered object placement for every trial and b) to provide a consistent measuring area for participant arm length and chair or seat position. A 10mm x 10mm Lego block, henceforth referred to as the home position, was installed using two-sided tape at 30 mm from the edge of the table (which would be nearest the participant), and in line with the vertical crosshair vector (figure 10). The home position was designed to allow participants to find and reorient themselves/their hand when performing tasks without vision, as well as to provide a consistent and controlled starting position for every trial executed. Participants were seated and centered with the crosshair and home position on the table (figure 11).

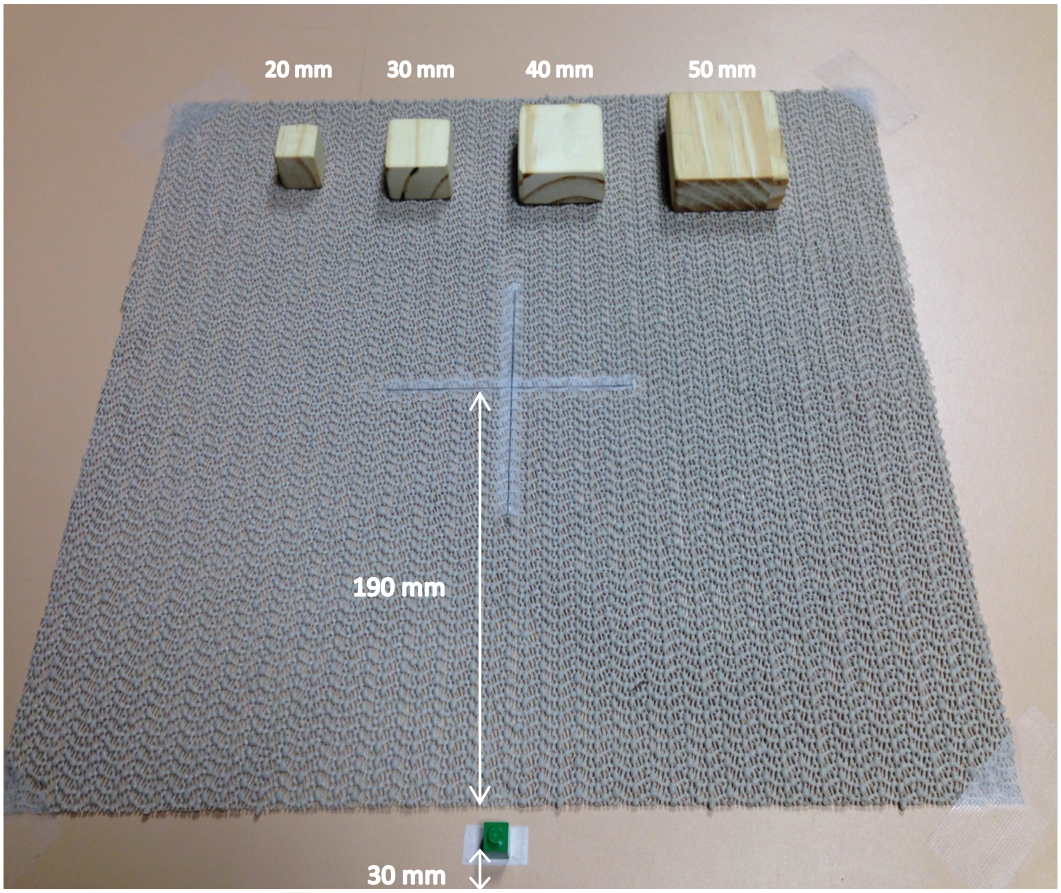

Figure 10 – Table top configuration with the home position (bottom of panel) and crosshair (center of panel). The object stimuli (at the top of the panel) used in experiments 1 and 2. The smallest object (20mm) to the largest object (50mm) could easily be manipulated by all participants' hands.

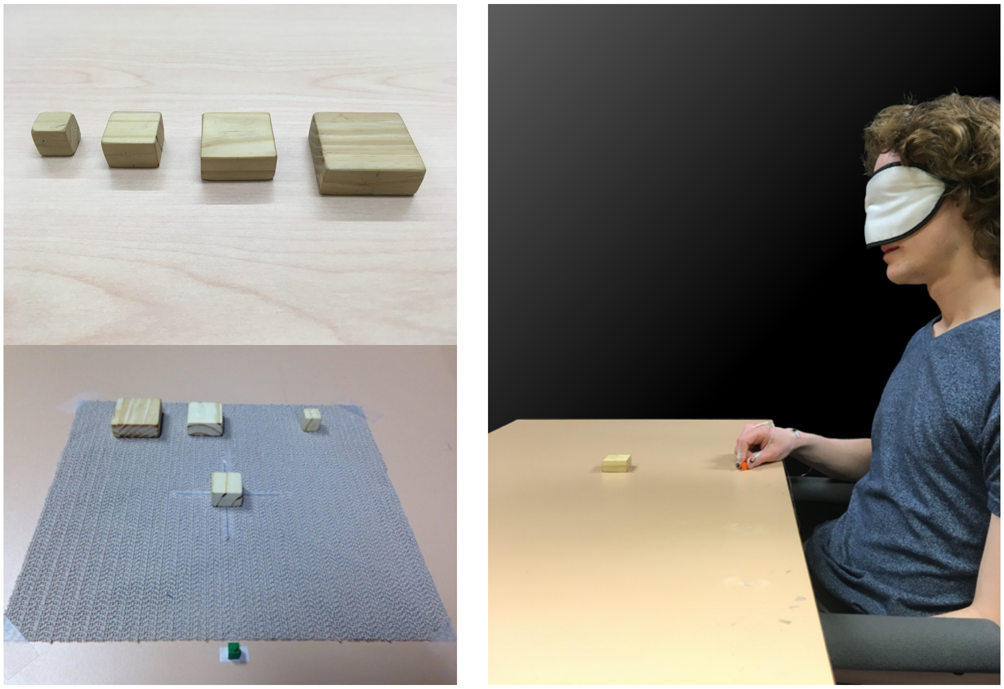

Figure 11 – The left panel shows the four different object sizes (top left) and an example of the block placement on the crosshair (bottom left). All objects were orientated the same way; square with the crosshair. The right panel shows a blindfolded participant seated comfortably and centered with the crosshair and home position.

Material and stimuli

The stimuli for these experiments consisted of four differently sized square wooden objects (20mm, 30mm, 40mm, 50mm) all with the same 20mm thickness (figure 10) Each sized-square was presented twelve times per hand-block (per participant) in a pseudorandom order according to participant number and condition. The orientation of the object placed at the crosshairs was always the same (figure 11). Participants in all conditions were instructed to produce behavior where the thumb was always closer to them while their index finger was further away in grasping or pantomiming the different objects (figure 12). Participants in both experiments and in all conditions were not given any information about the number of different objects for which they would be grasping or pantomiming.

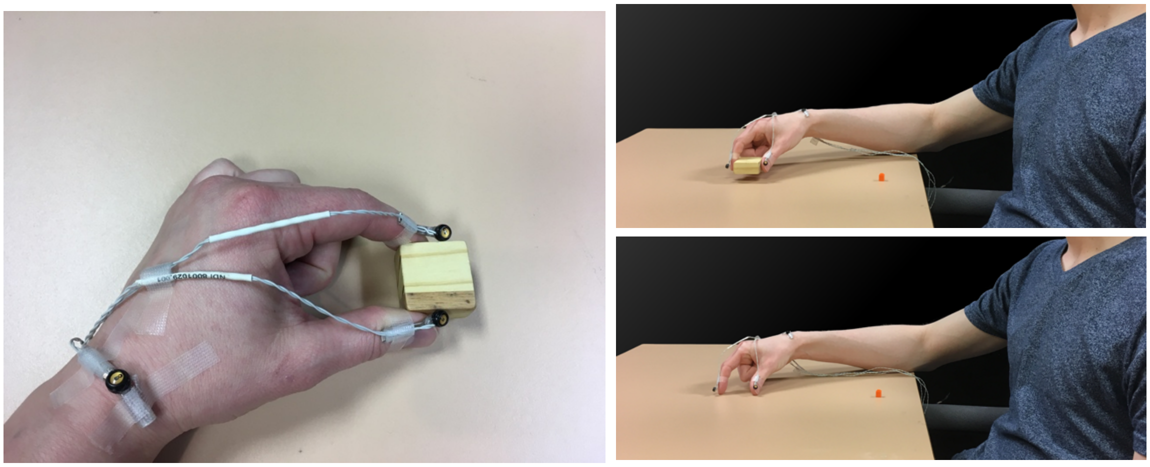

Figure 12 – The left panel shows a grasp from the participant's point of view where the thumb is proximal and the index is distal to the body. The top right panel shows the side view of a participant grasping a block in the haptic condition (blindfolded). The bottom right panel shows the side view of a participant pantomiming a block in the haptic condition (blindfolded).

General procedure

Prior to the first trial, participants were informed that the experiment was divided into two 48-trial blocks: one for each hand and that the entire session would last up to 75 minutes. Participants were told that they would be grasping or pantomiming different objects, one at a time, with the right or left hand. Once all the trials (48) were completed for one hand (one block) then the same would be repeated with the other hand. The participants' starting hand (right or left) was counterbalanced between participants so that approximately half of each group started the first block using the right hand whereas participants in the other half of the group started the first block using the left hand. They were also informed that the objects would always be placed in the same orientation and location on the table top for them to grasp (only applicable for the grasping conditions). Given the length of the experiment, different groups of participants were recruited for each of the between factors (modality – vision or haptic; task – grasp or pantomime; and temporal condition – immediate or delay).

Participants sat comfortably in a chair facing the testing table with their back against the chair-back. They were instructed to not lean or strain their body position during the "calibration" and testing of the study. Each participant was instructed to move the chair in which they were seated to line up with the vertical cross hair and the home position. To control for the reaching distance, the chair in which participants were seated was adjusted forward or back from the table without otherwise altering the participant's posture (causing them to lean forward or strain) until their wrist was centered at the horizontal crosshair. This ensured each participant full and comfortable reach-to-grasp mobility, from the home position to the centre of the crosshairs, for a block of trials (minimum of 48 trials per hand).

Once the seating position of each participant was achieved, participants were given an opportunity to learn the distance between the home position and the centre of the crosshairs by practicing the movement between the home position and the centre of the crosshairs where they would grasp a small roll of tape. Participants were instructed to use only a pincer grasp (the index finger and thumb) to grasp the home position. For the grasping groups, participants were also instructed to use only a pincer grasp to perform the grasping of the featured object stimuli. In the pantomime groups, participants were instructed to show the size of an object by separating the index and thumb to reflect the distance of the object size. These participants were required to place both the index and the thumb on the table and near the crosshair to provide a stable measure. After approximately five practice trials, or when participants were comfortable with the movements and seemed to move their hand in a stable manner, the IREDs were installed on the participant's thumb, index finger and wrist. A few more practice trials were encouraged to ensure the correct placement of the IREDs and that the Optotrak could consistently receive the signal. A mock trial was provided immediately prior to the start of the recorded experiment to ensure that the participant understood all the instructions and could execute the appropriate behavior (grasp or pantomime) for the given condition (immediate or delay-memory); the participant was told and shown the order of operation of a single trial for the given experiment.

