

Sensory Integration During Goal Directed Reaches:
The Effects of Manipulating Target Availability

By

Sajida Khanafer

Thesis submitted to the Faculty of Graduate and Postgraduate
Studies In partial fulfillment of the requirements for the degree
of Master's of Science in Human Kinetics

School of Human Kinetics

Health Sciences

University of Ottawa

Copyright © Sajida Khanafer, Ottawa, Canada, 2012

Abstract

When using visual and proprioceptive information to plan a reach, it has been proposed that the brain combines these cues to estimate the object and/or limb's location. Specifically, according to the maximum-likelihood estimation (MLE) model, more reliable sensory inputs are assigned a greater weight (Ernst & Banks, 2002). In this research we examined if the brain is able to adjust which sensory cue it weights the most. Specifically, we asked if the brain changes how it weights sensory information when the availability of a visual cue is manipulated. Twenty-four healthy subjects reached to visual (V), proprioceptive (P), or visual + proprioceptive (VP) targets under different visual delay conditions (e.g. on V and VP trials, the visual target was available for the entire reach, it was removed with the go-signal or it was removed 1, 2 or 5 seconds before the go-signal). Subjects completed 5 blocks of trials, with 90 trials per block. For 12 subjects, the visual delay was kept consistent within a block of trials, while for the other 12 subjects, different visual delays were intermixed within a block of trials. To establish which sensory cue subjects weighted the most, we compared endpoint positions achieved on V and P reaches to VP reaches. Results indicated that all subjects weighted sensory cues in accordance with the MLE model across all delay conditions and that these weights were similar regardless of the visual delay. Moreover, while errors increased with longer visual delays, there was no change in reaching variance. Thus, manipulating the visual environment was not enough to change subjects' weighting strategy, further indicating that sensory information is integrated in accordance with the reliability of a sensory cue.

Acknowledgements

This thesis would not have been possible without the support and help of several people who in one way or another contributed and extended their valuable assistance in the completion of this study.

First and foremost, I offer my utmost gratitude to my supervisor, Dr. Erin Cressman, who has supported me through my entire study with her patience and knowledge. I truly appreciate her encouragement, guidance and effort. Without her suggestions and advice, this thesis would not have been completed in such a short time. One simply could not wish for a better or friendlier supervisor.

I would like to thank the graduate and undergraduate students in Dr. Cressman's Lab, their comments were invaluable, and I look forward to continuing our collaborations. Special thanks also to the volunteers who provided their time to participate in my study.

I also would like to thank my parents, brothers and sisters. They always supported and encouraged me with their best wishes.

My deepest appreciation goes to my husband, Yamen Nasrallah, for instilling in me the confidence and a drive necessary to pursue a master's. He was always there cheering me up, and stood by me through the good and bad times, with his care and love.

To my little princesses, Wared and Rawand, who represent the source of joy and smile in my life.

Finally, and above all, thanks to God for giving me the strength to overcome the various challenges and lead me to a success that I am proud of. May your name be exalted, honoured, and glorified.

Table of Contents

Abstract	II
Acknowledgements	III
Table of Contents	IV
List of Figures	VI
List of Tables	VII
List of Abbreviations	VIII
Chapter One: Literature Review	1
I. Introduction	2
II. Sensory Systems	3
1. Visual System	4
2. Somatosensory System	5
III. Sensory Integration	7
1. Postural Control	14
2. Arm Reaching Movements	15
IV. Sensory Reweighting	22
1. Postural Control	23
2. Arm Reaching Movements	23
V. The Influence of Sensory Availability	25
1. Reaching to Remembered Visual Targets	25
2. Reaching to Remembered Proprioceptive Targets	27
Chapter Two: Research Paper	32
Abstract	33
I. Introduction	34
II. Methodology	39
1. Subjects	39
2. Experimental Set-Up	40
3. Procedures	42
III. Data Analysis	49
1. Kinematic Analysis	49
2. Sensory Reweighting	50
IV. Results	53
1. Group One	53

i.	Movement Time (MT).....	53
ii.	Reaching errors in V and P reaches	54
iii.	Reaching precision in V and P reaches.....	59
iv.	Reaching performance during VP reaches.....	62
v.	Reaching precision in VP reaches.....	67
vi.	Sensory reweighting.....	70
2.	Additional Analysis	72
V.	Discussion.....	77
1.	Reaches differed across target positions.....	78
2.	Reaches differed across target modalities	79
3.	Performance on VP trials / Sensory Integration	81
4.	Manipulation of Visual Information.....	83
5.	Sensory Reweighting.....	88
	References.....	90
	Chapter Three: General Discussion and Conclusions.....	94
	References as Cited in Thesis	100
	Appendix	109
	Edinburgh Handedness Inventory	109

List of Figures

Chapter One

Figure 1. Sensory Integration.....	8
------------------------------------	---

Chapter Two

Figure 1. Experimental set-up.....	41
------------------------------------	----

Figure 2. Breakdown of each trial type.....	44
---	----

Figure 3. Movement time.....	54
------------------------------	----

Figure 4. Endpoint positions - unimodal conditions.....	56
---	----

Figure 5. Angular errors - unimodal conditions.....	58
---	----

Figure 6. Variance of angular errors - unimodal conditions.....	61
---	----

Figure 7. Endpoint positions - bimodal vs. unimodal conditions.....	63
---	----

Figure 8. Angular errors - biomodal vs. unimodal conditions.....	64
--	----

Figure 9. Variance of angular errors - bimodal vs. unimodal conditions.....	68
---	----

Figure 10. Weight of vision.....	72
----------------------------------	----

Figure 11. Endpoint positions - Group Two.....	73
--	----

Figure 12. Angular errors - Group Two.....	74
--	----

Figure 13. Variance of angular errors - Group Two.....	75
--	----

List of Tables

Table 1. Breakdown of trials completed in each testing block by Group One.	45
Table 2. Breakdown of trials completed in each testing block by Group Two.	47
Table 3. EPx, EPy, and EP AE errors.	66
Table 4. EPx, EPy and EP AE precision.	69

List of Abbreviations

A	Auditory stimulus
AIP	Anterior intraparietal area
AV	Auditory-visual stimulus
B1	Block one of trials
B2	Block two of trials
B3	Block three of trials
B4	Block four of trials
B5	Block five of trials
BOLD	Blood-oxygen-level-dependent
CNS	Central Nervous System
C.T.	Center target position
2D	Two dimensions
3D	Three dimensions
D0	0 seconds delay condition
D1	1 seconds delay condition
D2	2 seconds delay condition
D5	5 seconds delay condition
DMS	Delayed matching-to-sample task
EBA	Extrastriate body area
EP AE	Endpoint angular errors
EP	Endpoint position errors
EPx	Endpoint position errors in the horizontal dimension
EPy	Endpoint position errors in the vertical dimension

fMRI	Functional magnetic resonance imaging
FV	Full vision condition
IREDs	Infrared-emitting markers
IPS	Intraparietal sulcus
LOC	Lateral occipital complex
L.T.	Left target position
MLE	Maximum-likelihood estimation
MOC	Middle occipital complex
ms	milliseconds
MT	Movement time
P	Proprioceptive
PMv	Premotor cortex
PPC	Posterior parietal cortex
PV AE	Angular errors at peak velocity
RM ANOVA	Repeated measures analysis of variance
R.T.	Right target position
s	seconds
TMS	Transcranial magnetic stimulation
V	Visual
VIP	Ventral intraparietal area
VP	Visual + proprioceptive
Wp	Weight assign to proprioception
Wv	Weight assigned to vision / Weight assigned to vision in the resultant direction
Wvx	Weight assigned to vision in the horizontal direction
Wvy	Weight assigned to vision in the vertical direction

Chapter One: Literature Review

I. Introduction

Throughout the day, we are constantly engaged in goal-directed actions, i.e., movements of the body performed in order to achieve a specific goal or task (Kröger, Kopp, & Lowit, 2009). Examples of these goal directed movements include activities such as reaching for a cup of tea, lifting a laundry basket, opening the refrigerator, picking up a pencil from the floor, climbing a set of stairs, or even walking around the room. In order to accomplish these movements in a controlled and coordinated manner, humans must process incoming sensory information and plan an appropriate movement. Typically, input from more than one sensory modality is available and may be necessary when performing a motor task. For example, to execute an appropriate movement towards an object (e.g. to reach for a cup of tea and bring it up to one's mouth), the central nervous system (CNS) processes the incoming sensory input from sensory receptors located in the eyes, ears, skin, muscles, and joints. These incoming sensory signals provide information on the body's orientation in space and help identify the location of the goal object relative to one's body, as well as the object's size, shape, weight, and texture (Jeannerod, 1988).

In some cases, information regarding an object's location in space can be provided by more than one sensory modality (Sober & Sabes, 2003, 2005). For example, if one is looking at a cup of tea he or she is holding in his or her right hand, then both visual information and proprioceptive information (i.e., information derived from sensory receptors located in the muscles, joints and skin), encode the cup's location. Such situations raise the question: How does the brain integrate these different sensory signals in order to ensure that the act of bringing the cup of tea to one's mouth is performed appropriately (i.e., no tea is spilt)?

In this research project, we will investigate this issue of sensory integration. Specifically, we will examine how the brain integrates sensory information during reaching movements when the target is defined by both visual and proprioceptive cues.

In order to provide the relevant background information pertaining to the research question of interest, this literature review will first outline the main sensory systems typically engaged in reaching actions. In particular, we will discuss the visual and somatosensory systems. We will then look to discuss how and where these sensory signals are integrated in the brain, by presenting previous literature which has investigated how multiple sources of sensory information are integrated. Studies will be discussed from work investigating both postural control and reaching literature. Finally, we will outline the typical errors achieved when reaching to visual and proprioceptive targets under conditions in which sensory feedback is no longer available, before laying out the research question of interest.

II. Sensory Systems

The central nervous system (CNS) receives information about the external environment and one's own body through sensory receptors specialized for vision, hearing, touch, smell, taste and balance. These sensory signals provide information on changes that occur in the environment and within one's own body (Moller, 2006; Rosdahl & Kowalski, 2007). In general, sensory information is transmitted to the brain through a series of relays: (1) sensory receptors in the periphery are activated (or stimulated) by a stimulus, (2) afferent neurons then transmit this information to the spinal cord and brain stem and finally (3) this information is sent to the brain (Moller, 2006; Rosdahl & Kowalski, 2007).

To start, we will consider how information is processed in the visual and somatosensory systems, as they have been shown to play a role in the execution of actions. For each system, we will briefly (1) discuss its sensory receptors, (2) describe how information is carried to the brain, and (3) outline areas of the brain responsible for processing the incoming sensory information. We will then discuss how and where visual and somatosensory (in particular proprioceptive) information is integrated in the brain.

1. Visual System

In general, vision is the sense that humans rely on the most to gather information regarding the spatial localization of one's own body or other objects in one's surroundings (Cohen, 1999; Bhatnagar, 2002; Rosdahl & Kowalski, 2007; Coon & Mitterer, 2008). Visual information is detected by visual (photo) receptors located at the back of the eye on the retina. These photoreceptors (rods and cones) are responsible for distinguishing light and dark and it is here where colour processing begins (Cohen, 1999; Bhatnagar, 2002; Scheiman, 2002; Kurtz, 2006; Rosdahl & Kowalski, 2007). Each retina contains approximately 100 to 120 million rods located in the peripheral portion of the retina (Kurtz, 2006; Rosdahl & Kowalski, 2007; Coon & Mitterer, 2008; Kalat, 2008). The rods are insensitive to color and are activated under dim light conditions (Kurtz, 2006; Rosdahl & Kowalski, 2007; Coon & Mitterer, 2008; Kalat, 2008). Thus they are best suited for night vision (Kurtz, 2006; Rosdahl & Kowalski, 2007; Coon & Mitterer, 2008; Kalat, 2008). As well, rods are responsible for peripheral vision due to their location on the retina (Kurtz, 2006; Rosdahl & Kowalski, 2007; Coon & Mitterer, 2008; Kalat, 2008). In contrast to the rods, there are about 6 to 7 million cones located in each retina (Kurtz, 2006; Rosdahl & Kowalski, 2007; Coon & Mitterer, 2008; Kalat, 2008). These receptors are insensitive to dim light and are responsible for the detection of colour and fine details in visual

images (Kurtz, 2006; Rosdahl & Kowalski, 2007; Coon & Mitterer, 2008; Kalat, 2008). In addition, they are involved in processing stimuli in central vision as they are abundant in the central area of the retina (the macula) (Rosdahl & Kowalski, 2007; Coon & Mitterer, 2008; Kalat, 2008). Cones are classified as one of three types depending on which wavelength they respond to the most (Eysenck, 2001; Koch, 2004). For example, they are referred to as either short-, middle-, or long-wavelength cones (Eysenck, 2001; Koch, 2004). Both rods and cones convert light rays into neural impulses (Bhatnagar, 2002; Kurtz, 2006; Rosdahl & Kowalski, 2007). These impulses are carried by the optic nerve to the lateral geniculate nucleus in the thalamus which sends the information to the primary visual cortex in the brain's occipital lobe (Bhatnagar, 2002; Kurtz, 2006; Rosdahl & Kowalski, 2007).