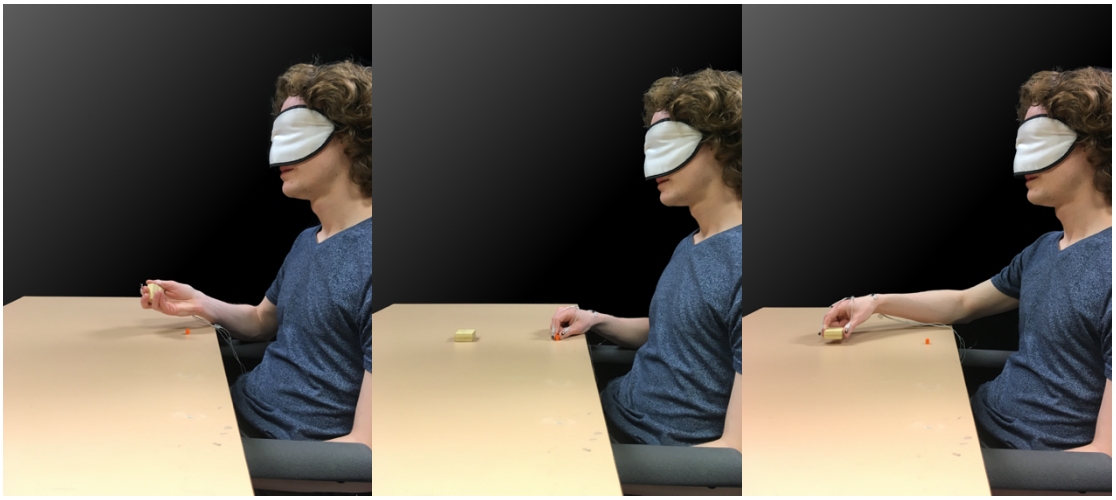

Figure 13 – General procedure for an experimental trial. Here, the haptic condition is shown with the participant wearing a blindfold to occlude vision. They start with the object exploration (left panel) for 5000ms, followed by grasping the home position using a pincer grasp (center panel), followed by the prescribed task (grasp or pantomime) (right panel) completing one trial. In vision experiments, everything was the same except participants had the use of vision and did not manually explore the target objects prior to performing a task as they received object stimuli information through vision.

Participants

A total of 153 participants were recruited from the University of Lethbridge. Participants were healthy, with no evidence of neurological impairment. According to a modified version of the Edinburgh/Waterloo Handedness Inventory (Brown, Roy, Rohr, & Bryden, 2006; Oldfield, 1971), which was always administered at the end of the testing session, six participants were identified as left-handed and were excluded from further analyses. Only right-handed participants were included in the analyses of this thesis for a total of 147 participants (111 females). Participants were naïve to the purpose of the study and informed consent was obtained prior to participation.

Experiment 1 - Vision

Experiment 1 was divided into four groups: immediate grasping (n = 20, 15 females), immediate pantomiming (n = 10, 9 females), delayed grasping (n = 10, 8 females), and delayed pantomiming (n = 10, 8 females). In all vision groups, once participants were prepared as outlined above, they were provided with the PLATO goggles to wear for the duration of the condition. Participants were informed that they would have three seconds to grasp or pantomime an object, using only their index and thumb, after hearing an audible prompt (beep). They were told to hold the object (grasp) or the stable position (pantomime) for three seconds until a second beep was heard, indicating the end of a trial. This was repeated in at least 47 more trials. All trials started with opaque, or "closed" PLATO goggles that occluded participant vision.

Procedures

Immediate grasping and immediate pantomiming groups in vision

For the immediate grasping group, participants were instructed to grasp the object centered on the crosshair once a beep was heard. A trial was programmed to start once an object was centered on the crosshairs and the participant grasped the home position using a pincer grasp. The three second data collection and recording began when the PLATO goggles opened and a beep sounded, signaling the participant to grasp the object they could now see. The participant grasped and held the object, just hovering above the table, until a second beep sounded and the goggles closed (became opaque), indicating the end of the trial.

The immediate pantomiming group entailed the same procedure as for the grasping group save for the task and object placement. Participants were instructed to pantomime the largest size of an object presented once a beep was heard. The object was placed to the side of the crosshair that was opposite the performing hand to provide an unobstructed trajectory between the home position and the finger "landing spot" on the table near the crosshair. The participant held this position for the remainder of the three second collection duration at which point a second prompt sounded and the PLATO goggles closed, indicating the end of the trial.

Delayed grasping and delayed pantomiming groups in vision

The delayed groups were conducted using the same procedures as the immediate task groups but included a 5000ms delay, creating a memory component for the task. This involved occluding vision for the 5000ms before the task was performed. Vision occlusion persisted through the three second task performance window after the 5000ms delay.

Participants were shown the object for three seconds and were instructed to grasp or pantomime the object shown to them after hearing a beep which would sound only after a 5000ms, no vision delay. Upon hearing the beep, participants then performed the task without vision, as eluded to previously.

Experiment 2 – Haptics

Experiment 2 was also divided into four groups: immediate grasping (n = 32, 21 females), immediate pantomiming (n = 33, 27 females), delayed grasping (n = 16, 13 females), and delayed pantomiming (n = 16, 13 females). In all haptic groups, once participants were prepared as outlined above, they were blindfolded for the entirety of the condition. This meant that participants had no vision available to process characteristics of an object stimuli. Instead, they had to rely on only the haptic information provided to them through haptic manipulation of an object placed in their hand. These participants were given the opportunity to explore an object placed in one of their hands for five seconds. They were limited to the use of one hand and were encouraged to feel and haptically-manipulate the object presented using the entirety of their hand for the five second duration. Participants in the haptic groups were never visually exposed to the objects, nor were they informed of the number of different objects for which they would be manipulating, grasping, or pantomiming. However, participants in the grasping conditions (both immediate and delay-memory) were told that the objects would always be in the same location and orientation (on the crosshair) to perform grasps.

Participants were informed they would have three seconds to grasp or pantomime the same object they had just manually explored, using the same hand, after hearing a second beep. They were told to hold the object (grasp) or the stable position (pantomime) during the three second recording period until a third beep was heard, indicating the end of a trial. This was repeated in at least 47 more trials, all of which started with a five second object exploration/stimuli exposure event.

For all haptic conditions, the trials started with a participant opening their hand, palm up, to receive and manually explore an object. A beep sounded after five seconds and the object was removed from the participant's hand and either placed on the crosshair (for a grasping condition) or off to the side (for a pantomime condition). In the meantime, the participant would locate and grasp the home position using a pincer grasp.

Procedures

Immediate grasping and pantomiming conditions in haptics

For the immediate grasping group, participants were instructed to grasp the object they had manually explored (for five seconds) which was now centered on the crosshair, once a beep was heard. A trial was programmed to start once an object was centered on the crosshairs and the participant grasped the home position using a pincer grasp. The three second data collection and recording began when a second beep sounded, signaling the participant to grasp the object they had just manipulated using the same hand. The participant grasped and held the object, just hovering above the table, until a third beep sounded, indicating the end of the trial.

The immediate pantomiming group entailed the same procedure as for the grasping group save for the task. Participants were instructed to pantomime the largest size of the recently manipulated object once a second beep was heard. The participant held this position for the remainder of the three second collection duration at which point a third beep sounded, indicating the end of the trial.

Delayed grasping and delayed pantomiming groups in haptics

The delayed groups were conducted using the same procedures as the immediate task groups but included a memory component (5000ms delay) before the task was performed. Participants were instructed to grasp or pantomime the object they had previously manipulated, but only after a 5000ms, no haptic feedback/information, delay.

Chapter 4. Results

Results

The results are divided into two sections to help maintain clarity of the statistical analysis: Object size scaling in MGAs and JNDs (individual group statistics), and repeated measures ANOVA. All results are subject to an α set to $p < 0.05$ for significance values, all p-values reported are two-tailed, and confidence intervals are reported at 95% lower and upper bounds.

The following six points are elucidated here in the interest of reducing literary redundancy in the results section. First, the Greenhouse-Geisser correction was used in all ANOVAs as Mauchly's test of sphericity was significant ($p < 0.001$). Second, the mean (M), standard error (SE), and 95% confidence interval (CI) for MGA and JND, of every group are presented in tables (to facilitate understanding of results). Third, a main effect of size in MGAs demonstrates that participants scaled smaller for smaller objects and scaled larger for larger objects. Fourth, a main effect of size in JNDs demonstrates an adherence to Weber's law while no effect of size in JNDs shows a violation of Weber's law. Fifth, only main effects ($p < 0.05$) and interactions are reported. Finally, sex was not included in the statistical analysis as very few males participated in my studies. As such, sex was collapsed across both experiments and in all groups.

Object size scaling in MGAs, GAs and JNDs

Repeated measures ANOVAs were used to demonstrate whether the MGAs and GAs show scaling for object size and whether the associated JNDs show a violation or an adherence to Weber's law in each group in both experiments. The within subject factors were hand (x2) and size (x4) and there was no between subject factor. Results for group 1, vision immediate grasp, are presented in table 1, table 2 and Figure 14; Results for group 2, vision immediate pantomime, are presented in table 3 and Figure 15; Results for group 3, vision delayed grasp, are presented in Table 4 and Figure 16; Results for group 4, vision delayed pantomime, are presented in Table 5 and Figure 17; Results for group 5, haptic immediate grasp, are presented in Table 6 and Figure 18; Results for group 6, haptic immediate pantomime, are presented in Table 7 and Figure 19; Results for group 7, haptic delayed grasp, are presented in Table 8 and Figure 20 ; And results for group 8, haptic delayed pantomime, are presented in Table 9 and Figure 21.

Experiment 1 – Vision

Group 1 – Vision immediate grasp – refer to table 1 and Figure 14.

Table 1. Results of Experiment 1, group 1: Vision, immediate grasp. Means and standard errors are reported for MGA and JND grasp kinematics.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
MGAs	20 mm	58.015	1.808	[54.231, 61.798]
	30 mm	67.428	1.868	[63.518, 71.337]
	40 mm	77.303	1.978	[73.162, 81.443]
	50 mm	86.551	1.882	[82.612, 90.491]
JNDs	20 mm	5.179	0.399	[4.343, 6.015]
	30 mm	5.009	0.337	[4.305, 5.714]
	40 mm	5.003	0.273	[4.431, 5.574]
	50 mm	4.879	0.330	[4.189, 5.569]

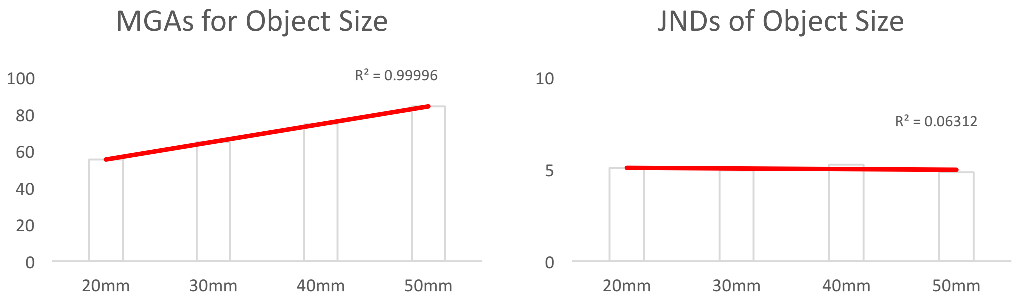

Figure 14 – MGAs and JNDs of vision immediate grasp group. The left panel shows MGA scaling for object size. The right panel shows invariant JNDs, creating a flat line suggesting non-adherence or violation to Weber's law.

MGAs

A main effect of size was found in MGAs, F (1.830, 34.775) = 1038.705, $p < 0.000$, $\eta^2 = 0.982$. Participants scaled larger for larger object sizes and scaled smaller for smaller objects. Follow-up pairwise comparisons showed that all sizes were significantly different from one another (p's < 0.001). A hand by size interaction was found, F (2.229, 42.357) = 3.258, $p < 0.043$, $\eta^2 = 0.146$. Follow-up paired-samples t-tests showed significant differences in the way each hand responded to the different object sizes (p's < 0.000). The right hand opened less wide (M = 58.034, SE = 2.148) when compared to the left hand (M = 57.995, SE = 1.931) for the 20mm object, but wider than the left for the other three object sizes (refer to table 2, below).

Table 2 – Paired samples t-test of hand by size interaction results. Means and standard errors are reported for left and right hand object grasps.

Hand	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
Left	20 mm	58.034	2.148	[53.540, 62.529]
	30 mm	66.722	2.168	[62.185, 71.260]
	40 mm	76.093	2.194	[71.500, 80.686]
	50 mm	85.700	2.128	[81.246, 90.154]
Right	20 mm	57.995	1.931	[53.953, 62.038]
	30 mm	68.133	2.001	[63.946, 72.320]
	40 mm	78.512	2.108	[74.100, 82.924]
	50 mm	87.403	2.041	[83.131, 91.675]

JNDs

There was no main effect of size in JNDs demonstrating a violation of Weber's law.