2. *Somatosensory System*

The somatosensory system is a diverse sensory system mediating the sensations of touch, pressure, vibration, temperature, pain, body position, and movement (Valentinuzzi, 1980; Cohen, 1999; Greenstein & Greenstein, 2000). Its specialized receptors are located in the skin, muscles, bones, joints, tendons, and internal organs (Valentinuzzi, 1980; Cohen, 1999; Greenstein & Greenstein, 2000). Touch receptors are mechanoreceptors that respond to mechanical stimulation such as touch, pressure, vibration, and movement (Valentinuzzi, 1980; Cohen, 1999; Greenstein & Greenstein, 2000). These receptors are embedded in the epidermal layer, dermal layer, and subcutaneous tissues of the skin (Valentinuzzi, 1980; Cohen, 1999; Greenstein & Greenstein, 2000) and include Meissner corpuscles, Merkel discs, Ruffini's corpuscles, and Pacinian corpuscles, (Valentinuzzi, 1980; Cohen, 1999; Greenstein & Greenstein, 2000). These receptors provide detailed information regarding the source of stimulation, as well as the exact

location, shape, size, texture, and movement of the stimulating source (Valentinuzzi, 1980; Cohen, 1999; Greenstein & Greenstein, 2000).

Proprioceptors are located primarily in muscles, tendons, joints and skin and provide information regarding body position and movement of one's own limbs and body (Cohen, 1999; Aquilla et al., 2003; Rosdahl & Kowalski, 2007). Proprioceptors in the muscles include muscle spindles which are distributed within the belly of a muscle, running parallel to the muscle fibers (Cohen, 1999; Cheatum & Hammond, 2000). These receptors detect changes in muscle length (Cohen, 1999; Cheatum & Hammond, 2000). Proprioceptors in the tendons are referred to golgi tendon organs (Cohen, 1999; Cheatum & Hammond, 2000). Golgi tendon organs are localized in the muscle-tendon junction, running in series with the muscle fibers and are specialized for detecting changes in muscle tension (Cohen, 1999; Cheatum & Hammond, 2000). Joints proprioceptors are found within the connective tissue, capsule, cartilage and ligaments of the joints. These receptors sense changes in the joint's position (Cohen, 1999; Cheatum & Hammond, 2000).

Touch and proprioceptive input from somatosensory receptors are carried to the spinal cord by sensory nerves. This information is then relayed up to the thalamus or cerebellum via the dorsal column-medial lemniscus system (Bhatnagar, 2002). From the thalamus information is carried to an area in the primary somatosensory cortex that corresponds to the area of stimulation (Bhatnagar, 2002). In other words, the primary somatosensory cortex has a somatotopic mapping.

III. Sensory Integration

As outlined in the last section, once visual and proprioceptive information enter the cortex through the thalamus, information is then passed onto primary sensory areas (visual information to the primary visual cortex in the occipital lobe and proprioceptive information to the primary somatosensory cortex in the parietal lobe). Traditionally, these primary sensory areas were believed to process information related to only one sensory modality (e.g. the primary visual cortex processed visual information only). Then, from these primary sensory areas, information was passed to unimodal sensory processing areas located in the posterior parietal lobe and the inferolateral surface of the occipital and temporal lobes (Kandel *et al.*, 2000). From there, information was thought to be conveyed to multimodal association areas which include the area between the parietal and the temporal lobe as well as the prefrontal cortex. It was thought that these multisensory areas were responsible for integrating sensory information as well as transferring information to higher order motor areas where the transformation of sensory information into planned movement took place (Weinrich & Wise, 1982; Kandel *et al.*, 2000) (see Figure 1.).

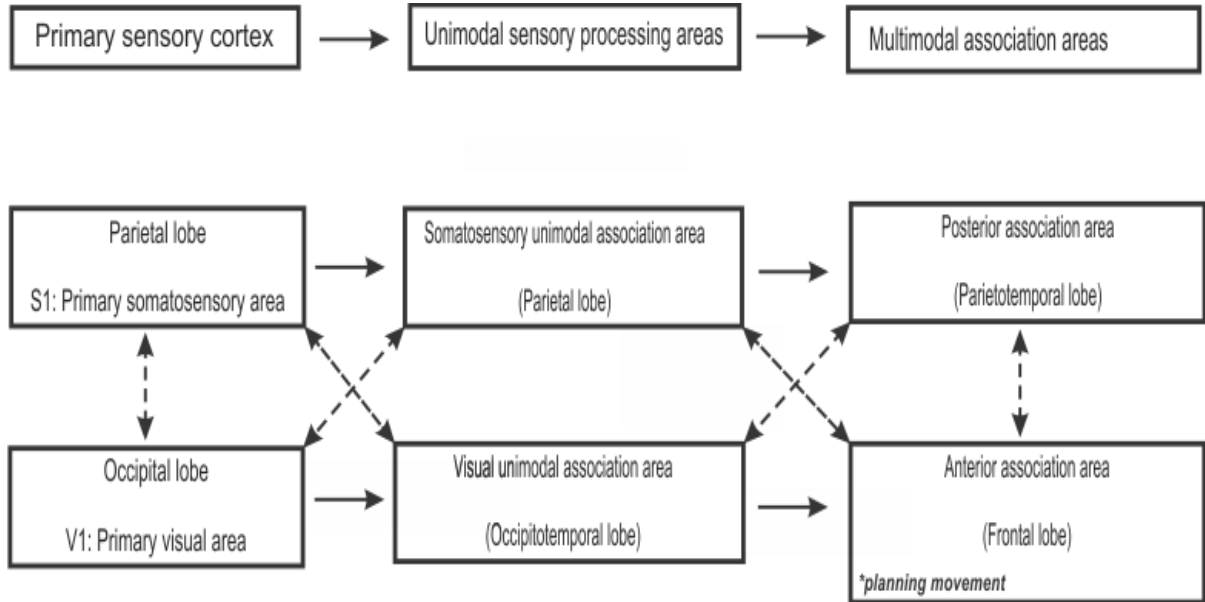


Figure 1. Sensory Integration

Visual and proprioceptive information enter the cortex through the thalamus, information is then passed to primary sensory areas (visual information to the primary visual cortex in the occipital lobe and proprioceptive information to the primary somatosensory cortex in the parietal lobe). Traditionally, these primary sensory areas were believed to process information related to only one sensory modality (e.g. the primary visual cortex processed visual information only). From these primary sensory areas information is transmitted to unimodal sensory processing areas located in the posterior parietal lobe and the inferolateral surface of the occipital and temporal lobes (Kandel *et al.*, 2000). From there, information is conveyed to multimodal association areas which include the area between the parietal and the temporal lobe as well as the prefrontal cortex. The solid lines indicate the flow of information in the cortex. The dotted lines indicate the source of sensory information that can be processed by each area. As shown in the figure, contrary to original ideas, primary and unimodal areas are capable of processing more than one source of sensory information.

Recent research suggests that sensory information is not simply processed and integrated in this hierarchical model. Moreover, multiple sources of sensory information can be processed in early (primary and unimodal) sensory areas and sensory information can actually be integrated before multimodal areas. In support of this suggestion, a growing body of literature has revealed that signals from different sensory modalities converge and interact within primary cortices in humans. For example, in a study by Sadato *et al.* (1996), the primary visual cortex was shown

to be activated in response to tactile stimuli in Braille readers who were blinded from an early age. Specifically, the primary visual cortex was activated when subjects were reading Braille and performing other tactile discrimination tasks. As well, Cohen *et al.* (1997) showed that when transcranial magnetic stimulation (TMS) was applied transiently to the primary visual cortex in early-blinded subjects, it induced errors and disrupted tactile identification of Braille letters. These results and other studies suggest that cortical areas thought to be reserved for visual processing are capable of receiving and processing somatosensory input (e.g. Sathian, Zangaladze, Hoffman, & Grafton, 1997; Kauffman, Theoret, & Pascual-Leone, 2002; van Bovan, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000). Along the same lines, Martuzzi *et al.* (2007) also examined whether neural processing in primary sensory cortices can be modulated in healthy individuals by interactions between the senses (Molholm *et al.*, 2002, Foxe *et al.*, 2002; Pekkola *et al.*, 2005). In their paradigm, healthy subjects were asked to perform a quick response upon detection of visual (V), auditory (A), or a simultaneous auditory-visual (AV) stimulus. Using fMRI, their results revealed that auditory stimuli activated primary visual cortices and visual stimuli activated primary auditory cortices. Moreover, analyses revealed facilitation of earlier peak BOLD (blood-oxygen-level-dependent) response latencies for multisensory stimuli versus conditions in which only one sensory modality was presented. Taken together these results provide evidence that multiple sensory signals can be processed within primary sensory cortices, even in healthy individuals.

➤ *Multimodal Cortical Regions - Evidences from monkeys and human brain imaging studies*

In addition, to showing that the same primary sensory area can respond to multiple sensory cues, over the past few decades, single-neuron studies in non-human primates have

identified neurons within the premotor and parietal cortices (i.e., multimodal association areas) that respond to visual, tactile and visuotactile stimuli related to the spatial location of a stationary limb. For example, Graziano (1999), studied the responses of neurons in the premotor cortex of the monkey's brain when moving a visual stimulus along the monkey's real arm under three different conditions; (1) the arm was visible (visual + proprioceptive information available) (2) the arm was covered (proprioceptive information available) and (3) the arm was replaced by a visible realistic false arm from a monkey of the same species (altered visual information). Graziano (1999) noticed that some of the neurons that responded to the position of the monkey's unseen own arm, also responded to the position of a visible fake arm. Moreover, the greatest response of these neurons was reported when the stimulus was moved along the monkey's seen real arm. These results indicate that premotor neurons can use both visual and proprioceptive inputs to encode the position of monkey's arm, and that these inputs converge on single neurons located in premotor cortex.

Likewise, Graziano, Cooke, and Taylor (2000) examined responses of single neurons in area 5 of a primate's parietal lobe while positioning a monkey's unseen real arm and a realistic seen false arm in the left or right directions. They found that the neurons which responded to the position of the unseen real arm, responded to the seen position of the fake arm as well. Moreover, the neurons' firing rate was highest when both the felt and seen positions were in the left direction, and lowest when both the felt and seen positions were in the right direction. Such findings further suggest that these neurons in the parietal lobe receive both proprioceptive and visual signals and those signals are combined in individual neurons to provide a possible code for static limb position.

In addition to coding static limb position in macaque monkeys, the posterior parietal (PPC) and ventral premotor (PMv) cortices have been shown to be crucially involved in the integration of neural signals from different sensory modalities for coding movement (Colby and Duhamel, 1996; Andersen, Snyder, Bradley, & Xing, 1997). For example, electrophysiological studies have highlighted a highly modular structural and functional specialization area within the macaque posterior parietal cortex that plays a role in multimodal motion processing (in addition to PMv). This area is known as the ventral intraparietal area (VIP) and it is located in the fundus of the intraparietal sulcus (IPS) (Colby & Duhamel, 1996; Andersen, Snyder, Bradley, & Xing, 1997).

While studies examining multisensory integration on a single neuron level in humans are lacking, neuroimaging studies in humans have highlighted a set of cortical and subcortical regions in the human brain where information from vision and proprioceptive are suggested to be combined. For example, Costantinia and colleagues (2011) recently recorded, using fMRI, bilateral activation in the lateral occipito-temporal area (extrastriate body area, EBA), which is typically involved in the visual perception of human body parts, during the haptic exploration of unseen real-size fake body parts. This finding suggests that EBA may integrate visual and somatosensory information for perception of body parts. The lateral occipital complex (LOC) has also been identified as an area that may be responsible for multimodal information processing during object recognition. In accordance with this suggestion, James and colleagues (2002) noticed activation in the LOC when subjects were presented with a set of three-dimensional novel objects made out of clay and were asked to study them either visually or haptically. Additionally, when Naumer *et al.* (2010) introduced artificial 3D objects to their subjects visually, haptically, or bimodally, their data showed an increase in neural activation in

bilateral lateral occipital cortex and anterior cerebellum during bimodal trials compared to unimodal trials.

Moreover, Gentile, Petkova, & Ehrsson (2011), have also identified a set of frontal, parietal and subcortical regions with multisensory integrative properties. Gentile *et al.* (2011) measured the blood-oxygen-level-dependent (BOLD) signal in these regions while applying visual, tactile, and visuotactile stimuli on participants' right hands. fMRI results revealed that certain regions were activated by both visual and tactile stimuli and that these areas exhibited greater activity in the visuotactile condition than in both unisensory conditions (i.e., the BOLD signal measured during visuotactile stimulation was greater than the sum of the responses registered during the two unisensory conditions). Specifically, activation was seen in the left (contralateral) ventral and dorsal premotor cortex, left anterior part of the intraparietal sulcus, left inferior parietal cortex (supramarginal gyrus), left postcentral sulcus, left insula, and bilateral parietal operculum. In addition, subcortical regions (left putamen, left thalamus, and right cerebellum), also showed greater activity in the visuotactile condition.