Group 2 – Vision, immediate pantomime – see table 3 and Figure 15.

Table 3 – Results of Experiment 1, group 2: Vision, immediate pantomime. Means and standard errors are reported for GA and JND pantomime kinematics.

Measure	Object size	Mean (mm)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
GAs	20 mm	29.143	1.890	[24.867, 33.419]
	30 mm	39.245	2.400	[33.816, 44.674]
	40 mm	50.035	2.661	[44.015, 56.054]
	50 mm	61.011	3.026	[54.166, 67.857]
JNDs	20 mm	3.069	0.398	[2.094, 4.044]
	30 mm	3.601	0.459	[2.477, 4.724]
	40 mm	4.499	0.556	[3.139, 5.860]
	50 mm	5.036	0.677	[3.380, 6.692]

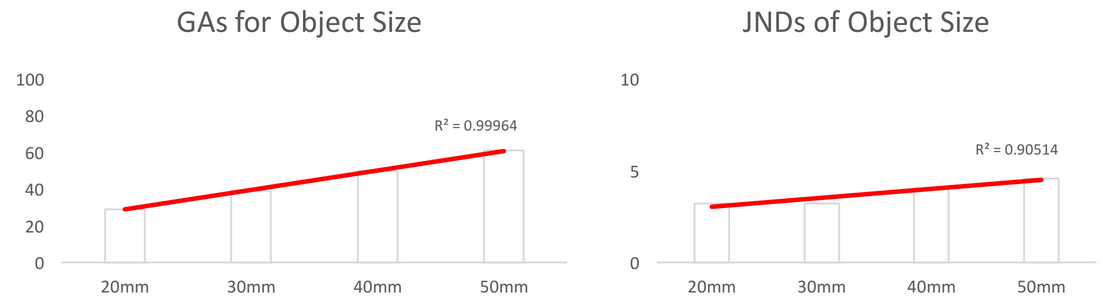

Figure 15 – GAs and JNDs of the vision immediate pantomime group. The left panel shows GA scaling for object size. The right panel shows increasing JNDs with increase object size, creating a positive linear relationship suggesting an adherence to Weber's law.

GAs

A main effect of size was found in GAs, F (1.456, 13.100) = 314.500, $p < 0.000$, $\eta^2 = 0.972$, demonstrating that participants scaled smaller for smaller objects and larger for larger objects. Follow-up pairwise comparisons showed that all sizes were significantly different from one another (p's < 0.001).

JNDs

A main effect of size, F (2.189, 19.705) = 8.236, $p = 0.002$, $\eta^2 = 0.478$ was found in JNDs which demonstrates an adherence to Weber's law. Follow-up paired-samples t-tests revealed that the 20mm object size JNDs were significantly smaller than the 50mm JNDs ($p = 0.039$), and that the 30mm object size JNDs were significantly smaller than the 40mm ($p = 0.05$), and 50mm ($p = 0.08$) JNDs.

A main effect of hand was also found in JNDs, $F(1, 9) = 21.318$, $p = 0.001$, $\eta^2 = 0.703$ showing that the left hand ($M = 4.159$, $SE = 0.411$) has greater JNDs (more variable) than the right hand ($M = 3.368$, $SE = 0.304$) does.

Group 3 – Vision, delayed grasp – see table 4 and Figure 16.

Table 4 – Results of Experiment 1, group 3: Vision, delayed grasp. Means and standard errors are reported for MGA and JND grasp kinematics.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
MGAs	20 mm	65.943	2.675	[59.892, 71.994]
	30 mm	73.750	2.017	[69.186, 78.313]
	40 mm	81.457	2.203	[76.732, 86.699]
	50 mm	86.457	2.463	[80.886, 92.027]
JNDs	20 mm	5.261	0.515	[4.097, 6.425]
	30 mm	6.341	0.471	[5.277, 7.405]
	40 mm	5.723	0.279	[5.092, 6.353]
	50 mm	5.918	0.396	[5.022, 6.813]

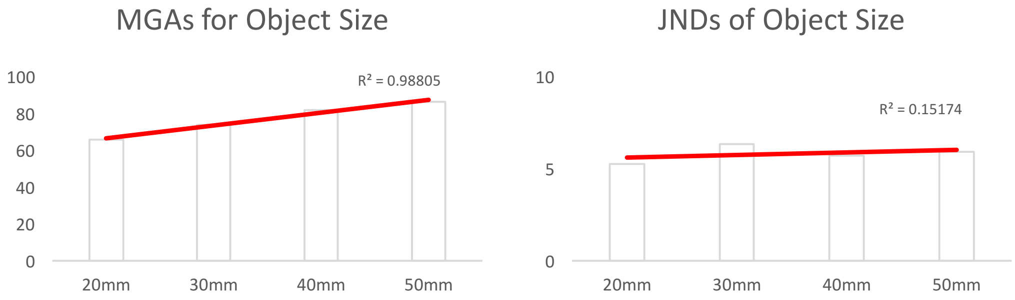

Figure 16 – MGAs and JNDs of the vision delay grasp group. The left panel shows MGA scaling for object size. The right panel shows invariant JNDs, creating a flat line suggesting non-adherence or violation to Weber's law.

MGAs

A main effect of size was found in MGAs, F (1.814, 16.330) = 150.876, $p < 0.000$, $\eta^2 = 0.944$, showing that participants scale smaller for smaller objects and scale bigger for bigger objects. Follow-up pairwise comparisons showed that all sizes were significantly different from one another (p's < 0.001).

JNDs

There was no main effect of size in JNDs demonstrating a violation of Weber's law.

A main effect of hand was found in JNDs, $F(1, 9) = 6.738$, $p < 0.029$, $\eta^2 = 0.428$. The left hand ($M = 6.162$, $SE = 0.442$) has greater JNDs than the right hand ($M = 5.460$, $SE = 0.269$) does and is therefore more variable than the right hand.

Group 4 – Vision, delayed pantomime – see table 5 and Figure 17.

Table 5 – Results of Experiment 1, group 4: Vision, delayed pantomime. Means and standard errors are reported for GA and JND pantomime kinematics.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
GAs	20 mm	31.448	1.817	[27.338, 35.557]
	30 mm	42.758	2.713	[36.621, 48.895]
	40 mm	54.672	3.517	[46.717, 62.628]
	50 mm	68.529	4.846	[57.567, 79.492]
JNDs	20 mm	4.678	0.355	[3.874, 5.482]
	30 mm	5.750	0.372	[4.908, 6.592]
	40 mm	6.905	0.686	[5.354, 8.457]
	50 mm	7.730	0.628	[6.310, 9.150]

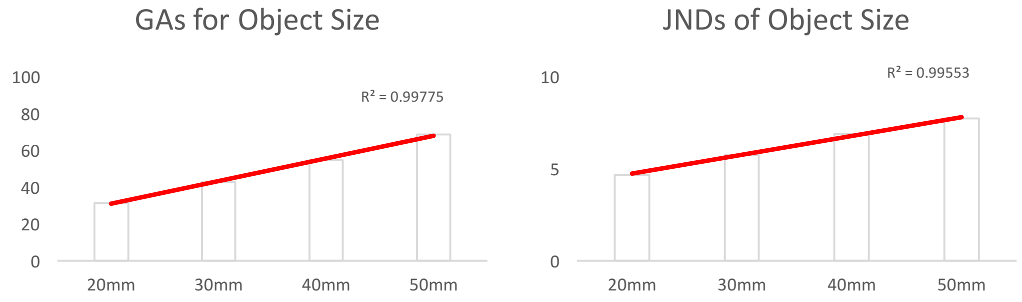

Figure 17 – GAs and JNDs of the vision delay pantomime group. The left panel shows GA scaling for object size. The right panel shows increasing JNDs with increase object size, creating a positive linear relationship suggesting an adherence to Weber's law.

GAs

A main effect of size was found in GAs, F (1.135, 10.219) = 75.362, $p < 0.000$, $\eta^2 = 0.893$, showing that participants scale smaller for smaller objects and scale bigger for bigger objects. Follow-up pairwise comparisons showed that all sizes were significantly different from one another (p's < 0.001).

JNDs

A main effect of size, F (2.012, 18.110) = 9.720, p = 0.001, $\eta^2 = 0.519$, was found in JNDs which demonstrates an adherence to Weber's law. Follow-up paired-samples t-tests revealed that the 20mm object size JNDs were significantly smaller than the 40mm ($p = 0.039$) and 50mm ($p = 0.024$) JNDs, and that the 30mm object size JNDs were significantly smaller than the 50mm ($p = 0.036$) JNDs.

Experiment 2 – Haptic

Group 5 – Haptic, immediate grasp – see table 6 and Figure 18.

Table 6 – Results of Experiment 2, group 5: Haptic, immediate grasp. Means and standard errors are reported for MGA and JND grasp kinematics.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
MGAs	20 mm	76.192	1.927	[72.252, 80.132]
	30 mm	83.468	1.934	[79.512, 87.424]
	40 mm	88.683	1.917	[84.762, 92.605]
	50 mm	94.306	2.040	[90.134, 98.477]
JNDs	20 mm	7.453	0.441	[6.552, 8.355]
	30 mm	7.215	0.383	[6.432, 7.998]
	40 mm	7.360	0.386	[6.570, 8.151]
	50 mm	7.208	0.445	[6.297, 8.118]

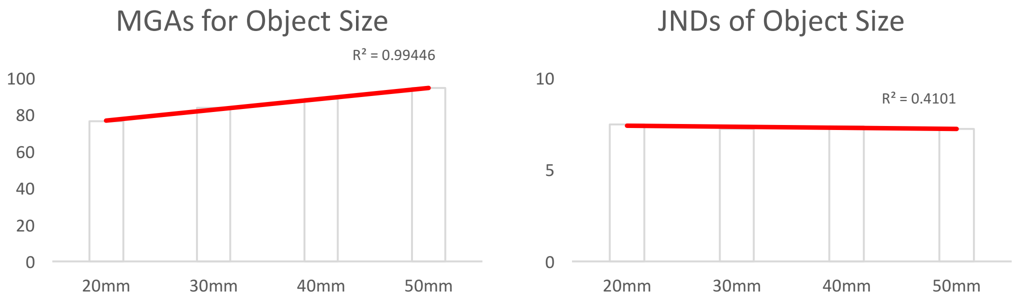

Figure 18 – MGAs and JNDs of the haptic immediate grasp group. The left panel shows MGA scaling for object size. The right panel shows invariant JNDs, creating a flat line suggesting non-adherence or violation to Weber's law.

MGAs

A main effect of size was found in MGAs, F (1.434, 41.587) = 184.262, $p < 0.000$, $\eta^2 = 0.864$, showing that participants scale smaller for smaller objects and scale bigger for bigger objects. Follow-up pairwise comparisons showed that all sizes were significantly different from one another (p's < 0.001).

JNDs

There was no main effect of size in JNDs demonstrating a violation of Weber's law.

Group 6 – Haptic, immediate pantomime – see table 7 and Figure 19.

Table 7 – Results of Experiment 2, group 6: Haptic, immediate pantomime. Means and standard errors are reported for GA and JND pantomime kinematics.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
GAs	20 mm	37.792	1.105	[35.531, 40.052]
	30 mm	51.293	1.309	[48.615, 53,970]
	40 mm	51.293	1.309	[48.615, 53,970]
	50 mm	75.841	1.383	[73.012, 78.670]
JNDs	20 mm	3.943	0.382	[3.161, 4.725]
	30 mm	5.025	0.323	[4.364, 5.685]
	40 mm	5.767	0.388	[4.974, 6.559]
	50 mm	6.218	0.471	[5.255, 7.181]

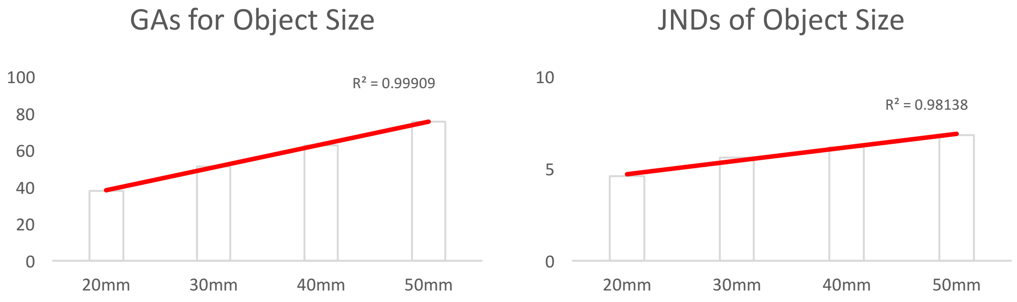

Figure 19 – GAs and JNDs of the haptic immediate pantomime group. The left panel shows GA scaling for object size. The right panel shows increasing JNDs with increase object size, creating a positive linear relationship suggesting an adherence to Weber's law.