In accordance with these results and the monkey work discussed previously, Grefeks and colleagues (2002) have suggested that multimodal object-related processing can take place in the anterior lateral bank of the IPS, and based on the observed functional properties and the anatomical location, they suggest that this area is the human equivalent of the macaque anterior intraparietal area (AIP, which is located in the lateral bank of the anterior portion of the macaque's intraparietal sulcus). In their experiment, Grefeks *et al.* (2002) used fMRI to measure changes in neural activity in subjects while they performed a crossmodal delayed matching-to-sample task (DMS). In this task, subjects were asked to encode abstract objects (such as pyramids, triangles, and squares) either visually or by tactile manipulation (encoding). After 5

seconds the object was removed and then, after a 1 second delay, replaced by either the same or different object. Another 5 seconds was given to assess the new object either visually or by tactile manipulation (recognition) and to decide whether the new object was identical to the one previously presented. Results showed that both visual or tactile object presentation (encoding and recognition) activated the anterior intraparietal cortex, and the neural activity in this area was further enhanced when subjects transferred object information between modalities (i.e., the task required crossmodal matching). The integrative properties of the posterior intraparietal sulcus in the human brain have been further established in an fMRI study conducted by Saito and colleagues (2003), as they found neural activation bilaterally in the posterior intraparietal sulcus when subjects were presented with patterns of 2D shapes, both haptically and visually. According to these findings, shape information from different sensory modalities may be integrated in the posterior intraparietal sulcus.

Neuroimaging studies in humans have also identified a set of areas in the parietal and frontal lobes that respond to multimodal motion processing and activation of these areas closely matches the pattern of activation observed in electrophysiological studies of the monkey brain. In fact, according to Bremmer *et al.* (2001), multimodal motion processing in humans and monkeys is supported by equivalent areas. Bremmer *et al.* (2001) used fMRI to measure the changes in neural activity when a moving visual, tactile, or auditory stimulus was presented. The conjunction analysis revealed an increase in neural activity evoked by all three stimulus modalities in the intraparietal sulcus (IPS), ventral premotor, and lateral inferior postcentral cortex. The responses of neurons in the IPS to multimodal motion stimulation and the anatomical location of this area implies that the IPS represents the human equivalent to the macaque area VIP. This growing body of evidence from recent neuroimaging studies with

humans supports the suggestion that there are cortical areas where visual and tactile signals converge for the purpose of object and/or body part perception and that these areas have similar properties to areas in the macaque brain.

With a better understanding of how sensory inputs are integrated in the central nervous system, we will now begin to examine the role of sensory integration in goal directed movements. We will focus on postural control and hand reaching movements, as these tasks have been used in previous research to explore sensory integration.

1. Postural Control

Maintaining an upright stance requires detection and utilization of sensory information from multiple sensory systems and translation of this information into coordinated muscle responses (Tideiksaar, 1997). Primarily, three sensory systems are involved in postural control: (1) the visual system which specifies the position of the body in relation to other objects in the environment, (2) the somatosensory system which identifies the spatial orientation and movement of a body part relative to other body segments, and (3) the vestibular system which detects the body's linear and angular accelerations with respect to gravity (Horak, Henry, & Shumway-Cook, 1997). The integration of these different sources of sensory information during the maintenance of postural control has been assessed experimentally by measuring body sway under various conditions in which sensory input has either been altered by the experimenter or limited by a certain pathology (Horak, Nashner, & Diener, 1990; Mahboobin, Loughlin, Redfen, & Sparto, 2005; Bugnariu & Fung, 2007). Typically, in these experiments, postural responses are recorded following a perturbation that is applied to a movable support surface and/or visual surroundings in order to diminish the accuracy of ankle proprioceptive and/or visual information

respectively (Kuo, 2005). According to Clark and Riley (2007), manipulating the accuracy of visual and proprioceptive information affects one's ability to control posture. This is especially true in the case of individuals with impaired vestibular function (Kuo, 2005), suggesting that multisensory integration plays a key role in postural control.

2. *Arm Reaching Movements*

In addition to postural control, reaching movements also require (and use) multiple sources of sensory information. Consider the action described at the beginning of this literature review - the act of reaching and grasping a cup of tea held in the left hand. In order to plan the movement of the right hand towards the cup (i.e., the target), the central nervous system needs to know where the cup is located relative to one's reaching hand (i.e. body part) or a location in the environment. This information can be gained from visual, haptic and proprioceptive cues, therefore, target location is encoded in different reference frames. While visual localization relies on extrinsic coordinates (i.e., using a reference frame external to the body), proprioceptive localization relies on intrinsic coordinates (i.e., using a reference frame internal to the body, such as joint angles) (Soechting & Flanders, 1989; van Beers *et al.*, 1996, 1999, & 2002; Sober & Sabes, 2005). Therefore, the image of the tea cup and reaching hand on the retina provide the brain with a visual estimate of the hand and target's position, while sensory receptors in the muscles joints and skin of the arm and hand provide a proprioceptive estimate¹ of target position (Batista, Buneo, Snyder, & Richard, 1999; Crawford, Medendorp, & Marotta, 2004; Smeets, Dobbelsteen, Grave, van Beers, & Brenner, 2006). This raises the question: **How does the brain**

¹ The terms "proprioceptive information" or "proprioceptive estimate" will be considered to include tactile information.

integrate these two sources of sensory inputs (i.e., visual and proprioceptive information), when they both provide information regarding the target's position?

In the following section we will review previous studies which have investigated sensory integration, either when the position of the target or the position of the reaching hand is specified by multiple sensory cues.

According to Ernst and Banks (2002), when the brain encounters multiple sources of sensory information regarding an object in the environment (in our example: visual and proprioceptive information about the location of the cup), the brain combines these multiple sensory inputs in an optimal manner to form a coherent estimate of the object (whether this estimate be a property related to the object or the object's location). This optimal integration hypothesis can be referred to as the maximum-likelihood estimation model (MLE) or minimum variance integration model and implies that the more reliable sensory inputs (i.e., sources providing more precise information) are assigned a higher weight (i.e., provide more input). For example, when localizing one's seen hand, localization is typically based on visual and proprioceptive cues (van Beers, Sittig, & van der Gon, 1999). With eyes closed, the visual estimate of the hand's position persists and can be updated with efferent information regarding the hand's movements (Smeets *et al.*, 2006). However, with movement of the unseen hand, uncertainty of the visual estimate arises (i.e., reliability of visual information decreases), due to the fact that the actual movement can differ from the planned movement. Thus, according to optimal integration accounts, due to increased uncertainty regarding the visual estimate of the hand's location, the proprioceptive estimate of the hand's position should be relied on to a greater extent than the visual estimate (Ernst & Banks, 2002).

Several studies have investigated this “**optimal integration**” hypothesis by examining how the brain integrates visual and proprioceptive information when the position of the target and/or reaching hand is defined by both visual and proprioceptive cues. In other words, these studies ask: “*Is the position at which we feel our limb the same location at which we see it?*”

Research suggests (e.g. work by Smeets *et al.* 2006), that sensory signals are not aligned, i.e., the position one feels his or her limb is not necessarily the same as the location one sees his or her limb. Instead, when both visual and proprioceptive information are available, this information is optimally combined in order to form a coherent estimate of the limb’s position in space (van Beers *et al.*, 1996, 1998, & 1999). According to optimal integration accounts (Ernst & Banks, 2002; Ernst & Bulthoff, 2004), noise in each single sensory modality’s estimate is mutually independent from the other estimates and the combination of these unimodal signals is weighted proportionally to the modality’s relative reliability. Based on this combination rule, the bimodal estimate would typically lie between the two signal modalities estimated positions and be more reliable (less variable) than either of the unimodal estimates. Therefore to summarize the tenants of the optimal integration hypothesis, when information regarding a target’s position is available from several modalities and the estimate associated with each sensory modality is independent from other estimates (i.e., the biases of unimodal estimates differ from each other): (1) the biases for bimodal estimates are expected to lie between the unimodal estimates, and (2) the variance of the bimodal estimate is expected to be smaller than that for unimodal estimates (van Beers and colleagues, 1996 & 1999, Ernst & Bulthoff, 2004; Reuschel, Drewing, Henriques, Rosler, & Fiehler, 2010).

To examine optimal integration experimentally, van Beers and colleagues (1996, 1998, & 1999), have measured the precision of hand localization (i.e., target) in two-dimensions. In

general, in their experiments, subjects were asked to match target positions presented above the table top with their left hand that was hidden under the table. The target positions were either a: (1) proprioceptive target (unseen right hand was the target), (2) visual target, or (3) proprioceptive + visual target (the seen right hand was the target). These targets were randomly placed in a workspace that was 40 cm left and right of subjects' midline and extended to 40 cm in front of subjects. The precision of hand estimates were determined by calculating localization errors in two-dimensions (x and y) for each condition. Results showed that subjects were more precise in localizing proprioceptive targets in the radial direction (perpendicular to the shoulders) compared to the azimuthal/horizontal direction (parallel to the shoulders), with precision equal to 0.6-1.1 degrees (van Beers *et al.*, 1998). In contrast, localizing visual targets was more precise in the azimuthal direction (mean azimuth error = 0.36 degrees and mean radial error = 0.44 degrees) (van Beers *et al.*, 1998). Moreover, and more importantly, by comparing the precision (or variance) in performance between "unimodal" conditions (i.e., proprioceptive only or visual only), and the "bimodal" condition (i.e., proprioceptive + visual), it was noticed that when both proprioceptive and visual cues were provided, subjects performed the matching task with a smaller variance than when using only proprioceptive or only visual information (van Beers *et al.*, 1996 & 1999). In accordance with the optimal integration hypothesis stated earlier (i.e., Ernst & Banks, 2002; Ernst & Bulthoff, 2004), these findings illustrate that when both visual and proprioceptive information are available, the CNS integrates both types of information in an effective manner. As well, proprioceptive information was found to be weighted more than visual information when subjects reached to bimodal targets in the radial direction. Conversely, visual information was weighted to a greater extent than proprioceptive information when subjects reached to bimodal targets in the azimuthal/horizontal direction.

Further evidence of optimal integration has been found by examining the integration of visual and proprioceptive information regarding the reaching hand. Generally, to plan a movement for the purpose of reaching to an object (i.e., a target), the initial position of the hand needs to be estimated in order to identify the required movement vector, and to convert this movement vector into a joint-based motor command (Sober & Sabes, 2003 & 2005). For both stages (i.e., movement vector or motor command), the estimation of reaching hand position can be obtained by integrating visual and proprioceptive information (Sober & Sabes, 2003 & 2005). To determine the weight assigned to each sensory cue in each stage, Sober and Sabes (2003) had subjects reach to visual targets in a virtual reality environment, where a visual cue could incorrectly indicate the initial hand position. In particular, the visual cue representing the hand's location was shifted to the left or right of the actual hand's position by 6 cm. Thus, proprioceptive information correctly indicated the hand's start position, but visual information provided inaccurate information. By examining reaching accuracy, results revealed that the position estimates utilized for planning the movement vector depended predominately on vision. However, the position estimates utilized to compute the joint-based motor command depended more on proprioception. Based on these results, one may conclude that when estimating position of the reaching hand, the CNS relies on different combinations of visual and proprioceptive information during each stage of reach planning.

Sober and Sabes (2005) then went on to investigate whether the relative weighting of visual and proprioceptive cues at each stage of movement planning could be adapted, such that it could be influenced by the sensory modality of the target (visual target vs. proprioceptive target) or by the information content of the visual feedback regarding the reaching hand. To manipulate visual feedback of the reaching hand, they showed only a bright white spot representing hand

location or a white polygon in the shape of the subject's arm. Results showed that the accuracy of the movement planning vector was influenced by the sensory modality of the target; subjects relied more on visual information when reaching to a visual target, while the movement planning vector relied more on proprioceptive information when planning a movement to a proprioceptive target. Moreover, it was noticed that the computation of the motor command was affected by the information content of the visual feedback. When the fingertip position was the only source of visual feedback available, proprioception dominated during the computation of the motor command. In contrast, when additional visual feedback was provided, the two sensory modalities contributed almost equally to the computation of the motor command. Similar to van Beers and colleagues (1996), this study shows that the weight that is assigned to sensory cues is context dependent. In this case, these results demonstrate that sensory weighting is dependent on the sensory modality of the target and the visual environment one is reaching in.