GAs

A main effect of size was found in GAs, F (1.473, 42.712) = 619.090, $p < 0.000$, $\eta^2 = 0.955$, showing that participants scale smaller for smaller objects and scale bigger for bigger objects. Follow-up pairwise comparisons showed that all sizes were significantly different from one another (p's < 0.001).

JNDs

A main effect of size, F (2.106, 61.069) = 17.220, $p < 0.000$, $\eta^2 = 0.373$, was found in JNDs which demonstrates an adherence to Weber's law. Follow-up pairwise comparisons showed that all sizes were significantly different from one another (p's < 0.001).

Group 7 – Haptic, delayed grasp – see table 8 and Figure 20.

Table 8 – Results of Experiment 2, group 7: Haptic, delayed grasp. Means and standard errors are reported for MGA and JND grasp kinematics.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
MGAs	20 mm	75.442	2.231	[70.686, 80.198]
	30 mm	81.010	2.514	[75.652, 86.369]
	40 mm	86.050	2.320	[81.105, 90.995]
	50 mm	86.050	2.320	[81.105, 90.995]
JNDs	20 mm	8.058	0.363	[7.284, 8.832]
	30 mm	6.940	0.420	[6.044, 7.836]
	40 mm	6.918	0.404	[6.056, 7.780]
	50 mm	6.818	0.506	[5.739, 7.896]

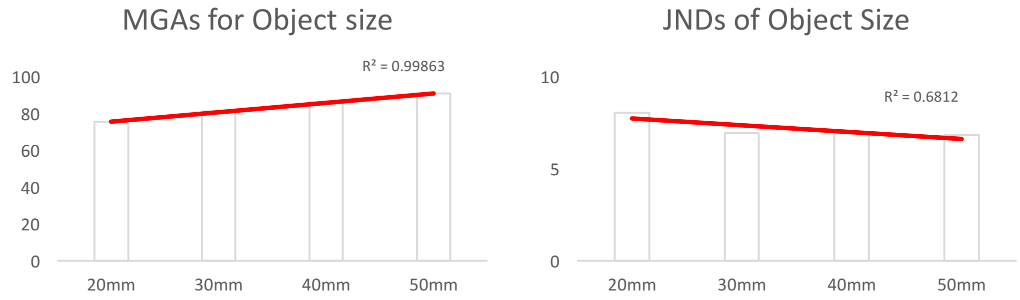

Figure 20 – MGAs and JNDs of the haptic delay grasp group. The left panel shows MGA scaling for object size. The right panel shows invariant (decreasing) JNDs, creating a flat, declining line suggesting non-adherence or violation to Weber's law (as Weber's law posits that perceptual relationships must be a positive linear relationship rather than inverse or negative)

MGAs

A main effect of size was found in MGAs, F (1.853, 27.801) = 237.517, $p < 0.000$, $\eta^2 = 0.855$, showing that participants scale smaller for smaller objects and scale bigger for bigger objects. Follow-up pairwise comparisons showed that all sizes were significantly different from one another (p's < 0.001).

JNDs

A main effect of size, $F(2.839, 42.591) = 11.594$, $p < 0.038$, $\eta^2 = 0.172$, was found in JNDs. However, follow-up pairwise comparisons reveals no significant differences between the sizes after Bonferroni correction (p's > 0.085).

Group 8 – Haptic, delayed pantomime – see table 9 and figure 21.

Table 9 – Results of Experiment 2, group 8: Haptic, delayed pantomime. Means and standard errors are reported for GA and JND pantomime kinematics.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
GAs	20 mm	31.048	1.159	[28.577, 33.519]
	30 mm	43.978	1.454	[40.880, 47.076]
	40 mm	55.032	1.789	[51.218, 58.846]
	50 mm	68.662	1.955	[64.494, 72.829]
JNDs	20 mm	4.148	0.252	[3.612, 4.685]
	30 mm	5.492	0.315	[4.821, 6.164]
	40 mm	6.159	0.373	[5.365, 6.953]
	50 mm	6.738	0.323	[6.050, 7.427]

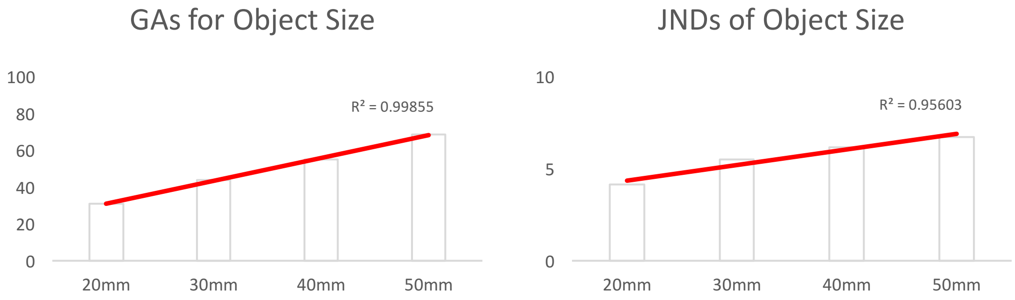

Figure 21 – GAs and JNDs of the haptic delay pantomime group. The left panel shows GA scaling for object size. The right panel shows increasing JNDs with increase object size, creating a positive linear relationship suggesting an adherence to Weber's law.

GAs

A main effect of size was found in GAs, F (1.575, 23.628) = 409.545, $p < 0.000$, $\eta^2 = 0.965$, showing that participants scale smaller for smaller objects and scale bigger for bigger objects. Follow-up pairwise comparisons showed that all sizes were significantly different from one another (p's < 0.001).

JNDs

A main effect of size, F (2.130, 31.947) = 17.318, $p < 0.000$, $\eta^2 = 0.536$, was found in JNDs which demonstrates an adherence to Weber's law. Follow-up paired-samples t-tests revealed that the 20mm object size JNDs were significantly smaller than the 30mm ($p < 0.000$), 40mm ($p < 0.000$), and the 50mm ($p < 0.000$) JNDs.

An “almost” main effect of hand was found in JNDs, F (1, 15) = 4.519, p = 0.051, $\eta^2 = 0.232$. The left hand JNDs (M = 6.117, SE = 0.359) are more variable than the right hand (M = 5.152, SE = 0.264**)** for pantomiming.

Repeated measures ANOVA for all groups

A repeated measures ANOVA was used to investigate significant JND differences between vision and haptics, grasping and pantomiming, and immediate and delayed groups. The between factors were modality (vision, haptic), task (grasp, pantomime), and temporality (immediate, delayed), and the within-subject factors were hand (X2), and size (X4 object sizes). No main effect or interaction with the hand factor (F (1, 134) = 3.590, $p < 0.060$, $\eta^2 = 0.026$) were found so in the interest of brevity, hand was collapsed across analyses. The Huynh-Feldt correction was applied as Mauchley's test of sphericity was found to be significant ($p = 0.012$) and as the epsilon value was found to be > 0.75.

Main effects

Between variables – modality, task, and temporality

Three main effects were found for between subject analyses. A main effect of modality (F (1, 134) = 19.976, $p < 0.000$, $\eta^2 = 0.130$) showed that the vision groups (M = 5.214, SE = 0.228) were less variable than the haptic groups (M = 6.484, SE = 0.169); a main effect of task (F (1, 134) = 11.488, $p = 0.001$, $\eta^2 = 0.079$) demonstrated that the grasping groups (M = 6.330, SE = 0.919) were more variable than the pantomime groups (M = 5.368, SE = 0.210); and a main effect of temporality (F (1, 134) = 6.957, $p = 0.009$, $\eta^2 = 0.049$) showed that the immediate task groups (M = 5.474, SE = 0.180) were less variable than the delayed (memory) task groups (M = 6.223, SE = 0.220).

Within variables – size – refer to table 10 and figure 22.

Table 10 – Results of repeated measures ANOVA on object size JNDs. Means, standard errors, and 95% confidence intervals are reported for JND size comparisons.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
JNDs	20 mm	5.323	0.179	[4.970, 5.676]
	30 mm	5.699	0.160	[5.383, 6.015]
	40 mm	6.035	0.164	[5.711, 6.358]
	50 mm	6.339	0.188	[5.968, 6.710]

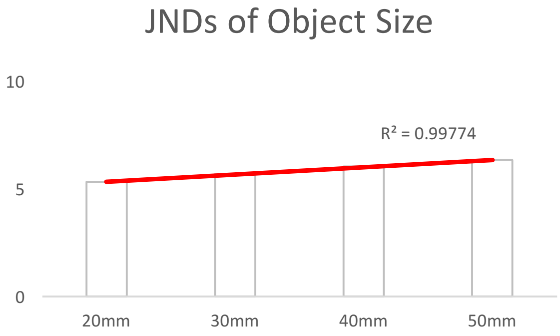

Figure 22 – Results of repeated measures ANOVA for object size JNDs. The graph shows increasing JNDs with increasing object size, creating a positive linear relationship and thereby suggesting an adherence to Weber's law.

Overall, a main effect was found for size JNDs, F (2.997, 401.555) = 14.805, $p < 0.000$, $\eta^2 = 0.099$, showing a general adherence to Weber's law. Pairwise comparisons revealed significance values for some (although not all) sizes. Follow-up paired-samples t-tests revealed that the 20mm JNDs were significantly smaller than the 40mm ($p < 0.000$) and 50mm ($p < 0.000$) JNDs, and that the 30mm object size JNDs were significantly smaller than the 50mm ($p = 0.001$) JNDs.

Interactions

Task by size JNDs

A significant interaction between task by size JNDs (F (2.997, 401.555) = 24.645, $p < 0.000$, $\eta^2 = 0.155$), suggests that JNDs vary according to the task performed (grasping or pantomiming). Paired sample t-tests were conducted where data were split by task and revealed that in grasping there were no significant differences between the JNDs of differently sized objects. The inverse was found in pantomiming: there were significant differences between the JNDs of *all* sizes (p's < 0.024). In other words, JNDs across all grasping tasks were found to be less variable than JNDs across all pantomiming tasks. This shows that grasping does not adhere to Weber's law, while pantomiming does.

Between subject interactions

Modality by temporality

A between-subject interaction was found for modality and temporality (F (1, 134) = 10.006, p = 0.002, η^2 = 0.069). A follow-up one-way ANOVA, split by modality, revealed a significant difference between vision groups (F (1, 49) = 15.935, p < 0.000). The vision immediate groups (M = 4.391, SE = 0.299) were less variable than the vision delay groups (M = 6.038, SE = 0.345). No such difference was found in the haptic modality.

A further follow-up one-way ANOVA, split by temporality this time, revealed a significant difference (F (1, 89) = 22.156, p < 0.000) between the immediate groups. The immediate vision groups (M = 4.391, SE = 0.299) were less variable than the immediate haptic groups (M = 6.558, SE = 0.199). No such difference was found between the delay groups.

Modality by task

Another between-subject interaction was found between modality and task (F (1, 134) = 3.931, p = 0.049, η^2 = 0.028). A one-way ANOVA (split by modality) showed a significant difference (F (1, 91) = 18.613, p < 0.000) between the haptic groups. Haptic grasp groups (M = 7.246, SE = 0.239) were more variable than the haptic pantomime groups (M = 5.721, SE = 0.239). No such difference was found in the vision modality.

A further follow-up one-way ANOVA, this time split by task, showed a significant difference (F (1, 75) = 31.423, p < 0.000) between the grasp groups. Grasping haptic groups (M = 7.246, SE = 0.239) were more variable than the grasping visual groups (M = 5.414, SE = 0.299). No such difference was found between the pantomime groups.

Three-way interactions

Task by modality by size JNDs

A three-way interaction was found between task, modality, and size JNDs (F (2.997, 401.555) = 2.616, p = 0.050, η^2 = 0.019). A follow-up (3-way ANOVA) test, split by task, revealed no main effect of size and no interaction for grasping tasks (refer to Figure 23, Figure 24, and Table 11). A main effect of size was found for the pantomiming tasks (F (2.119, 135.588) = 39.41, p < 0.000, η^2 = 0.381), and no interaction was found (Figure 23, right panel). Pairwise comparisons showed that all object size JNDs were significantly different from each other (p’s < 0.043). The results suggest that regardless of modality, grasping violates Weber’s law whereas pantomiming adheres to Weber’s law (Figure 24).

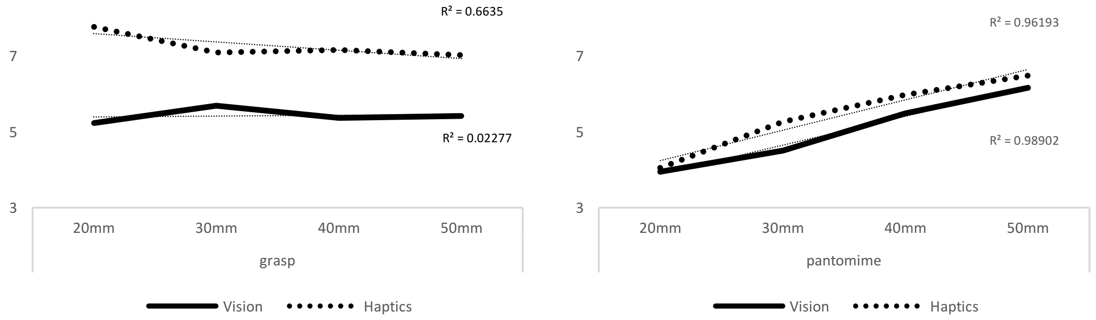

Figure 23 – Results from follow-up paired samples t-tests split by modality and task for size JNDs. The left panel shows the grasping task groups for vision and haptics across all size JNDs. The right panel shows the pantomiming task groups for vision and haptics across all size JNDs.

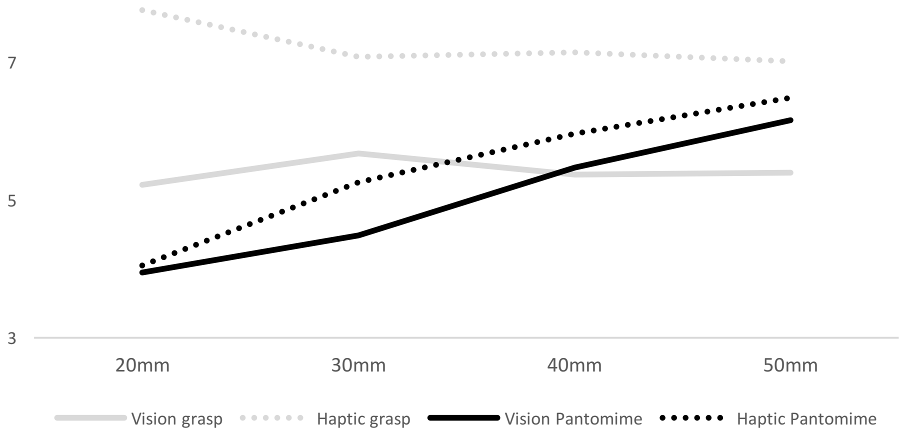

Figure 24 – Results for the modality, task, and size threesome. The black solid line and the black dotted line represent the groups in which JNDs increased as a function of object size. Notice that only the two pantomime task groups show an adherence to Weber’s law.

Table 11 – Results of follow-up 3-way ANOVA on object size JNDs, split by task. Means, standard errors, and 95% confidence intervals are reported for JND size comparisons.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
Grasping JNDs	20 mm	6.435	0.232	[5.973, 6.897]
	30 mm	6.287	0.214	[5.861, 6.713]
	40 mm	6.224	0.198	[5.830, 6.618]
	50 mm	6.148	0.235	[5.679, 6.617]
Pantomiming JNDs	20 mm	4.192	0.255	[3.682, 4.701]
	30 mm	5.031	0.238	[4.555, 5.508]
	40 mm	5.820	0.270	[5.280, 6.360]
	50 mm	6.481	0.299	[5.884, 7.077]

Further follow-up univariate tests of task by modality conducted for the different object sizes revealed the following for the JNDs of each object size:

The 20mm object size JNDs revealed the following: A main effect of modality (F (1, 138) = 18.172, $p < 0.000$, $\eta^2 = 0.116$) where vision groups were less variable (smaller JNDs) (M = 4.576, SE = 0.281) than the haptic groups (M = 6.051, SE = 0.203); A main effect of task (F (1, 138) = 42.028, $p < 0.000$, $\eta^2 = 0.233$) where grasping groups were more variable (M = 6.435, SE = 0.228) than pantomime groups (M = 4.192, SE = 0.260); And a task by modality interaction (F (1, 138) = 8.056, $p = 0.005$, $\eta^2 = 0.55$) where vision groups show less variability between grasp and pantomime tasks (grasp M = 5.206, SE = 0.355; pantomime M = 3.945, SE = 0.435) than the haptic groups (grasp M = 7.664, SE = 0.287; pantomime M = 4.438, SE = 0.287).

The 30mm object size JNDs revealed a main effect of modality (F (1, 138) = 18.416, $p < 0.000$, $\eta^2 = 0.118$) where vision groups were less variable (smaller JNDs) (M = 4.970, SE = 0.260) than the haptic groups (M = 6.348, SE = 0.188), and a main effect of task (F (1, 138) = 15.304, $p < 0.000$, $\eta^2 = 0.100$) where grasping groups (M = 6.287, SE = 0.212) were more variable than pantomime groups (M = 5.031, SE = 0.241).

The 40mm object size JNDs revealed a main effect of modality (F (1, 138) = 16.391, $p < 0.000$, $\eta^2 = 0.106$) where vision groups were less variable (smaller JNDs) (M = 5.357, SE = 0.267) than the haptic groups (M = 6.688, SE = 0.193). No other effects or interactions were found.

The 50mm object size JNDs revealed a main effect of modality (F (1, 138) = 11.004, $p < 0.000$, $\eta^2 = 0.074$) where vision groups were less variable (smaller JNDs) (M = 5.690, SE = 0.305) than the haptic groups (M = 6.938, SE = 0.220). No other effects or interactions were found.

Temporality by modality by size JNDs

A three-way interaction was found between temporality, modality, and size JNDs (F (2.997, 401.555) = 2.698, p = 0.046, $\eta^2 = 0.020$). A follow-up 3-way ANOVA test, split by modality, revealed a main effect of size for both modalities (Vision: F (2.890, 138.702) = 7.661, $p < 0.000$, $\eta^2 = 0.138$; Haptics: F (2.577, 231.939) = 5.244, p = 0.003, $\eta^2 = 0.055$) indicating that JNDs increased as object size increased (refer to figures 26 and 27, and table 12). Pairwise comparisons showed that object size JNDs were not all significantly different from each other in both the vision and haptic modalities. In vision groups, the 20mm object size JNDs were found to be significantly smaller than the 40mm (p = 0.016), and the 50mm (p = 0.002) object size JNDs. In haptic groups, the 20mm JNDs were found to be significantly smaller than the 40mm (p = 0.044), and the 50mm (p = 0.030) object size JNDs.

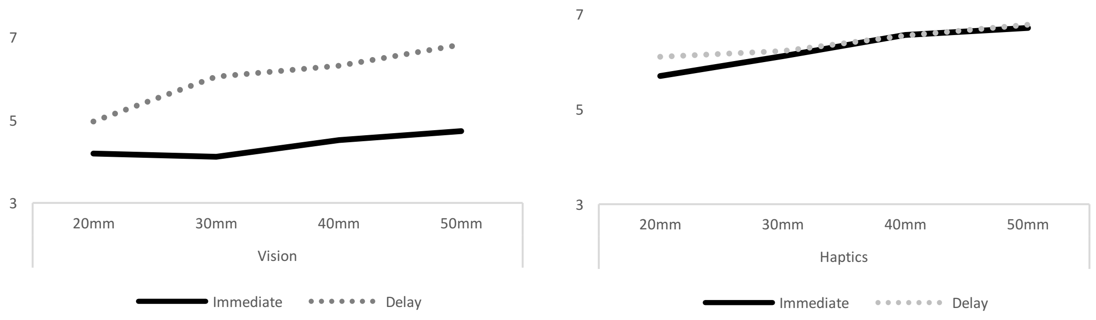

Figure 25 – Results from the three-way ANOVA test, split by modality, for JNDs across object sizes in immediate and delay groups. The left panel shows the vision groups for immediate and delay task execution across all size JNDs. The right panel shows the haptic groups for immediate and delay task execution across all size JNDs.

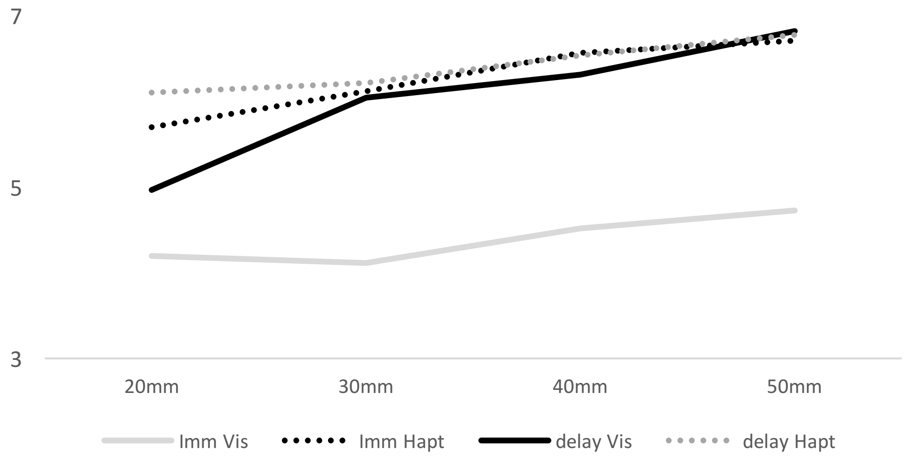

Figure 26 – Results for the modality, temporality, and size three-way interaction. The black solid line and the black dotted line represent the groups in which JNDs increased significantly as a function of object size. Notice that there is no clear demonstration of violation or adherence to Weber's in any group here.

Table 12 - Results of follow-up 3-way ANOVA on object size JNDs, split by modality. Means, standard errors, and 95% confidence intervals are reported for JND size comparisons.

Measure	Object size	Mean (M)	Standard Error (SE)	95% Confidence Interval (lower bound, upper bound)
Vision JNDs	20 mm	4.747	0.238	[4.268, 5.225]
	30 mm	5.230	0.218	[4.792, 5.669]
	40 mm	5.497	0.217	[5.062, 5.932]
	50 mm	5.802	0.239	[5.321, 6.282]
Haptics JNDs	20 mm	6.063	0.293	[5.480, 6.646]
	30 mm	6.317	0.223	[5.875, 6.759]
	40 mm	6.653	0.217	[6.221, 7.085]
	50 mm	6.901	0.243	[6.417, 7.385]

An interaction between temporality and size ($F(2.890, 138.702) = 4.541$, $p = 0.005$, $\eta^2 = 0.086$) was also found, but only in the vision modality where immediate task execution showed no change in JNDs with object sizes whereas delay task execution showed increasing JNDs with object size. Further follow-up univariate tests of temporality by modality conducted for the different object sizes revealed the following for the JNDs of each object size:

The 20mm object size JNDs revealed a main effect of modality (F (1, 138) = 9.383, $p < 0.000$, $\eta^2 = 0.064$) where vision groups were less variable (smaller JNDs) (M = 4.746, SE = 0.343) than the haptic groups (M = 6.063, SE = 0.260).