Sarlegna & Sainburg (2007) later examined if planning movement distance would alter how sensory information was integrated, as in addition to movement direction, movement distance is considered to be another aspect of reach planning that could rely on both visual and proprioceptive information. Sarlegna and Sainburg (2007) looked at how target modality influenced the contributions of vision and proprioception when planning movement distance. In their experiment, subjects' movements were constrained to one dimension such that they extended their elbow in order for their right index fingertip to reach the target (either a visual target or a proprioceptive target defined by their unseen left index finger). For the purpose of this study, the movement distance was manipulated by performing a reach towards targets at three different distances from three different starting positions. The subjects were provided with visual feedback of the reaching right index fingertip location just before movement onset. Like

the studies of Sober and Sabes discussed above, this experiment created a discrepancy between actual and seen starting position of the right index finger tip by using a virtual reality display (i.e., a mismatch was created between visual and proprioceptive cues regarding initial reaching hand position). By analyzing reaching accuracy, results revealed that planning of movement distance towards visual targets depended more on visual information of starting hand location, whereas planning of movement distance towards proprioceptive targets depended more on proprioceptive information regarding starting hand location. These results again indicate that the sensory nature of the target modality changes the relative contributions of vision and proprioception during movement planning. Thus, taken together the findings of Sober and Sabes (2003 & 2005) and Sarlegna and Sainburg (2007) indicate the target modality influences how much different sensory cues regarding hand position are weighted during movement planning. In addition to the effect of target position (van Beers *et al.*, 1996, 1998 & 1999), target modality (Sober & Sabes, 2005; Sarlegna & Sainburg, 2007) and the availability of visual information of the reaching hand (Sober & Sabes, 2005), the visual environment and attention have been shown to influence sensory integration. For example, by manipulating the visual information of the surroundings (i.e., light vs. dark room), Mon-Williams and colleagues (1997) looked at the effect of environmental conditions on perception of reaching hand position. In their study, subjects were asked to align the unseen index finger (of their right or left hand) under the table with their opposite visible index finger above the table. Subjects wore displacing prisms during the task, creating a spatial discrepancy between the visual and proprioceptive estimates of hand position, i.e., subjects saw their finger in a location that was shifted either left or right up to 34° relative to the actual finger position. Results indicated that subjects depended more on visual cues to

specify hand position in a rich visual environments (light condition), while in a sparse visual environment (dark condition), proprioceptive cues were given more weight.

In addition to environment conditions, Warren and Schmitt (1978) have shown that attention can also influence sensory integration. In their paradigm, subjects performed a pointing task with their unseen hand (either left or right hand) to a multisensory target (one's seen finger of the opposite hand). Subjects were instructed to concentrate on one modality more than the other and a conflict between sensory cues was created by having subjects wear prism goggles. The prisms displaced the perceived location of the target about 11° to the subject's right or left. Warren and Schmitt (1978) found that subjects who were instructed to concentrate on the visual cues tended to depend heavily on the visual information, compared to subjects who were to concentrate on proprioceptive information. Such findings show that attention also influences sensory integration processes.

IV. Sensory Reweighting

From the studies discussed above, it is evident that the brain combines visual and proprioceptive information to generate an estimate of where the target position (defined as either the reaching hand or the goal object) is located in space. How this sensory information is combined depends on target position, target modality, vision of the reaching hand, environmental conditions, and attention.

The question that now arises from these previous studies concerns one's ability to change the way the brain integrates sensory information. Can one learn to reweight sensory cues in a given environment? In other words, *is the brain able to change which modality it "listens" to the most when estimating a target position?*

1. Postural Control

This issue of sensory reweighting has been investigated extensively in the field of postural control. In order to examine the ability of the brain to quickly adjust the weight assigned to sensory cues, Mahboobin and colleagues (2005) assessed changes in postural sway after exposing subjects to a visual perturbation (i.e., watching a prolonged random moving scene) while standing on a sway-referenced platform. They noticed that immediately after exposure to a random scene, there was a significant decrease in postural sway, suggesting that when visual information was perturbed, the brain reweighted the incoming sensory information by decreasing its dependence on the visual input and increasing its dependence on other inputs, i.e., proprioceptive and vestibular cues. Moreover, Bugnariu and Fung (2007) confirmed the ability of the CNS to dynamically reweight multiple sensory inputs by examining the influence of a visual perturbation in combination with a synchronized proprioceptive perturbation in the opposite direction (i.e., the surface was perturbed in the opposite direction of a visual perturbation). Results indicated that subjects reweighted sensory information and that sensory reweighting was dependent on age. Young adults paid more attention to proprioceptive inputs while older adults placed an increased reliance on visual inputs.

2. Arm Reaching Movements

In the reaching literature, little is known about how (or if) the CNS dynamically reweights sensory information. Recently, Block and Bastian (2010) investigated this issue by examining the possibility that certain contextual cues may lead one to change his or her reliance on a particular sensory modality more than another when estimating the position of a multimodal target. In their paradigm, subjects reached with the index fingertip of their dominant

hand to a visual target, a proprioceptive target (unseen index fingertip of the subject's non-dominant hand touching a tactile marker underneath the reaching surface) and a multisensory target (visual and proprioceptive information regarding target position were available) in a virtual reality environment without receiving visual feedback of the positions of either of their limbs. In this study, three cues were manipulated in separate experiments: conscious effort, error history and target salience. In the conscious effort condition, subjects were instructed to intentionally aim to one modality rather than the other when reaching to the multisensory target. For example, during reaches to the multisensory target, subjects were asked to consciously aim for the visual component and ignore the proprioceptive component in one block, and aim for the proprioceptive component and ignore the visual component in the other block of trials. In the error history manipulation, reaching errors were manipulated such that subjects saw greater errors when reaching to either visual or proprioceptive targets. Finally, in the last manipulation, the target was made more or less salient by changing the brightness of the visual target or altering the nature of proprioceptive target (i.e., to increase the salience of the proprioceptive target, the target finger was placed directly on the tactile marker, while in the low salience condition it was placed on the bottom of a soft 10 cm-diameter plush ball). Results showed that aiming to one modality rather than the other (i.e., consciously aiming strategy) and changing the target's salience led to reweighting of sensory input. Specifically, subjects placed more reliance on visual input when instructed to aim to the visual target and when the visual target was more salient (increased visual reliance by 51% and 20% respectively). In contrast, subjects relied less on vision when told to aim to the proprioceptive target position and when the proprioceptive target was more salient (decreased visual reliance by 17% and 20% respectively). However, manipulating error history did not lead to changes in sensory reweighing. This ability to

dynamically reweight sensory modalities suggests that human behaviour is flexible in that the brain can adjust how it integrates sensory information.

V. **The Influence of Sensory Availability**

In this research proposal, we will continue to explore the circumstances under which one is able to reweight sensory information. In particular, we will look to see if the time a sensory cue is available for will cause changes in how sensory information is integrated. Before outlining our research question and hypotheses in more detail, we will first review literature regarding errors achieved when reaching to remembered visual and proprioceptive targets. This will provide insight onto what errors can be expected if one is relying on one sensory modality more than the other when reaching to multimodal targets.

1. *Reaching to Remembered Visual Targets*

Generally, we rely heavily on visual cues in order to localize a target's spatial localization and when visual cues are available, we are able to reach to a target very accurately (Soechting & Flanders 1989; Berkinblit, Fookson, Smetanin, Adamovich, & Poizner, 1995). *So, what happens if the target is not visible when the action takes place?* According to Berkinblit *et al.* (1995), pointing to a visual target in the absence of visual information, i.e., in darkness or with eyes closed, significantly reduces pointing accuracy (i.e., increases pointing errors). Berkinblit *et al.* (1995) examined pointing accuracy towards visual targets presented in three-dimensional space (3D), while manipulating the visual information from the pointing finger and the target. Specifically, subjects reaches to targets with: (1) visual information of both the finger and the target, (2) visual information from either the finger or the target, or (3) no visual information from either the finger or the target. In all conditions, subjects started their

reaches 1 s after visual information was removed. Results indicated that pointing errors (3D error values) were greatest in the no-vision condition (mean error = 9.16 cm), in which the pointing action was performed without visual information from either the pointing finger or the target. Pointing accuracy increased with vision of the reaching finger (mean error = 5.23 cm) and increased even further with vision of the target (mean error = 2.78 cm), as well as with both vision of the target and vision of the finger (mean error = 2.16 cm). These results suggest that one's representation of the target decays quickly.

In support of this claim, Elliott and Madalena (1987) had subjects reach with a stylus under five visual conditions: full vision, no vision with a 0 s delay (occluding vision with the onset of the response), and no vision with 2, 5, or 10 s delay (i.e., 2, 5, or 10 s visual occlusion prior to movement onset). The results indicated no significant difference in pointing error between the full vision (total error = 4.8 mm) and no vision 0 second delay (total error = 6.8 mm) conditions. However, subjects had a twofold increase (total error = 9.8 mm) in pointing error after only 2 s of visual occlusion prior to movement onset. Based on these findings, Elliott and Madalena concluded that accurate information about the movement environment is not available to the motor system after a period of time (< 2 s) following visual occlusion. Westwood, Roy, and Heath (2001 & 2003) further investigated this proposal by examining reaching accuracy to targets in full vision, no vision 0 s delay and delay conditions (specifically, visual occlusion 500, 1000, 1500 or 2000 ms prior to movement onset). In this study, results indicated that reaching errors were greater for the 0 s delay (average error = 15.6 mm approximately) than full vision reaches (average error = 8 mm approximately), and were greatest for delayed reaching, with similar errors associated with all delay conditions (i.e., from 500-2000 ms) (average error = 30 mm approximately). Thus, based on the work of Elliott and Madalena (1987) and Westwood *et*

al. (2001 & 2003), results indicate that memory-guided movements are typically less accurate compared to a visually guided ones. Such results suggest that visually guided and delayed reaching represent two distinct modes of visuomotor processing, and the transition between modes, i.e., on-line visual information to a degraded, stored representation, occurs very quickly (< 500 ms) if one does not immediately reach following visual occlusion.

2. *Reaching to Remembered Proprioceptive Targets*

Even in the absence of visual information, one can estimate the position of a body part based on proprioceptive information (Lovelace, 1989). In fact, researchers have found that one is able to localize a body part with minimal error in the absence of visual information, and in some cases proprioceptive targets can be localized more accurately than visual targets (Lovelace, 1989; van Beers *et al.*, 1998). To support this claim, Lovelace (1989) studied the accuracy of reaching to a target whose location had been coded either visually, proprioceptively or by both sensory modalities. Lovelace (1989) found that when subjects reached to multisensory targets (i.e., a visual and proprioceptive target), performance was slightly poorer (mean error = 2.02 cm) than reach errors achieved when subjects reached to a proprioceptive target (mean error = 1.77 cm), but better than reach errors to a visual target (mean error = 2.89 cm). This implies that reaching movements can be more accurate for proprioceptively coded targets compared to visually coded targets. When Jones and colleagues (2009) examined the accuracy of proprioceptive-guided reaching by asking subjects to reach with their seen hand (i.e., either their left or right hand) to the unseen location of their other hand, they also found that subjects were relatively good at estimating the location of each hand such that directional errors fell within 2 cm of the actual target location.

With respect to reaching to a proprioceptive target after a delay has been introduced between when the proprioceptive target is first placed in position and the reach begins, it has been suggested that reaching accuracy degrades over time when a subject relies exclusively on proprioception to estimate the location of his or her hand in space (Wann and Ibrahim, 1992). In an experiment by Craske and Crawshaw (1975), the position sense of a stationary arm was investigated by asking blindfolded subjects to localize the position of their right index finger with their left index finger. As the experiment proceeded, they noticed a unidirectional drift of perceived limb position toward the left. This suggests that proprioception may drift when not continuously calibrated by vision. To study this proprioceptive drift more directly, Wann and Ibrahim (1992) had subjects estimate the position of their occluded hand with the other hand following 0, 7, 15, 30, 45, 60, 75, 90, 105 and 120 s without vision of the occluded hand. Wann and Ibrahim (1992) found that when subjects performed the task immediately after occlusion (i.e., at delay time = 0), they reached with an average constant error of 16.1 mm. This constant error increased by 4 mm in the 7 s visual delay condition (i.e., constant error = 20.1 mm at 7 s). Reach errors continued to increase at a steady rate up to 120 s (the delay limit in this experiment). These results imply that the accuracy with which proprioception transmits information regarding limb position may change during prolonged periods of visual occlusion.

However, Desmurget and colleagues (2000) argued that the diminished accuracy observed by Wann and Ibrahim (1992) following visual occlusion could be attributed to factors other than proprioceptive drift. Desmurget and colleagues (2000) claimed that the reach errors observed by Wann and Ibrahim (1992) may be due to degradation of the visual representation of the movement environment as they removed vision of the reaching hand. Thus, to examine proprioceptive estimates of hand location following a delay, Desmurget et al. (2000) had subjects

indicate the location of their unseen right hand with a visual dot on the screen, whose location was controlled by the left hand via a joystick. Results indicated that mean accuracy was similar regardless of whether the localization task was performed immediately after the positioning of the target hand or after a 10-s delay without vision of the target hand. In contrast to previous results, these findings suggest the proprioception remains a reliable source of limb position information after prolonged time following visual occlusion if the visual environment remains constant.

In accordance with Desmurget and colleagues (2000), Chapman and colleagues (2001), have also found that proprioceptive cues do not decay after 10 s without vision of the hand. Chapman and colleagues (2001), had subjects performed a pointing task during which their hand was passively moved to a target position and maintained there for 2 s. The subject's hand was then returned to the starting position and the subject was asked to reach to the remembered target location after delay of 1, 2, or 10 s. Results showed that accuracy did not change over the various delay conditions. Thus, contrary to visual information, proprioceptive cues seem to continue to reliably indicate target position following visual occlusion when the visual representation of the movement environment is kept constant.

Furthermore, recent work by Monaco and colleagues (2010) suggests that reaching accuracy improves with the addition of proprioception to visual information, even under delayed reaching conditions. In their paradigm, subjects performed reaching movements with their right index finger to a visual target (LED mounted on top of a dowel), or a visual + proprioceptive target (LED attached to subject's left index finger). The LED was lit for 100 ms, and reaching actions either started (1) immediately (no visual memory/delay condition), or (2) 1 s after the offset of a 100 ms LED light at the top of the dowel or on the subject's left index finger (visual

memory/delay condition). By analyzing the absolute and variable endpoint errors of reaching movements along two orthogonal axes (i.e., along a horizontal and vertical axis with respect to the reaching vector), results revealed that reaches to visual + proprioceptive targets were performed with less errors (absolute and variable errors = 9 mm approximately in both axes) compared to reaches toward visual targets (e.g. horizontal axis: absolute and variable errors = 15 mm approximately, vertical axis: absolute and variable errors = 25 mm approximately) in the no delay conditions. Moreover, when the subjects reached to multimodal targets in the delay condition, they were just as accurate and precise at localizing their left index finger as when there was no delay (e.g. absolute and variable errors = 10 mm approximately in both axes). Subjects were slightly less accurate and precise when localizing the visual target under the delay condition compared to the no delay condition (e.g. errors in the delay condition in the horizontal axis: absolute and variable errors = 19 mm approximately, while in vertical axis: absolute and variable errors = 25 mm approximately). These results not only accentuate how the presence of proprioceptive information improves the precision of reaching movements, but also emphasizes that proprioceptive information has a slower rate of decay than visual information, as suggested previously by Desmurget *et al.* 2000, and Chapman *et al.* 2001.

In this research, we will examine the ability of the brain to reweight sensory information when the availability of visual information is manipulated. In particular subjects will reach to visual (V), proprioceptive (P) and visual + proprioceptive (VP) targets under different visual cue delay conditions. We hypothesize that in order to produce the most accurate reaching movement, the brain will combine the available sources of sensory information regarding target location in an optimal manner. Specifically, (1) the bias of a bimodal estimate will lie between the unimodal estimates and, (2) the variance for bimodal estimates will be smaller than that for

unimodal estimates. Moreover, we anticipate that manipulating the availability of visual cues will result in subjects placing more weight on proprioceptive cues. By examining how subjects weight sensory cues in a changing environment, we will gain insight into the brain's ability to dynamically adjust how it processes sensory information and the time course over which this reweighting takes place.

Chapter Two: Research Paper

Abstract

When using visual and proprioceptive information to plan a reach, it has been proposed that the brain combines these cues to estimate the object and/or limb's location. Specifically, according to the maximum-likelihood estimation (MLE) model, more reliable sensory inputs are assigned a greater weight (Ernst & Banks, 2002). In this research we examined if the brain is able to adjust which sensory cue it weights the most. Specifically, we asked if the brain changes how it weights sensory information when the availability of a visual cue is manipulated. Twenty-four healthy subjects reached to visual (V), proprioceptive (P), or visual + proprioceptive (VP) targets under different visual delay conditions (e.g. on V and VP trials, the visual target was available for the entire reach, it was removed with the go-signal or it was removed 1, 2 or 5 seconds before the go-signal). Subjects completed 5 blocks of trials, with 90 trials per block. For 12 subjects, the visual delay was kept consistent within a block of trials, while for the other 12 subjects, different visual delays were intermixed within a block of trials. To establish which sensory cue subjects weighted the most, we compared endpoint positions achieved on V and P reaches to VP reaches. Results indicated that all subjects weighted sensory cues in accordance with the MLE model across all delay conditions and that these weights were similar regardless of the visual delay. Moreover, while errors increased with longer visual delays, there was no change in reaching variance. Thus, manipulating the visual environment was not enough to change subjects' weighting strategy, further indicating that sensory information is integrated in accordance with the reliability of a sensory cue.

I. Introduction

Throughout the day, we are constantly engaged in goal-directed actions (i.e., movements of the body performed in order to achieve a specific goal or action; Kröger, Kopp, & Lowit, 2009). In order to accomplish these movements in a controlled and coordinated manner, we must process incoming sensory information and plan an appropriate movement. Typically, input from more than one sensory modality is available, and necessary, when performing a motor task. For example, in order to reach for a cup of tea and bring it up to one's mouth, the central nervous system (CNS) must process incoming sensory input from visual, proprioceptive and tactile receptors.

Previous research suggests that when multiple sources of sensory input are available, the brain integrates these sensory cues in an optimal manner according to the maximum-likelihood estimation model (MLE), or minimum variance integration model, to form a coherent estimate of the target and/or limb's location. This optimal integration consists of the brain combining unimodal sensory estimates in a linear manner, such that the how much a sensory cue is weighted depends on its precision. That is, the more reliable unimodal estimate (i.e., visual or proprioceptive estimate of target position) is assigned a greater weight than the less reliable source (van Beers *et al.*, 1996, 1998, & 1999; Ernst & Banks, 2002; Ernst & Bulthoff, 2004; Ghahramani, Wolpert, & Jordan, 1997).

The reliability of different sensory modalities, and hence the weights assigned to them when reaching to multimodal targets has been shown to differ under a variety of circumstances. For example, it has been shown that the integration of visual and proprioceptive information is dependent on target position (van Beers *et al.*, 1996, 1998, & 1999), target modality (Sober &

Sabes, 2005; Sarlegna & Sainburg, 2007), vision of the reaching hand (Sober & Sabes, 2005), the visual environment (Mon-Williams, Wann, Jenkinson, & Rushton, 1997), and attention (Warren & Schmitt 1978). Moreover, recent results indicate that one may be able to change the way the brain integrates sensory information (Block & Bastian, 2010). Specifically, recent work by Block and Bastian (2010) has suggested that subjects reweight sensory information regarding the location of a multisensory target after being instructed to pay attention to a particular sensory modality and when the saliency of the target is manipulated within or between blocks of trials.

The aim of the current research was to further investigate the ability of the brain to reweight sensory information. Specifically, we asked whether manipulating the time that a visual cue was available for prior to movement initiation could change how visual and proprioceptive information was integrated. Furthermore, we examined the time course of this sensory reweighting by having subjects reach to bimodal targets under various visual delay conditions.

Previously, it has been shown that one is less accurate when reaching to a remembered visual target compared to a target that is still visible (Soechting & Flanders 1989; Berkinblit, Fookson, Smetanin, Adamovich, & Poizner, 1995; Rossetti, 1998; Westwood & Goodale, 2003; Goodale, Westwood, & Milner, 2004; Heath, Westwood, & Binsted, 2004). For example, when Berkinblit *et al.* (1995) asked subjects to reach to a visual target 1 second after vision of the target was removed, subjects exhibited significantly greater reaching errors compared to errors achieved when vision of the target was available. It has been suggested that this decline in reaching accuracy under delayed conditions is due to the fact that visual memory fades quickly following visual occlusion (Elliott and Madalena, 1987). In fact, Westwood, Roy, and Heath (2001 & 2003) found that reaching errors were greater under a 0 second delay condition (i.e.,

vision was occluded with the onset of the reaching response), compared to when reaching with vision of the target available, suggesting that visual memory fades almost immediately. Westwood and colleagues also reported that reaching accuracy decreased even more when the visual delay increased from 0 to 500 ms, with similar errors associated with all additional delay conditions (i.e., 500, 1000, 1500 or 2000 ms of visual occlusion). Elliott and Madalena (1987) have also shown a levelling off of errors, reporting that there was no further increase in reaching errors when the visual delay was extended from 2 seconds to 5 or 10 seconds of visual occlusion. In addition, reaches to remembered visual targets (i.e., delayed reaching) have been shown to be more variable than movements to a visual target (Berkinblit *et al.*, 1995; Elliott & Madalena, 1987). Thus, it has been suggested (Elliott & Madalena, 1987; Goodale & Milner, 1992; Westwood *et al.*, 2001 & 2003) that visually guided and delayed reaching are driven by two distinct modes of visuomotor processing, and the transition between online visual information to a stored representation occurs very quickly (within less than 500 ms).

In contrast to reaching to remembered visual targets, studies examining reaches to proprioceptive targets (i.e., reaching to the hand after it has been at the target position for a length of time), have found similar levels of accuracy across delay conditions. Specifically, Desmurget and colleagues (2000) have shown reaches to proprioceptive targets are just as accurate under no delay conditions as 10 second delay conditions, and that any deterioration in reaching accuracy experienced during delayed proprioceptive reaches (e.g. that shown by Paillard & Brouchon 1968; Craske & Crawshaw 1975; Wann & Ibrahim 1992) is not due to a decay in proprioceptive information but rather can be attributed to the rapid degradation of the stored representation of the movement environment following visual occlusion. Chapman and colleagues (2001) further confirmed that proprioceptive information does not decay over time, as

they illustrated that subjects' reaching accuracy did not differ between delay conditions of 1, 2, or 10 s. Consequently, these results suggest that proprioception remains a reliable source of information after a prolonged period of visual occlusion when the visual environment is kept constant. Finally, recent work by Monaco and colleagues (2010) emphasizes that proprioceptive information has a slower rate of decay than visual information and demonstrates that the addition of proprioceptive to visual information can actually improve reaching accuracy, even under delayed reaching conditions.

Given the differences in how subjects reach to remembered visual and proprioceptive targets previously reported, in the current research we examined the ability of the brain to reweight sensory information and the time course of this reweighting when the availability of visual information was manipulated. In particular, subjects reached to visual (V), proprioceptive (P) and visual + proprioceptive (VP) targets under different visual delay conditions. In accordance with optimal integration accounts of sensory integration (van Beers *et al.*, 1996 & 1999, Ernst & Banks, 2002; Ernst & Bulthoff, 2004; Helbig & Ernst 2007; Reuschel *et al.*, 2010), we hypothesized that on reaches to bimodal targets, the brain will combine the available sources of sensory information regarding target location in an optimal manner. Specifically, (1) the bias observed on reaches to VP targets will lie between biases observed on V and P reaches, (2) the variance achieved on reaches to VP targets will be smaller than that for reaches to V and P targets. Moreover, we anticipated that manipulating the availability of visual cues will result in subjects changing how they weight proprioceptive cues. Specifically, given that reaches to visual targets have been shown to be less accurate and more variable under delayed reaching conditions, we expect that subjects will weight the more reliable proprioceptive cue when a greater delay between the offset of the visual target and go-signal onset is introduced. By

determining how subjects weigh sensory cues in a changing environment, we will gain insight into the brain's ability to dynamically adjust how it processes sensory information and the time course by which it determines a source of sensory input is not as reliable.

II. Methodology

Subjects were required to perform a reaching movement with their right index finger (reaching hand) to: (1) a visual target (V) (i.e., a white circle 10 mm in diameter), (2) a proprioceptive target (P) (i.e., their unseen left index finger; target hand), or (3) a multisensory target (visual + proprioceptive target, VP) (i.e., a white circle displayed above the position of their left index finger). Subjects were instructed to reach as accurately as possible, with no speed or time constraints. Subjects received endpoint visual feedback only on reaches to the V and P targets. Specifically, a yellow dot appeared on the screen to show reaching errors with respect to the white circular target. No feedback was provided on reaches to VP targets, as these reaches were used to determine how subjects weighted visual and proprioceptive cues when estimating the position of the target when both sensory modalities were available under different visual delay conditions.

1. Subjects

Twenty-four subjects (14 females, 10 males, aged 18-32 years old) from the University of Ottawa student population volunteered to participate in this study. Five of the volunteers (3 females, 2 males, aged 21-31 years old) were re-tested a second time, in which they performed the reaching action using their non-dominant hand (i.e., left hand). All subjects were healthy, had normal or corrected to normal vision, and had no history of neurological, sensory, or motor disorders. All subjects were right-handed as indicated by their responses to the modified version of the Edinburgh handedness inventory (mean score = 90.05 ± 13.25 SD) (Oldfield, 1971). All subjects provided informed consent prior to the start of the experiment in accordance with the ethical guidelines set by the University of Ottawa's Research Ethics Board.