The 30mm object size JNDs revealed a main effect of modality (F (1, 138) = 10.311, p = 0.002, $\eta^2 = 0.070$) where vision groups were less variable (smaller JNDs) (M = 5.230, SE = 0.270) than the haptic groups (M = 6.317, SE = 0.205); A main effect of temporality (F (1, 138) = 4.442, p = 0.037, $\eta^2 = 0.050$) where immediate task execution groups (M = 5.417, SE = 0.209) were less variable than the delayed task execution groups (M = 6.130, SE = 0.266); And a temporality by modality interaction (F (1, 138) = 7.328, p = 0.008, $\eta^2 = 0.050$) where vision groups showed more variability between immediate and delay task execution (immediate M = 4.415, SE = 0.341; delay M = 6.045, SE = 0.418) than did the haptic groups (immediate M = 6.418, SE = 0.241; pantomime M = 6.216, SE = 0.330).

The 40mm object size JNDs revealed a main effect of modality (F (1, 138) = 12.135, $p < 0.000$, $\eta^2 = 0.081$) where vision groups were less variable (smaller JNDs) (M = 5.497, SE = 0.264) than the haptic groups (M = 6.653, SE = 0.200); A main effect of temporality (F (1, 138) = 4.471, p = 0.036, $\eta^2 = 0.031$) where immediate task execution groups (M = 5.724, SE = 0.205) were less variable than the delayed task execution groups (M = 6.426, SE = 0.261); And a temporality by modality interaction (F (1, 138) = 7.895, p = 0.006, $\eta^2 = 0.054$) where vision groups showed more variability between immediate and delay task execution (immediate M = 4.680, SE = 0.334; delay M = 6.314, SE = 0.410) than did the haptic groups (immediate M = 6.768, SE = 0.236; pantomime M = 6.538, SE = 0.324).

The 50mm object size JNDs revealed a main effect of modality (F (1, 138) = 8.815, p = 0.004, $\eta^2 = 0.060$) where vision groups were less variable (smaller JNDs) (M = 5.802, SE = 0.295) than the haptic groups (M = 6.901, SE = 0.224); A main effect of temporality (F (1, 138) = 5.893, p = 0.016, $\eta^2 = 0.041$) where immediate task execution groups (M = 5.902, SE = 0.229) were less variable than the delayed task execution groups (M = 6.801, SE = 0.291); And a temporality by modality interaction (F (1, 138) = 9.545, p = 0.002, $\eta^2 = 0.065$) where vision groups showed more variability between immediate and delay task execution (immediate M =

4.780, SE = 0.373; delay M = 6.823, SE = 0.457) than did the haptic groups (immediate M = 7.023, SE = 0.264; pantomime M = 6.778, SE = 0.361). Together, these results suggest that Weber's law is only violated when a task (dorsally- or ventrally- driven) is executed with vision and immediately.

Chapter 5. Discussion and Future Directions

Discussion

Overall, the findings of this thesis suggest that action and perception streams of *haptic* processing relate with Weber's law of human perception differently from each other. Action stream processes such as grasping were found to violate Weber's law, while perception stream processes such as pantomiming adhered to Weber's law. My contributions to this field are as follows:

1- I establish that the rules of psychophysics apply in *haptics*. Specifically, that action (grasping) and perception (pantomiming) tasks engender respective action- and perception- driven behaviors in *haptics* according to Weber's Law of human perception.
2- I contribute to the growing body of evidence in hemispheric localization for the left-hemisphere specialization for the visual control of actions and the right-hemisphere specialization for haptic processing.
3- Memory-guided tasks may not be, or involve, perception-stream processes, as previously thought.

The following is a breakdown of the results for each hypothesis and question asked.

Two experiments were conducted, one in the visual modality and one in the haptic modality. Each modality was comprised of four groups: a grasp task, a pantomime task, an immediate condition, and a delayed condition. For the vision modality, participants grasped or pantomimed an object with the use of full vision, whereas in the haptic modality, participants never saw the object, but rather they manually explored it before executing a grasp or pantomime behavior. Two additional groups were included in the design to test if memory guided behaviours within the visual and haptic domains are action or perception driven. In this condition, a 5000ms delay was observed before participants were able to perform the prescribed grasp or pantomime task. In this thesis, grasp and pantomime tasks were used to elicit behaviors (JNDs) that reflect their respective action- and perception-stream processes.

According to the PAM, different systems mediate the visual control of action and perception. Visually-guided grasping is known to be mediated by the dorsal visual stream of information processing (Ganel, Chajut, & Algom, 2008; Goodale & Ganel, 2015; Goodale & Milner, 1992; Goodale & Milner, 2006; Goodale et al., 1991). The dorsal visual stream, also referred to as the action stream, involves constant online feedback of visual information. As such, the dorsal stream processes absolute metrics through an egocentric frame of reference. This online processing allows us to interact with our environment very accurately (Hu, Eagleson, & Goodale, 1999). For example, appropriately shaping our hands and fingers to grasp an object, and low variability in terms of JNDs (Dijkerman & De Haan, 2007; Ganel, Chajut, & Algom, 2008; Goodale & Ganel, 2015; Goodale et al., 1991; Lederman & Klatzky, 2009). The JNDs produced in grasping tasks, reflect dorsal (action) stream processes and are said to be refractory to Weber's psychophysical law of human perception. On the other hand, pantomime actions are known to tap into perceptual processes and thus JNDs adhere to Weber's law. Previous research has in fact shown that action (grasping) and perception (pantomiming) tasks produce JNDs that respectively violate and adhere to Weber's law in visuomotor experiments (Ganel, Chajut, & Algom, 2008). Other research exploring the *tactile* component of haptics have found similar results for action- and perception- driven tasks (Davarpanah Jazi & Heath, 2014). The purpose of my thesis was to examine how the haptic (tactile and proprioception) action and perception streams, as proposed by Dijkerman and de Haan's SPM, relate with Weber's law in purely haptic (no vision) grasping and pantomime tasks. Remember that in the work of Heath and colleagues, participants sometimes had previous visual exposure to the target (Davarpanah Jazi & Heath, 2014, 2016, 2017; Davarpanah Jazi, Hosang, et al., 2015; Davarpanah Jazi, Yau, et al., 2015) which did not provide a purely haptic (no vision) experience.

Hypothesis I

MGA and GA scaling to object size

Grasping and pantomiming tasks produce behaviors (MGAs and GAs) that scaled to object size. The findings for the individual group analyses (hypothesis I) showed main effects of MGAs (grasp) and GAs (pantomime) for different object sizes in all groups. This effect demonstrates that participants scaled for object size both for grasp (action) and pantomime (perception) tasks and confirms that the measures (MGAs and GAs) were sensitive to changes in object sizes. In other words, participants scaled smaller for smaller objects and bigger for bigger objects regardless of the task. These results have been found in other studies for grasping (Ganel, Chajut, & Algom, 2008; Holmes & Heath, 2013; Hu & Goodale, 2000; Smeets & Brenner, 1999) and to a lesser extent for pantomiming (Davarpanah Jazi & Heath, 2014, 2016, 2017; Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, et al., 2008; Holmes & Heath, 2013; Utz, Hesse, Aschenneller, & Schenk, 2015).

JNDs violate or adhere to Weber's law

Overall, a clear distinction can be made between the behaviors (JNDs) of groups that performed grasp or pantomime tasks. Grasping tasks elicited JNDs that violated Weber's law, whereas pantomiming tasks produced JNDs that adhered to Weber's law.

The results of the analyses for the individual group JNDs of object sizes show that all groups performing grasping tasks (regardless of sensory modality) displayed no main effect in JNDs for object size. This means that in all grasping groups, participants did not vary the standard deviation of their MGAs in accordance with the object size, but rather maintained proportional JNDs for each object. The consistent MGAs for each object size is reflected as low standard deviations which translate to invariant JNDs across all object sizes. The invariant JNDs to object size, in turn, demonstrate a violation of Weber's law. Conversely, all groups executing pantomime tasks showed main effects in JNDs for object size. These participants varied their MGAs relative to the object, thereby producing increasingly variable JNDs for each increasing object size. The increasing JND relationship to object size shows an adherence to Weber's law.

The results from the task by modality by size (three-way) interaction suggest that grasping tasks, regardless of sensory modality, elicit behaviors (JNDs) that violate Weber's law. These same results also suggest that pantomime tasks, regardless of modality, elicit behaviors (JNDs) that adhere to Weber's law.

These results are consistent with those from previous studies that examined the JNDs in grasp (action) and pantomime (perception) tasks (Davarpanah Jazi & Heath, 2014; Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, et al., 2008; Ganel & Freud, 2011; Ganel, Namdar, & Mirsky, 2017; Goodale & Ganel, 2015; Heath, Mulla, Holmes, & Smuskowitz, 2011; Holmes & Heath, 2013; Utz et al., 2015). Ganel and colleagues (2008) found that grasping did not adhere to Weber's law whereas pantomiming did adhere to Weber's law in a series of visuomotor tasks. Similarly, Davarpanah Jazi & Heath (2014) found the same results in their study for tactile action and perception. To my knowledge, the present thesis is the first to explore the effects of object size on *haptic* resolution. Davarpanah Jazi and colleagues' (2014, 2016; 2015; 2015) studies were delimited to the tactile aspect of haptics. As reviewed in the introduction, haptics refers to the senses of touch/tactile and proprioception, collectively.

Hypothesis II

Do memory-guided behaviours affect JNDs?

Previous research has shown that memory-guided grasping (in the context of visuomotor experiments) is kinematically different than on-line control of grasping and it has been argued that memory-guided actions are influenced by perceptual streams (Davarpanah Jazi, Hosang, et al., 2015; Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, et al., 2008; Holmes, Mulla, Binsted, & Heath, 2011). Consistent with this view Ganel and colleagues (2008) found that JNDs for memory-guided grasps were commensurate with those elicited in perceptual tasks (i.e., pantomiming). They argue that their results support the PAM's contention that delay in the task execution is guided by perceptual (relative) visual information through the ventral stream as soon as 2000ms after vision is occluded (Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, et al., 2008; Holmes et al., 2011). Davarpanah Jazi and Heath (2015) also found similar results for tactile processing. They argue from the basis of the SPM that introducing a memory component (2000 – 5000ms delay) in grasping and pantomiming tasks would draw out the relative percepts that drive tactile perception (Davarpanah Jazi, Hosang, et al., 2015).

Findings from my thesis disagree with these views. The results for the individual analyses of JNDs showed that memory-guided grasping is NOT perceptually-driven. JNDs for the memory-guided grasping condition in both vision and haptics, violated Weber's law. So, from this result one can only conclude that memory-guided grasping is mediated by the dorsal (not the ventral) stream. One other paper found similar results to mine. Holmes and comrades (2011) examined time-dependent scaling to Weber's law in immediate- and memory- guided visual conditions of grasping. They found that JNDs did not adhere to Weber's law in either immediate or 0 – 2000ms delayed (memory) conditions. Holmes and colleagues could not provide an explanation to account for the between-experiment difference in (JND) results between what they found and that of others. One way that I think the implications of my results (and Holmes) can be reconciled with the theoretical frameworks (and previous results of memory-guided actions) is by thinking about the interaction of streams. Milner and Goodale (1992) and Dijkerman and de Haan (2007) assert in their respective proposals of the PAM and the SPM, that action and perception streams do (necessarily) interact. While the perception stream is known to use memory resources (so you can remember what your car looks like), this does not mean that memory, as a higher-level process, does not also influence action stream behaviours. In other words, I argue that memory is not a function exclusive to the perception-stream. It is possible that more memory processes are associated with the haptic domain than in vision. This is to say that the haptic modality might rely and draw on more memory processes to perform behaviors. This offers an explanation for why we perform better in *haptic* memory-guided tasks than in *vision* memory-guided tasks. Another possibility (not mutually exclusive) is that memory-guided grasping lands somewhere in between the action and perception streams. In fact, it might serve as the interface between these two streams, and therefore should be treated as its own process. Future research should address these possibilities.