2. *Experimental Set-Up*

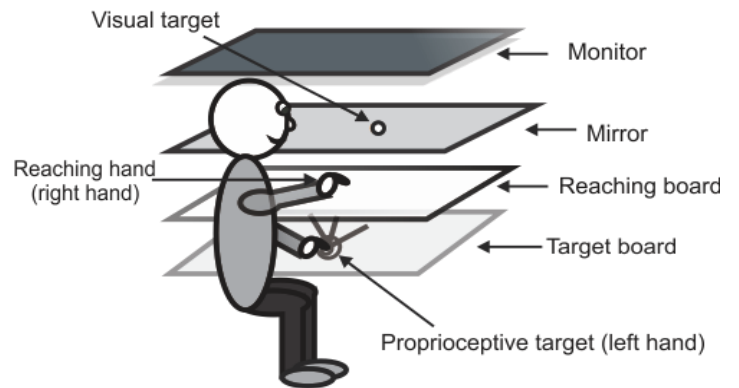
A view of the experimental set-up is provided in Figure 1A and 1B. Subjects were seated in a height adjustable chair so that they could comfortably see and reach to all targets. As well, the distance of the chair from the experimental apparatus was adjusted, such that on average, subjects were seated 29 cm away from the edge of the apparatus. Visual stimuli were projected from a monitor installed 66 cm above the horizontal surface on which the target hand (usually the left hand) was positioned for P and VP reaches. Subjects viewed the visual stimuli projected from the monitor as a reflective image in a mirror that was positioned half way between the monitor and the surface on which the target hand was placed into position. Thus visual and proprioceptive targets appeared to lie in the same plane and at the same locations. A subject's right reaching hand rested on a horizontal surface, placed 7.5 cm above the left target hand. A tactile marker (1 cm in diameter) indicated the start position of the right hand, approximately 17 cm in front of subject's midline. The room lights were dimmed and subjects' view of their right and left hands was blocked by the reflective surface and a black cloth draped between the experimental set-up and subjects' shoulders. To move the left index finger to the required proprioceptive target positions, a 50 cm x 60 cm target board was placed in the same plane as the left hand (see Figure. 1A and 1B). As shown in Figure 1C, located at the bottom and in the middle of the target board was a circle (10 cm in diameter). The circle had a groove cut out (4 cm long and 1.5 cm wide) that could be rotated with a stepper motor (Light Machinery, rotating at 12 rpm) so that it matched up with one of three grooved paths cut into the target board. Subjects were instructed to slide their left index finger out along the grooved path (1.5 cm wide) to the desired proprioceptive target position. The left index finger was pronated. The targets were located 28.5 cm from the home position, directly in front of the home position (center target

position) or 20° to the left or right of the center target. Visual targets (i.e., in V and VP reach trials) were displayed such that the visual targets were vertically aligned with the proprioceptive targets.

A



B



C

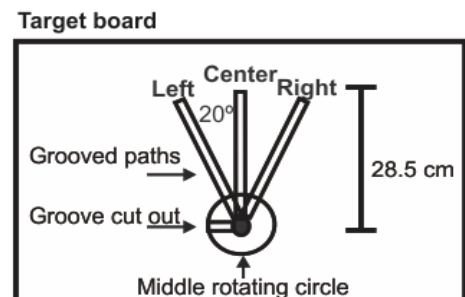


Figure 1. Experimental set-up.

A: Experimental set-up. **B:** Subjects viewed the stimuli (visual targets) projected from the monitor as a reflected image in a horizontal mirror that was positioned halfway between the monitor and the surface on which the target hand (left hand, proprioceptive target) was positioned. Thus, visual and proprioceptive targets appeared to lie in the same plane. A subject's right reaching hand rested on a horizontal surface, placed 7.5 cm above the left target hand. **C:** A 50 cm x 60 cm target board was placed in the same plane as the left target hand. Located at the bottom and in the middle of the target board was a circle (10 cm in diameter). The circle had a groove cut out (4 cm long and 1.5 cm wide) that could be rotated to match up with one of three grooved paths cut into target board. Subjects were to slide their left index finger out along the grooved path to the desired proprioceptive target position. The targets (visual, proprioceptive and visual + proprioceptive) were located 28.5 cm from the home position, at center and 20° to the left and right of the center target.

Infrared-emitting markers (IREDS) (approximately 5 mm in diameter) were attached to subjects' right and left index fingertips to monitor the position of the reaching and target hands

using an Optotrak camera system (Northern Digital). The positions of the fingertips were recorded with a sampling frequency of 500 Hz.

3. Procedures

An overview of the sequence of events in each trial is displayed in Figure 2. A trial began with subjects placing their left index finger at the home position on the target board. The right index finger was placed in its starting position, such that the left and right index fingers were aligned vertically. These home positions were represented visually by a white dot (10 mm in diameter). The trial was initiated when the home position became larger in size (20 mm in diameter) and changed colour to red. At this point, subjects attempted to move their left target hand into position (on V reaches, subjects' left hands were blocked from moving outwards).

A breakdown of each trial type:

- a. *Visual (V) trials:* On visual target trials (Figure. 2, top rows), the target appeared 500 ms after the disappearance of the red dot. The target was shown for 500 ms. Subjects were then instructed to wait for an auditory “beep” before starting their reach. In one condition (the full vision condition, FV, top row Figure. 2), vision of the target was available throughout the reach. In a second condition, the target disappeared at the same time that the auditory go signal sounded (0 second delay condition). Three other delay conditions were used (1, 2 and 5 second delay conditions, second row Figure. 2). On these trials, the visual target disappeared after 500 ms, and the go signal was provided after a delay of 1, 2 or 5 seconds. On all trials, the home position disappeared at the same time as the go-signal. Once a reach was completed (i.e., subjects had moved less than 2 mm over 500

ms as detected online via Optotrack), subjects were provided with visual feedback regarding their performance. Specifically, the target position was presented as a white dot (10 mm in diameter) and feedback of their endpoint position was provided by a yellow dot (10 mm in diameter). Following this feedback, the white dot representing the home positions reappeared, cuing subjects to return back to the home positions in order to initiate the next trial.

b. Proprioceptive (P) trials: On proprioceptive trials (Figure. 2, third row), subjects moved their left finger to the target position. 500 ms after this position was achieved, the auditory go signal sounded, cuing subjects to reach to their left hand with their right reaching hand. Once subjects completed their reach, we provided visual feedback indicating their endpoint position. Like the visual trials discussed above, feedback of the final hand position was represented by a yellow dot appearing over the reaching finger's endpoint position. As well, we indicated the target position (i.e., position of the left index finger) by showing its position with a white circle 10 mm in diameter. Similar to the visual trials, following this feedback, the white dot representing the home positions reappeared, cuing subjects to return back to the home positions in order to initiate the next trial. The next trial started immediately after the subjects returned to the home positions.

c. Visual + Proprioceptive (VP) trials: These trials were a combination of the visual and proprioceptive trials outlined above. Subjects moved their left target hand to the required target position. Once this position had been detected, the visual target was presented for 500 ms. After 500 ms, similar delayed reaching conditions were completed as introduced in the visual trials (bottom two rows Figure. 2).

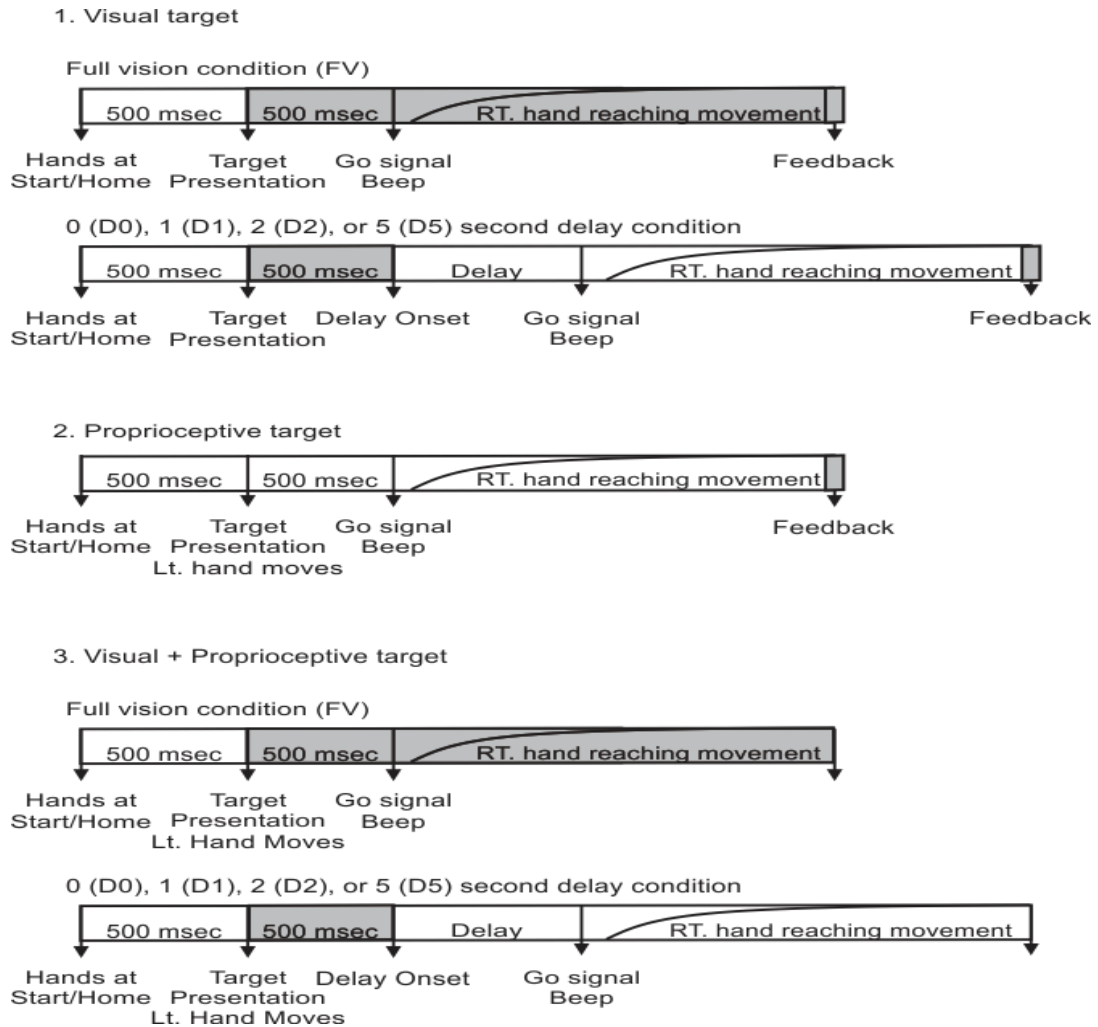


Figure 2. Breakdown of each trial type.

A trial began with subjects placing their left index finger at the home position on the target board. The right index finger was placed in its starting position, such that the left and right index fingers were aligned vertically. Starting positions were maintained for 500 ms before target presentation. 1: Visual (V) trials: On visual target trials, the target appeared 500 ms after the hands were detected at the home positions. The target was shown for 500 ms. Subjects were instructed to wait for an auditory “beep” before starting their reach. In one condition (top row), vision of the target was available throughout the reach (full vision condition, FV). In a second condition the target disappeared after 500 ms, and the go signal was provided after a delay of 1, 2 or 5 seconds respectively. When subjects completed their reach, they were provided with feedback, such that the position of the target and the endpoint that they reached to were shown. 2: Proprioceptive (P) trials: subjects moved their left hand to the target position. 500 ms after this position was achieved, the auditory go signal was sounded, cuing subjects to reach to their left target hand with their right hand. Once subjects completed their reach, visual feedback indicating the target and reach endpoint position was provided. 3: Visual + Proprioceptive (VP) trials: These trials (bottom two rows) were a combination of the V and P trials. Subjects moved their left target hand to the target position. Once this position had been detected, the visual target was presented for 500 ms. After 500 ms, similar delay conditions were completed as introduced in the Visual trials. For all trials, the grey/shaded area represents the time in the trial when visual feedback (of the target or performance) was presented.

Subjects were divided into two groups. Group One (7 females, 5 males, aged 18-32 years old) performed five blocks of 90 reaches. In each block, subjects reached to each of the 3 target positions (center, left and right) defined by the different sensory modalities (V, P, or VP) 10 times for a total of 90 trials (see Table. 1). The visual delay condition was the same across all V and VP reaches within a given block of trials. For example, a subject may have completed the first block of trials when the V and VP trials were presented under the full vision condition. The presentation of target modality and location were randomized within a block of trials and the block order in which the different delay conditions were completed was randomized across subjects.

Table 1. Breakdown of trials completed in each testing block by Group One.

V indicates reaches to visual targets, P reaches to proprioceptive targets and VP reaches to visual + proprioceptive targets. L.T., C.T. and R.T. correspond to the left, center and right targets respectively. Within each block, subjects completed reaches to the V and VP targets under a given delay condition (full vision: FV; 0 second delay: D0; 1 second delay: D1; 2 second delay: D2 and 5 second delay: D5).

Block	Group One									
	V			P			VP			Total Reaches
	L.T.	C.T.	R.T.	L.T.	C.T.	R.T.	L.T.	C.T.	R.T.	
FV	10	10	10	10	10	10	10	10	10	90
D0	10	10	10	10	10	10	10	10	10	90
D1	10	10	10	10	10	10	10	10	10	90
D2	10	10	10	10	10	10	10	10	10	90
D5	10	10	10	10	10	10	10	10	10	90

The second group of subjects (Group Two: 7 females, 5 males, aged 19-28 years old) also performed 5 blocks of 90 reaches. For one block, subjects completed the full vision condition trials like Group One. This was considered the control block. For the remaining 4 blocks, the 4 other visual delay conditions (0, 1, 2, and 5 seconds delay) were intermixed within a block. Subjects completed two or three reaches to each target under the different sensory and visual delay conditions within a block so that across all four blocks of trials, 10 reaches were completed in total for each of the different target combinations (see Table. 2).

Table 2. Breakdown of trials completed in each testing block by Group Two.

V indicates reaches to visual targets, P reaches to proprioceptive targets and VP reaches to visual + proprioceptive targets. L.T., C.T. and R.T. correspond to the left, center and right targets respectively. In Block 1 (B1) all subjects completed 10 reaches to each of the different targets for each sensory modality under the full vision (FV) no-delay condition. In Block 2 through 5, subjects completed reaches to the V and VP targets under different delay conditions (0 second delay: D0; 1 second delay: D1; 2 second delay: D2 and 5 second delay: D5). Specifically, subjects completed 2-3 reaches per delay condition per block per target.

Block	Group Two									
	V			P			VP			Total Reaches
	L.T.	C.T.	R.T.	L.T.	C.T.	R.T.	L.T.	C.T.	R.T.	
B1	10 FV	10 FV	10 FV	10 P	10 P	10 P	10 FV	10 FV	10 FV	90
B2	3 D0 2 D1 2 D2 3 D5	3 D0 2 D1 2 D2 3 D5	3 D0 2 D1 2 D2 3 D5	10 D0	10 D0	10 D0	3 D0 2 D1 2 D2 3 D5	3 D0 2 D1 2 D2 3 D5	3 D0 2 D1 2 D2 3 D5	90
B3	2 D0 3 D1 3 D2 2 D5	2 D0 3 D1 3 D2 2 D5	2 D0 3 D1 3 D2 2 D5	10 D0	10 D0	10 D0	2 D0 3 D1 3 D2 2 D5	2 D0 3 D1 3 D2 2 D5	2 D0 3 D1 3 D2 2 D5	90
B4	3 D0 2 D1 2 D2 3 D5	3 D0 2 D1 2 D2 3 D5	3 D0 2 D1 2 D2 3 D5	10 D0	10 D0	10 D0	3 D0 2 D1 2 D2 3 D5	3 D0 2 D1 2 D2 3 D5	3 D0 2 D1 2 D2 3 D5	90
B5	2 D0 3 D1 3 D2 2 D5	2 D0 3 D1 3 D2 2 D5	2 D0 3 D1 3 D2 2 D5	10 D0	10 D0	10 D0	2 D0 3 D1 3 D2 2 D5	2 D0 3 D1 3 D2 2 D5	2 D0 3 D1 3 D2 2 D5	90

Three subjects from Group One (1 female, 2 males, aged 22-31 years old) and two subjects from Group Two (2 females, aged 21 years old) were re-tested a second time under conditions in which the hands were switched. Specifically, subjects reached with their non-

dominant hand (i.e., left hand) and the right index finger indicated the position of the proprioceptive target. These five subjects completed the same 5 blocks as performed by the first group of subjects. In other words, subjects performed five blocks of 90 reaches and within a given block of trials, the visual delay condition was the same across all V and VP reaches.

In all trials, the task was to reach to the specified target position as accurately as possible. Before the actual experiment started, subjects performed two sets of practice trials to familiarize themselves with the apparatus and task. The first set consisted of 20 trials in which only the visual target was displayed at different delay conditions. In the second set (another 20 trials), the three target types were introduced (V, P and VP targets), in order to get subjects used to switching between different trial types.

To ensure that subjects did not become fatigued, 5 minute breaks were scheduled between blocks (approximately every 15-20) minutes and subjects were asked frequently if they would like longer or more frequent break periods. The entire experiment took approximately 2 hours to complete.

III. Data Analysis

1. Kinematic Analysis

Kinematics of the right reaching hand data were analyzed using custom written programs in Matlab and SPSS software. In order to determine how subjects' reaches varied when different sources of sensory information were available under the different delay conditions, we compared movement time (MT), movement angular errors at peak velocity (PV AE) and movement endpoint (EP AE), and movement endpoint position errors (EP) across the different types of trials completed.

Movement time was taken as the interval of time between movement initiation (defined as the point in time at which movement velocity increased above 0.01 m/s) and movement termination (defined as the point in time at which movement velocity fell below 0.01 m/s and remained below 0.01 m/s for more than 50 ms).

With respect to accuracy, we examined endpoint position errors and angular errors. In particular, movement endpoint position errors (EP) were calculated as the distance between the actual target position and the final position of the right index finger in both the horizontal (EP_x) and vertical (EP_y) dimensions. A positive horizontal error indicates that the hand was to the right of the target and a positive vertical error indicates that the hand landed above the target.

We examined angular errors (AE) at the end of the movement (EP AE), and at peak velocity (PV AE). The EP AE was defined as the angular difference between a movement vector (from the home position to reach endpoint) and a reference vector (joining the home position and the target). Similarly, the PV AE was defined as the angular difference between a movement vector (from the home position to the position of the right index finger at PV) and a reference vector (joining the home position and the target).

In addition to biases in performance, variability (or precision) of reaching movements (specifically EP variability and EP AE variability) for each sensory modality at each of the different targets under the different delay conditions was calculated. To further investigate reaching variability between target modalities and delay conditions, we fitted 95% confidence interval ellipses to each subject's data (i.e., all reaches completed to a specific target modality at a given target position within a block of trials). Using these ellipses, we then calculated ellipse area.

All variables were analyzed in a repeated measures analysis of variance (RM ANOVA). In order to compare reaching performance between unimodal conditions (V targets vs. P targets), a 2 (target modality) x 3 (target position) RM ANOVA was conducted, whereas a 3 (target modality) x 3 (target position) RM ANOVA was applied to compare performance on bimodal trials (VP targets) to the unimodal trials (V targets & P targets). Additionally, to examine the effect of manipulating the availability of visual information on reaching performance between blocks, we included the factor of visual delay condition (i.e., 5 visual delay conditions) to the analysis. Moreover, to ensure that subjects did not correct their movements online, a t-test was performed to compare mean angular errors achieved at the end of the reach and peak velocity.

2. *Sensory Reweighting*

From the analysis above, we found that reaches to visual versus proprioceptive targets were biased in different directions, and biases to VP targets lay between V & P biases. Therefore, to determine how subjects weighted visual and proprioceptive cues within a block of trials and if these weights changed across blocks of trials, we compared the endpoint position on a VP trial to mean endpoint positions achieved on V and P reaches within a block of trials. In

accordance with Block and Bastian (2010, 2011, & 2012), we assumed that if subjects assigned more weight to visual cues on reaches to VP targets, then they would point closer to their mean V endpoint position. However, if they assigned more weight to proprioceptive cues, they would point closer to their mean P endpoint position. Thus, we considered W_v to be the experimental weight assigned to vision and W_p to be the experimental weight assigned to proprioception (P), and if W_v was greater than 0.5, it indicated that subjects relied more on vision.

W_v and W_p were calculated as follows and determined with respect to the resultant distance between different reach endpoint positions, as well as the horizontal and vertical differences in reach endpoint positions:

$$W_v = (\text{P-to-VP endpoint distance}) / ((\text{P-to-VP endpoint distance}) + (\text{V-to-VP endpoint distance})),$$

$$W_p = 1 - W_v$$

For Group One (and the few subjects who completed the reaching tasks with their left hand), we calculated W_v and W_p for each subject for each VP trial within a block of trials (with respect to a resultant distance, as well as with respect to the horizontal and vertical dimension). Given that proprioception has been shown to drift over trials (Craske & Crawshaw, 1975; Wann & Ibrahim, 1992), in order to calculate the W_v for each VP trial, we used the mean endpoint positions of the four V and four P reaches occurring closest in time. These mean endpoint positions were compared to the mean position of three VP reaches (specifically the VP trial of interest (VP_i) and the preceding (VP_{i-1}) and following VP trial (VP_{i+1})). Thus, like Block and Bastian (2010, 2011, & 2012), we estimated the weight of vision on a trial-by-trial basis. The resultant, horizontal and vertical W_v and W_p assigned to each VP reach within a block of trials were then averaged across VP trials and these averages were compared across the 5 different blocks of trials with a RM ANOVA.

For Group Two, we calculated the W_v and W_p for each VP reach in a block of trials by a similar method. We then compared the results in the control block (full vision condition) to performance on the remaining blocks of trials, which included all other visual delays. Again, the resultant, horizontal and vertical W_v (and W_p) assigned to each VP reach within a block of trials were averaged across VP trials and these averages were then compared across the different 5 blocks of trials with RM ANOVA.

All ANOVA results are reported with Greenhouse-Geisser corrected values. Differences with a probability of less than .05 were considered to be significant and multiple comparisons with Bonferroni correction were used to determine the locus of these differences.

IV. Results

1. Group One

In this experimental group, subjects reached with the same visual delay condition across all V and VP reaches within a block of trials.

i. Movement Time (MT)

All trials that started before the go signal were excluded. Based on this criterion, 116 trials out of 5400 trials (or 2.1%) were excluded from analyses. As seen in Figure 3, MT differed depending on which target position subjects reached to ($F(2, 22) = 13.776, p < 0.001$), such that subjects completed their reaches faster to the right target (white bar: mean MT = 919 ± 213 ms) compared to the targets positioned at the center (grey bar: mean MT = 975 ± 224 ms), or on the left (black bar: mean MT = 986 ± 208 ms). Analysis revealed that MT did not vary with target modality ($F(2, 22) = 3.100, p = 0.073$) and did not change across the blocks of trials with different visual delay times. That is, subjects reached with a similar MT regardless of the sensory modality of the target (i.e., V target vs. P target vs. VP target) or the visual delay condition (i.e., full vision vs. 0 s delay vs. 1 s delay vs. 2 s delay vs. 5 s delay).

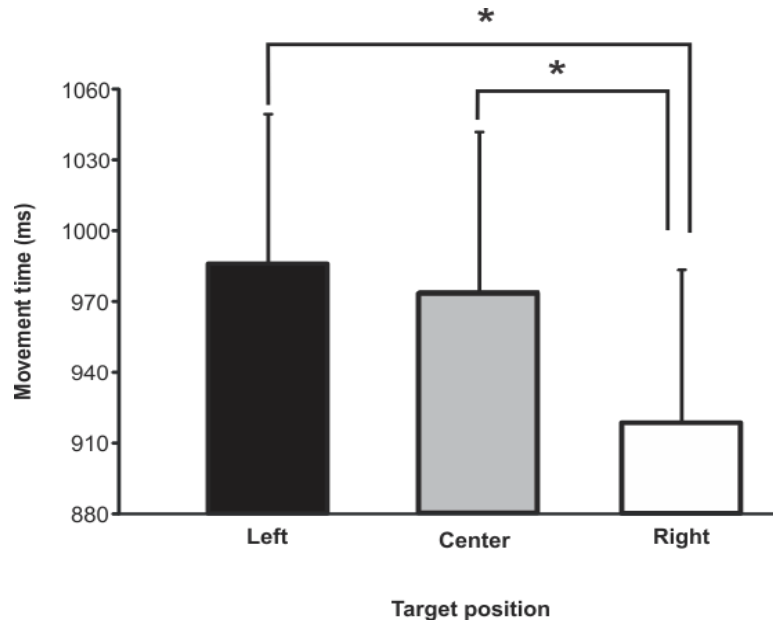


Figure 3. Movement time.

Mean movement times (ms) for reaches to the left (black bar), center (grey bar), and right (white bar) targets. Subjects were faster to reach to the right target compared to the targets positioned at the center, or on the left. Error bars reflect standard errors of the mean.

ii. Reaching errors in V and P reaches

Before determining how subjects weighted visual and proprioceptive cues across the different blocks of trials, we first established if reaches to V and P targets were biased in different directions (as shown previously by van Beers *et al.*, 1998, 1999, & 2002; Block & Bastian, 2010). To determine biases in subjects' reaches, we compared the final position of the reaching hand (e.g. with respect to final horizontal endpoint position (EP_x), final vertical endpoint position (EP_y), and angular errors (EP AE)) when subjects reached to V and P targets at the three different target locations.

As seen in Figure 4A, subjects' reaches differed when subjects reached to visual and proprioceptive targets; the average distance between mean V and P endpoint positions was 24 mm. Specifically, subjects reached to the left of and overshot the target when it was defined by

proprioception (as illustrated by the white shapes in Figure 4A), while they reached to the right of and undershot the target when it was defined by vision (as illustrated by the black shapes in Figure 4A).