Hypothesis III

JND translation across modalities for Action and Perception

This thesis brings forth evidence supporting Dijkerman and de Haan's SPM that action and perception tasks in the haptic domain are mediated via dissociated frames of references (egocentric, allocentric) and respective processing streams (dorsal, ventral). When considering all groups and conditions together, the results from the haptic domain mimic those from the visual domain. Grasping (action stream) task JNDs violated Weber's law while pantomiming (perceptual stream) task JNDs adhered to Weber's law. Therefore, the biggest contribution of my thesis is the support that it lends to the knowledge of different streams of information processing across sensory modalities.

Limitations

While my thesis provides a valuable contribution to the growing body of knowledge on haptics, it is not free from critique. The following five points are aspects worth greater consideration in future studies.

Group n-sizes

This study tested 147 participants distributed over eight different experimental groups. While there was sufficient number of participants in each group to validate significance, the N's of each group were not the same. The haptic groups always had more participants than the corresponding (temporality and task) vision group. Ideally, an even distribution of participants in each group would ensure more accurate statistical analyses.

Stimulus block design

Three dimensional (3D) objects are defined through their quantitative qualities along the x, y, and z axes (length, width, and height). All 3D objects used in this study were squares meaning that in each object size, the x and y metric values were the same (figure 10 in methods). Also, all objects were designed with a 20mm height (thickness). This meant that the smallest object (20mm) was, in fact a cube (all of its' dimensions were the same metric value) whereas the larger three objects were, while still three dimensional, characterized by two different values: one value for the height (20mm) and a second value for both its' length, and width. Previous studies have shown that action and perception streams compute 2D and 3D information differently (Freud & Ganel 2015, review; Holmes & Heath, 2013; Snow et al 2011). There is a possibility that the smallest object was processed differently (more easily) since it had one less metric value to compute (all dimensions were the same value). This could account for some of the differences/effects/interaction found in our experiment and requires further investigation.

Stimulus block sizes

Two recent studies have shown differences in the way JNDs adhere or violate Weber's law depending on the size of the object. Bruno and colleagues (2016) found that JNDs increased as a function of object size for smaller objects and decreased for larger objects. In my thesis, I noticed that the three-way interactions with size as a factor were always driven by the small block object. When this block was removed only one 2-way interaction (size X task) was observed. This interaction is much simpler to interpret as it indicated that JNDs adhered to Weber's law when pantomiming an action whereas JNDs violated Weber's law for grasping. It would be interesting to examine MGAs and JNDs in the haptic domain for very small objects (5mm, 10mm, and 15mm) as action and perception systems seem to deal with small object differently than for big objects.

Differences between hands

We did not specifically investigate hand differences. Although some main effects were found in the visual conditions (right hand actions were less variable than left hand actions), these disappeared in the haptic domain. This could be explained by literature that has shown a left-hemisphere specialization for the *visual* control of actions (i.e., visually-guided grasping), and a right-hemisphere specialization for haptic processing. Visually-guided actions (such as grasping) engage the left-hemisphere, which also controls the right hand. As such, right-handed visually-guided actions have been shown to be more accurately performed (i.e., smaller

JNDs) than those executed by the left hand. Conversely, the right-hemisphere, which controls the left hand, has been shown to house spatial representations and tactile processing functions; the left hand has been shown to have better performance than the right hand for tactile discrimination (Cormier & Tremblay, 2013; Fagot, Drea, & Wallen, 1991; Harada et al., 2004; Stone & Gonzalez, 2014a, 2014b). This could explain why the left hand demonstrates less variance (i.e., smaller JNDs) than the right hand during haptically-guided (no vision) tasks. Inquiring if these differences persist for pantomimed actions would open a new avenue of inquiry. These possibilities need further investigation.

Hand size and sex

Previous studies have shown that hand size and perception of hand (size) can affect task performance (Longo & Haggard, 2010). One study specifically found that females overestimated width and underestimated length whereas males only underestimated finger length (Coelho, Zaninelli, & Gonzalez, 2017). Hand size nor perception of hand (allocentric/perceptual stream process) was not taken into account in the experiments for this thesis but would be something to investigate further with respect to differences of hand size through sex.

Future Directions

Other than those proposed studies mentioned in the limitations section, writing this thesis sparked much excitement regarding further studies in how haptic information is processed for action and for perception. The following outlines a few (although not exhaustive or comprehensive) feasible studies to conduct in succession of the completion of my thesis (…and for the remainder of my lifetime working in the Brain in Action lab).

Lateralization studies show the tendency for some neural functions (cognitive processes) to be more localized in one hemisphere than the other. For example, Stone and Gonzalez (2015) showed a right hand preference for visually-guided grasping but this preference disappears when vision is occluded (guided by haptics). This demonstrates that visually-guided movements are lateralized to the left hemisphere whereas haptically-guided grasping is lateralized to the right hemisphere. A slight modification to the existing experimental design has allowed us to test whether the haptic action and perception streams between the hands are lateralized. Using the same experimental set-up as previously described, participants are required to haptically manipulate an object with one hand and grasp or pantomime the same object with their other hand. To date, data for a total of 34 participants (18 – haptic, cross-grasp condition; 16 – haptic, cross-pantomime condition) await analyses. This will offer some insight on whether haptic-action and haptic-perception information is specialized to a hand/hemisphere or to a task (action-grasping or perception-pantomiming). This will also provide an answer for whether there is a difference in JNDs and violation or adherence to Weber's law when information is shared across modalities and across hemispheres.

A next step would be to investigate how the JNDs of grasp and pantomime tasks relate to Weber's law in haptic illusions with the use of a haptic version of the Müller-Lyer illusion (Heller et al., 2002). No investigations have been conducted on how a haptic illusion would affect the action and perception streams and whether the behaviours produced violate or adhere to Weber's law. In other words, we would be examining whether haptic illusions affect haptic perception the way visual illusions affect visual perception.

Another exciting point of departure for a subsequent follow-up study would explore haptic memory and information transfer between the haptic and visual modalities. This would involve cross-modality tasks between vision and haptics. Object (stimuli) information would be received and processed haptically, through manual exploration, and then subsequently (with and without a memory delay) reported on using vision by matching the target object to the one experienced haptically. This would help to provide an explanation on the role of memory in haptics and whether there are degrees of differences in JNDs violation or adherence to Weber's law in memory tasks.

In conclusion, psychophysical principles of human perception provide a quantitative measure by which we better understand our subjective experience of the world. The psychophysical principle of Weber's law of human perception entails a relation between the intensity of a stimulus and our subjective experience of the stimulus intensity *change* (JNDs). The positive linear nature of this relationship renders it a robust principle in human perception. In other words, Weber's law helps us get a firmer grasp on perception in our world.

References

Aglioti, S., Smania, N., Manfredi, M., & Berlucchi, G. (1996). Disownership of left hand and objects related to it in a patient with right brain damage. *Neuroreport, 8*(1), 293-296.

Allman, J., & Kass, J. (1975). The dorsomedial cortical visual area: A third tier area in the occipital lobe of the owl monkey (Aotus trivirgatus). *Brain Research, 100*(3), 473-487.

Anema, H. A., van Zandvoort, M. J., de Haan, E. H., Kappelle, L. J., de Kort, P. L., Jansen, B. P., & Dijkerman, H. C. (2009). A double dissociation between somatosensory processing for perception and action. *Neuropsychologia, 47*(6), 1615-1620.

Baird, J. C., & Noma, E. J. (1978). *Fundamentals of scaling and psychophysics*: John Wiley & Sons.

Binkofski, F., & Buxbaum, L. J. (2013). Two action systems in the human brain. *Brain and Language, 127*(2), 222-229.

Binkofski, F., Kunesch, E., Classen, J., Seitz, R., & Freund, H.-J. (2001). Tactile apraxia: Unimodal apractic disorder of tactile object exploration associated with parietal lobe lesions. *Brain, 124*(1), 132-144.

Bonda, E., Petrides, M., & Evans, A. (1996). Neural systems for tactual memories. *Journal of Neurophysiology, 75*(4), 1730-1737.

Brown, S., Roy, E., Rohr, L., & Bryden, P. (2006). Using hand performance measures to predict handedness. *Laterality: Asymmetries of Body, Brain, and Cognition, 11*(1), 1-14.

Bruno, N., Uccelli, S., Viviani, E., & de'Sperati, C. (2016). Both vision-for-perception and vision-for-action follow Weber's law at small object sizes, but violate it at larger sizes. *Neuropsychologia, 91*, 327-334.

Caselli, R. J. (1991). *Rediscovering tactile agnosia.* Paper presented at the Mayo Clinic Proceedings.

Caselli, R. J. (1993). Ventrolateral and dorsomedial somatosensory association cortex damage produces distinct somesthetic syndromes in humans. *Neurology, 43*(4), 762-762.

Chan, J. S., & Newell, F. N. (2008). Behavioral evidence for task-dependent “what” versus “where” processing within and across modalities. *Attention, Perception, & Psychophysics, 70*(1), 36-49.

Coelho, L. A., Zaninelli, G., & Gonzalez, C. L. (2017). A kinematic examination of hand perception. *Psychological Research, 81*(6), 1224-1231.

Cohen, N. R., Cross, E. S., Tunik, E., Grafton, S. T., & Culham, J. C. (2009). Ventral and dorsal stream contributions to the online control of immediate and delayed grasping: a TMS approach. *Neuropsychologia, 47*(6), 1553-1562.

Cormier, J.-M., & Tremblay, F. (2013). Asymmetry in corticomotor facilitation revealed in right-handers in the context of haptic discrimination. *Laterality: Asymmetries of Body, Brain and Cognition, 18*(3), 365-383.

Culham, J. C., Danckert, S. L., De Souza, J. F., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research, 153*(2), 180-189.

Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Current Opinion in Neurobiology, 16*(2), 205-212.

Danckert, J., & Rossetti, Y. (2005). Blindsight in action: what can the different sub-types of blindsight tell us about the control of visually guided actions? *Neuroscience & Biobehavioral Reviews, 29*(7), 1035-1046.

Davarpanah Jazi, S., & Heath, M. (2014). Weber’s law in tactile grasping and manual estimation: feedback-dependent evidence for functionally distinct processing streams. *Brain and Cognition, 86*, 32-41.

Davarpanah Jazi, S., & Heath, M. (2016). Pantomime-grasping: advance knowledge of haptic feedback availability supports an absolute visuo-haptic calibration. *Frontiers in Human Neuroscience, 10*.

Davarpanah Jazi, S., & Heath, M. (2017). The spatial relations between stimulus and response determine an absolute visuo-haptic calibration in pantomime-grasping. *Brain and Cognition, 114*, 29-39.

Davarpanah Jazi, S., Hosang, S., & Heath, M. (2015). Memory delay and haptic feedback influence the dissociation of tactile cues for perception and action. *Neuropsychologia, 71*, 91-100.

Davarpanah Jazi, S., Yau, M., Westwood, D. A., & Heath, M. (2015). Pantomime-grasping: the ‘return’of haptic feedback supports the absolute specification of object size. *Experimental Brain Research, 233*(7), 2029-2040.

DeYoe, E. A., & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neurosciences, 11*(5), 219-226.

Dijkerman, H. C., & De Haan, E. H. (2007). Somatosensory processing subserving perception and action: Dissociations, interactions, and integration. *Behavioral and Brain Sciences, 30*(2), 224-230.

Fagot, J., Drea, C. M., & Wallen, K. (1991). Asymmetrical hand use in rhesus monkeys (Macaca mulatta) in tactually and visually regulated tasks. *Journal of Comparative Psychology, 105*(3), 260.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex (New York, NY: 1991), 1*(1), 1-47.

Gallagher, S. (2005). Dynamic models of body schematic processes. *Advances in Consciousness Research, 62*, 233.

Ganel, T., Chajut, E., & Algom, D. (2008). Visual coding for action violates fundamental psychophysical principles. *Current Biology, 18*(14), R599-R601.

Ganel, T., Chajut, E., Tanzer, M., & Algom, D. (2008). Response: When does grasping escape Weber's law? *Current Biology, 18*(23), R1090-R1091.

Ganel, T., & Freud, E. (2011). Weber's law during grasping. *Proceedings of Fechner Day, 27*(1), 159-162.

Ganel, T., Namdar, G., & Mirsky, A. (2017). Bimanual grasping does not adhere to Weber's law. *Scientific Reports, 7*(1), 6467.

Goodale, M. A. (1983). Neural mechanisms of visual orientation in rodents: targets versus places. *Spatially Oriented Behavior* (pp. 35-61): Springer.

Goodale, M. A. (1996). Visuomotor modules in the vertebrate brain. *Canadian Journal of Physiology and Pharmacology, 74*(4), 390-400.

Goodale, M. A. (2011). Transforming vision into action. *Vision Research, 51*(13), 1567-1587.

Goodale, M. A., & Ganel, T. (2015). Different modes of visual organization for perception and for action. *Oxford Handbook of Perceptual Organization, 3*(1), 1-19.

Goodale, M. A., Meenan, J. P., Bülthoff, H. H., Nicolle, D. A., Murphy, K. J., & Racicot, C. I. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology, 4*(7), 604-610.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15*(1), 20-25.

Goodale, M. A., & Milner, A. D. (2006). One brain-two visual systems. *Psychologist, 19*(11), 660-663.

Goodale, M. A., Milner, A. D., Jakobson, L., & Carey, D. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature, 349*(6305), 154-156.

Goodale, M. A., Westwood, D. A., & Milner, A. D. (2004). Two distinct modes of control for object-directed action. *Progress in Brain Research, 144*, 131-144.

Grunwald, M. (2008). *Human Haptic Perception: Basics and Applications*. Berlin: Birkhäuser.

Harada, T., Saito, D. N., Kashikura, K.-I., Sato, T., Yonekura, Y., Honda, M., & Sadato, N. (2004). Asymmetrical neural substrates of tactile discrimination in humans: a functional magnetic resonance imaging study. *Journal of Neuroscience, 24*(34), 7524-7530.

Heath, M., Mulla, A., Holmes, S. A., & Smuskowitz, L. R. (2011). The visual coding of grip aperture shows an early but not late adherence to Weber's law. *Neuroscience Letters, 490*(3), 200-204.

Held, R. (1970). Two modes of processing spatially distributed visual stimulation. *The Neurosciences: Second Study Program, MIT Press*, 317-324.

Heller, M. A., Brackett, D. D., Wilson, K., Yoneyama, K., Boyer, A., & Steffen, H. (2002). The haptic Müller-Lyer illusion in sighted and blind people. *Perception, 31*(10), 1263-1274.

Hendry, S. H., & Hsiao, S. S. (2014). Fundamentals of sensory systems. *Fundamental Neuroscience Fourth Edition* (pp. 499-511): Elsevier.

Holmes, S. A., & Heath, M. (2013). Goal-directed grasping: the dimensional properties of an object influence the nature of the visual information mediating aperture shaping. *Brain and Cognition, 82*(1), 18-24.

Holmes, S. A., Mulla, A., Binsted, G., & Heath, M. (2011). Visually and memory-guided grasping: Aperture shaping exhibits a time-dependent scaling to Weber's law. *Vision Research, 51*(17), 1941-1948.

Hu, Y., Eagleson, R., & Goodale, M. A. (1999). The effects of delay on the kinematics of grasping. *Experimental Brain Research, 126*(1), 109-116.

Hu, Y., & Goodale, M. A. (2000). Grasping after a delay shifts size-scaling from absolute to relative metrics. *Journal of Cognitive Neuroscience, 12*(5), 856-868.

Ingle, D. (1973). Evolutionary Perspectives on the Function of the Optic Tectum (Part 1 of 2). *Brain, Behavior and Evolution, 8*(3), 211-223.

James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. *Brain, 126*(11), 2463-2475.

Jeannerod, M., & Rossetti, Y. (1993). Visuomotor coordination as a dissociable visual function: experimental and clinical evidence. *Baillieres Clinical Neurology, 2*(2), 439-460.

Johansson, R. S., & Vallbo, Å. B. (1983). Tactile sensory coding in the glabrous skin of the human hand. *Trends in Neurosciences, 6*, 27-32.

Jones, E., & Powell, T. (1973). Anatomical organization of the somatosensory cortex *Somatosensory System* (pp. 579-620): Springer.

Kaas, J. H., & Hackett, T. A. (2000). Subdivisions of auditory cortex and processing streams in primates. *Proceedings of the National Academy of Sciences, 97*(22), 11793-11799.

Kaas, J. H., Krubitzer, L. A., Chino, Y. M., Langston, A. L., Polley, E. H., & Blair, N. (1990). Reorganization of retinotopic cortical maps in adult mammals after lesions of the retina. *Science, 248*(4952), 229.

Kaas, J. H., Nelson, R. J., Sur, M., Lin, C.-S., & Merzenich, M. M. (1979). Multiple representations of the body within the primary somatosensory cortex of primates. *Science, 204*(4392), 521-523.

Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience, 11*(6), 417-428.

Kolb, B., & Whishaw, I. Q. (2009). *Fundamentals of Human Neuropsychology*. New York: Worth Publishers.

Kolb, B., Whishaw, I. Q., & Teskey, G. (2014). *An Introduction to Brain and Behavior (4th Ed.)* (Vol. 1273). New York: Worth Publishers.

Lederman, S. J., & Klatzky, R. L. (2009). Haptic perception: A tutorial. *Attention, Perception, & Psychophysics, 71*(7), 1439-1459.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth- Anatomy, physiology, and perception. *Science, 240*(4853), 740-749.

Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences, 107*(26), 11727-11732.

Mai, J. K., & Paxinos, G. (2011). *The Human Nervous System*. San Diego: Academic Press.

Marks, L. E., & Algom, D. (1998). In Birnbaum MH (1998) Measurement, judgment, and decision making. *San Diego, Calif., London: Academic Press. xviii, 367*, 81-178.

Martin, J., & Jessell, T. (1991). Anatomy of the somatic sensory system. *Principles of Neural Science, ed. ER Kandel, JH Schwartz & TM Jessell. Appleton & Lange.[aHCD]*.

Milner, A. D., & Goodale, M. A. (1995). Oxford psychology series, No. 27. The visual brain in action. New York: *Oxford University Press*.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia, 46*(3), 774-785.

Milner, A. D., Perrett, D. I., Johnston, R. S., Benson, P. J., Jordan, T. R., Heeley, D. W., . . . Terazzi, E. (1991). Perception and action in 'visual form agnosia'. *Brain, 114*(1), 405-428.

Mishkin, M., & Ungerleider, L. G. (1982). Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behavioural Brain Research, 6*(1), 57-77.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences, 6*, 414-417.

Mountcastle, V. B. (1957). Modality and topographic properties of single neurons of cat's somatic sensory cortex. *Journal of Neurophysiology, 20*(4), 408-434.

Mountcastle, V. B. (1975). The view from within: Pathways to the study of perception. *The Johns Hopkins Medical Journal, 136*(3), 109-131.

Mountcastle, V. B. (1984). Central nervous mechanisms in mechanoreceptive sensibility. *Handbook of Physiology, the Nervous System: Sensory Processes, 3*, 789-878.

Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H., & Acuna, C. (1975). Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *Journal of Neurophysiology, 38*(4), 871-908.

Nelson, R. J. (2001). *The somatosensory system: Deciphering the brain's own body image*: CRC Press.

Nicolelis, M. A. L., & Fanselow, E. E. (2002). Thalamocortical optimization of tactile processing according to behavioral state. *Nature Neuroscience, 5*(6), 517-523.

Nicolelis, M. A. L., & Ribeiro, S. (2002). Multielectrode recordings: The next steps. *Current Opinion in Neurobiology, 12*(5), 602-606.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113.

Paillard, J. (1999). Body Schema and body image-a double dissociation. *Motor Control, Today and Tomorrow*, 197-214.

Paillard, J., Michel, F., & Stelmach, G. (1983). Localization without content: A tactile analogue of 'blind sight'. *Archives of Neurology, 40*(9), 548-551.

Pause, M., Kunesch, E., Binkofski, F., & Freund, H.-J. (1989). Sensorimotor disturbances in patients with lesions of the parietal cortex. *Brain, 112*(6), 1599-1625.

Penfield, W. (1953). *A consideration of the neurophysiological mechanisms of speech and some educational consequences.* Paper presented at the Paper presented at the Proceedings of the American Academy of Arts and Sciences Conference.

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms: I. Different aspects of the deficit in reaching for objects. *Brain, 111*(3), 643-674.

Purves, D., Augustine, G., Fitzpatrick, D., Hall, W., LaMantia, A., McNamara, J., & White, L. (2012). Neuroscience. 5: e uppl: Sinauer Associates, Massachusetts USA.

Reed, C. L., Klatzky, R. L., & Halgren, E. (2005). What vs. where in touch: An fMRI study. *Neuroimage, 25*(3), 718-726.

Rode, G., Rossetti, Y., & Boisson, D. (2001). Prism adaptation improves representational neglect. *Neuropsychologia, 39*(11), 1250-1254.

Rossetti, Y., Desmurget, M., & Prablanc, C. (1995). Vectorial coding of movement: Vision, proprioception, or both? *Journal of Neurophysiology, 74*(1), 457-463.

Schiller, P. H., Logothetis, N. K., & Charles, E. R. (1990). Role of the color-opponent and broad-band channels in vision. *Visual Neuroscience, 5*(4), 321-346.

Schneider, G. E. (1967). Contrasting visuomotor functions of tectum and cortex in the golden hamster. *Psychological Research, 31*(1), 52-62.

Schneider, G. E. (1969). Two visual systems. *Science, 163*(3870), 895-902.

Schott, G. D. (1993). Penfield's homunculus: A note on cerebral cartography. *Journal of Neurology, Neurosurgery & Psychiatry, 56*(4), 329-333.

Sedda, A., & Scarpina, F. (2012). Dorsal and ventral streams across sensory modalities. *Neuroscience Bulletin*, 1-10.

Sheth, B. R., Sharma, J., Rao, S. C., & Sur, M. (1996). Orientation maps of subjective contours in visual cortex. *Science, 274*(5295), 2110-2115.

Smeets, J. B., & Brenner, E. (1999). A new view on grasping. *Motor control, 3*(3), 237-271.

Stern, M. K., & Johnson, J. H. (2010). Just noticeable difference. *Corsini Encyclopedia of Psychology*.

Stevens, S. S. (1975). *Psychophysics*: Transaction Publishers.

Stone, K. D., & Gonzalez, C. L. (2014a). Grasping with the eyes of your hands: hapsis and vision modulate hand preference. *Experimental Brain Research, 232*(2), 385-393.

Stone, K. D., & Gonzalez, C. L. (2014b). Grasping without sight: insights from the congenitally blind. *PLoS One, 9*(10), e110175.

Stone, K. D., & Gonzalez, C. L. (2015). The contributions of vision and haptics to reaching and grasping. *Frontiers in Psychology, 6*.

Striemer, C. L., Yukovsky, J., & Goodale, M. A. (2010). Can intention override the "automatic pilot"? *Experimental Brain Research, 202*(3), 623-632.

Thaler, L., & Goodale, M. A. (2011). Reaction times for allocentric movements are 35 ms slower than reaction times for target-directed movements. *Experimental Brain Research, 211*(2), 313-328.

Tresch, M. C., Sinnamon, H. M., & Seamon, J. G. (1993). Double dissociation of spatial and object visual memory: Evidence from selective interference in intact human subjects. *Neuropsychologia, 31*(3), 211-219.

Trevarthen, C. B. (1968). Two mechanisms of vision in primates. *Psychological Research, 31*(4), 299-337.

Utz, K. S., Hesse, C., Aschenneller, N., & Schenk, T. (2015). Biomechanical factors may explain why grasping violates Weber's law. *Vision Research, 111*, 22-30.

Volpe, B. T., LeDoux, J. E., & Gazzaniga, M. S. (1979). Spatially oriented movements in the absence of proprioception. *Neurology, 29*(9 Part 1), 1309-1309.

Westwood, D. A., & Goodale, M. A. (2003). A haptic size-contrast illusion affects size perception but not grasping. *Experimental Brain Research, 153*(2), 253-259.

Woolsey, C. N., Erickson, T. C., & Gilson, W. E. (1979). Localization in somatic sensory and motor areas of human cerebral cortex as determined by direct recording of evoked potentials and electrical stimulation. *Journal of Neurosurgery, 51*(4), 476-506.