The difference in reaches observed between V targets and P targets was further illustrated by comparing the mean final position errors of the reaching hand in both the horizontal (EP_x) and vertical axis (EP_y) across the three target locations. As seen in Figure 4B, reaches to P targets had a greater leftwards bias (white bars: mean EP_x = -6.8 ± 19.6 mm) compared to reaches completed to V targets (black bars: mean EP_x = 5.8 ± 22.6 mm), ($F(2, 22) = 17.514$, $p < 0.001$). A similar trend was seen at all target positions; however, post hoc analysis revealed that EP_x was only significantly different between the two target modalities when subjects reached to the center ($p = 0.003$) or right target ($p = 0.002$). Similar to errors in the horizontal dimension, errors in the vertical dimension differed significantly between V and P targets ($F(2, 22) = 13.587$, $p = 0.001$), target positions ($F(2, 22) = 15.731$, $p = 0.001$), and the interaction of target modality by target position was significant ($F(4, 44) = 13.864$, $p < .001$). As seen in Figure 4C, subjects reached significantly farther when reaching to a P target (white bars: mean EP_y across all target positions = -1.6 ± 13.4 mm) at the left ($p = 0.002$) and center ($p = 0.005$) target locations compared to a V target (black bars across all target positions: mean EP_y = -9.6 ± 12.3 mm) at the same locations.

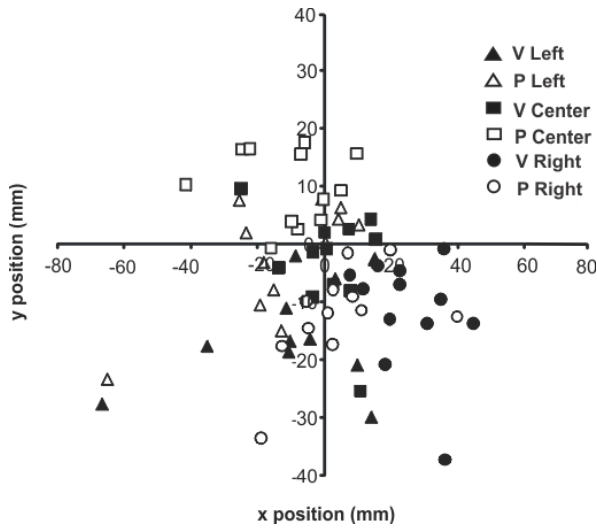
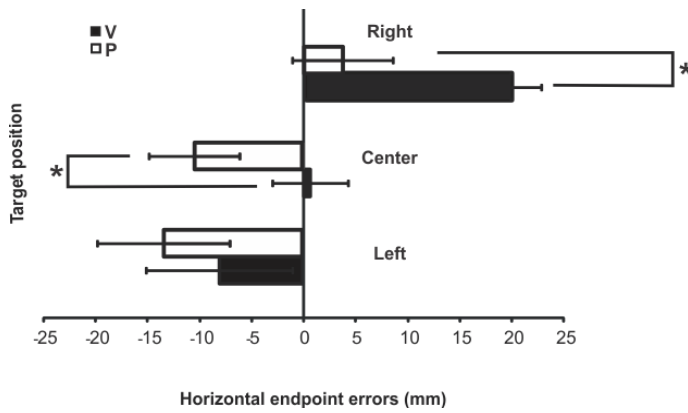
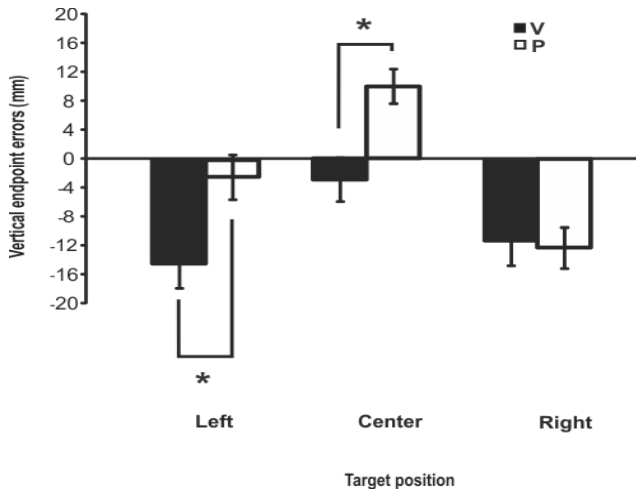
A**B****C**

Figure 4. Endpoint positions - unimodal conditions.

A: Mean endpoint positions for reaches to visual (V: black symbols) and proprioceptive targets (P: white symbols), when subjects reached to the left target (triangles), center target (squares) and right target (circles). Final positions of the reaching hand differed depending on target modality. Subjects reached to the right of and undershot the visual targets, while they reached to the left of and overshot the proprioceptive targets. Mean (B) horizontal and (C) vertical endpoint position errors for reaches to visual (V: black bars) and proprioceptive targets (P: white bars), when subjects reached to the left, center and right targets. The difference in biases between these unimodal conditions is illustrated by comparing the mean endpoint errors in V and P reaches across the three target positions. A significant difference between means is marked by an asterisk. Error bars reflect standard errors of the mean.

In accordance with these observations, analysis of angular errors at reaching endpoint (EP AE) revealed a main effect of target modality ($F(2, 22) = 16.35, p < 0.001$), target position ($F(2, 22) = 9.24, p = 0.008$), and significant target modality by target position interaction ($F(4, 44) = 15.915, p < 0.001$). Post hoc analysis showed that this difference between reaches to visual and proprioceptive targets was significant when subjects reached to the center target ($p = 0.002$) and to the right target ($p < 0.001$), but not in reaches to the left target ($p > 0.05$) (Figure 5A). Analysis of angular errors at peak velocity (PV AE) showed a trend similar to EP AE. As illustrated in Figure 5B subjects' biases differed between the two target modalities ($F(2, 22) = 17.963, p < 0.001$), target positions ($F(2, 22) = 8.611, p = 0.002$), and the interaction of target modality with target position ($F(4, 44) = 14.349, p < 0.001$). Moreover, there was no significant difference between angular errors achieved at the end of the reach and peak velocity ($t(8) = 0.386, p = 0.710$), suggesting that subjects did not correct their movements online.

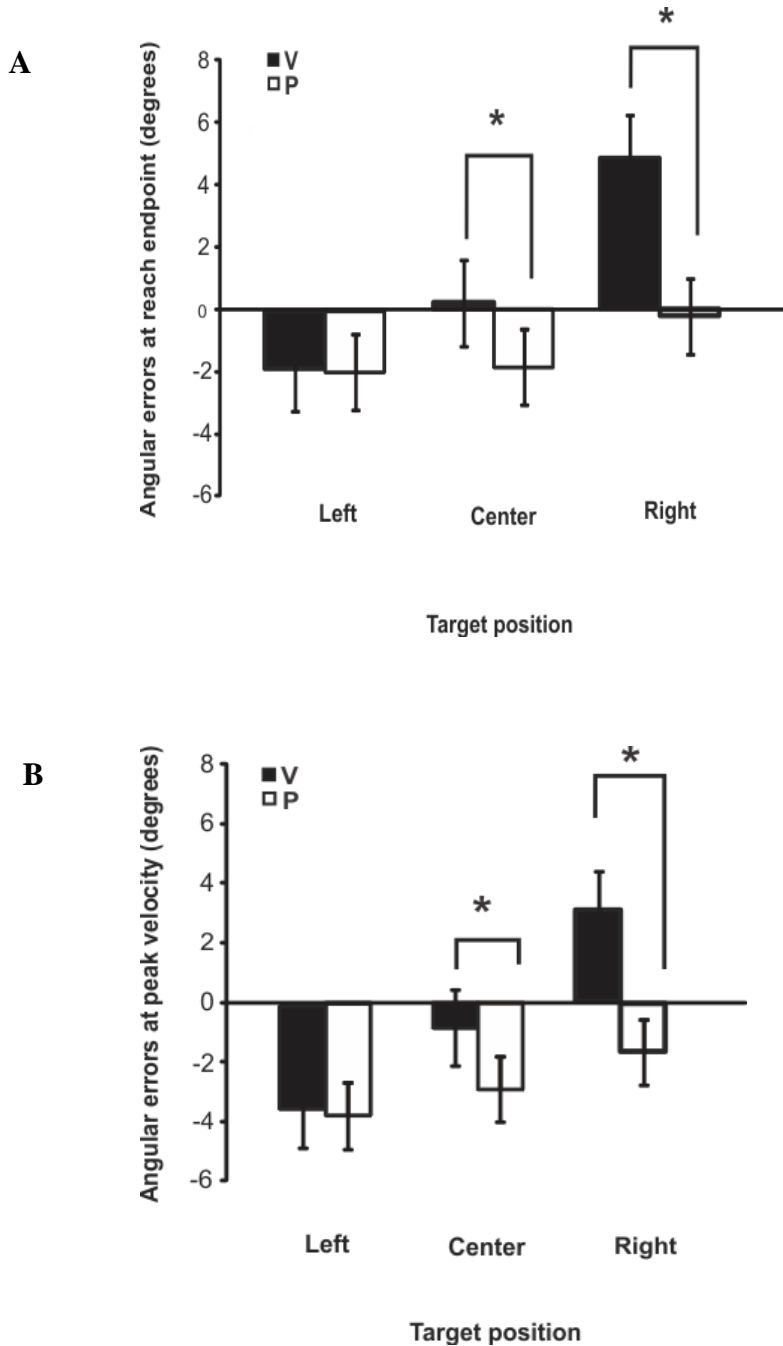


Figure 5. Angular errors - unimodal conditions.

(A) Mean angular errors at reach endpoints (EP AE) for reaches to visual (V: black bars) and proprioceptive targets (P: white bars), when subjects reached to the left, center and right targets. (B) Mean angular errors at peak velocity (PV AE) for reaches to visual (V: black bars) and proprioceptive targets (P: white bars), when subjects reached to the left, center and right targets. The difference in biases between these unimodal conditions is illustrated by comparing the angular errors in V and P reaches across the three target positions. A significant difference between means is marked by an asterisk. Error bars reflect standard errors of the mean.

After establishing that subjects had different biases when reaching to visual versus proprioceptive targets, we next examined whether manipulating the time of visual information available influenced subjects' reaching accuracy. In particular, errors in pointing to actual (online) and remembered visual targets were studied under the five visual delay conditions (i.e.,

FV, D0, D1, D2, and D5). A 5 (visual delay condition) x 2 (target modality) x 3 (target position) RM ANOVA illustrated that errors in EP_x did not change between visual delay blocks ($F(4, 44) = .0087, p = 0.952$). However, errors in EP_y were influenced by visual delay such that analysis revealed a significant visual delay x target modality interaction ($F(4, 44) = 2.847, p = 0.038$), visual delay x target position interaction ($F(8, 88) = 9.767, p < 0.001$), and a significant visual delay x target modality x target position interaction ($F(16, 176) = 6.957, p < 0.001$). According to post hoc analysis, subjects' reaches to proprioceptive targets did not change across the blocks of trials. However, subjects reached with differing amounts of errors to the left visual target between the delay conditions of D0 vs. D1, and D0 vs. D2. As well, subjects did not reach as far and hence had greater errors in the delay condition D5 compared to the remaining four delay blocks when reaches were made towards the right target.

In contrast to errors in the horizontal and vertical dimensions, statistical analysis revealed no main effect for visual delay condition with respect to both EP AE ($F(4, 44) = 0.069, p = 0.974$), and PV AE ($F(4, 44) = 0.702, p = 0.555$). Additionally, analysis of EP AE and PV AE showed that visual delay condition did not interact significantly with target modality and/or target position (i.e., $p > 0.05$). In summary, errors in subjects' reaches increased in the vertical dimension when reaching towards actual versus remembered visual targets.

iii. Reaching precision in V and P reaches

In addition to reaching errors, we also examined reaching precision in horizontal, vertical, and angular directions. Precision with respect to EP_x differed as a function of target modality ($F(2, 22) = 8.345, p = 0.003$), such that subjects were more precise in localizing visual targets (mean EP_x = 12.1 ± 3.2 mm) compared to proprioceptive targets (mean EP_x = 13.7 ± 4.2 mm). In addition, precision differed across the 3 target positions ($F(2, 22) = 16.137, p = 0.001$),

such that reaches to the right target were less precise (mean EPx = 14.77 ± 5.46 mm) than reaches to the left (mean EPx = 12.1 ± 3.2 mm) and center (mean EPx = 10.5 ± 2.4 mm) targets. Finally, a significant target modality by target position interaction ($F(4, 44) = 2.998, p = 0.045$) revealed that reaches to the left V target (mean EPx = 11.3 ± 3.5 mm) were significantly less variable than reaches to the left P target (mean EPx = 14.3 ± 4.5 mm) ($p = 0.007$).

Precision in EPy was influenced by target position ($F(2, 22) = 7.715, p = 0.006$), but not by target modality ($F(2, 22) = 3.020, p = 0.087$) and there was no significant target modality x target position interaction ($F(4, 44) = 1.977, p = 0.138$). Reaches to the right target position (mean EPy = 13.2 ± 3.4 mm) were more variable compared with reaches to the center (mean EPy = 11.9 ± 3.1 mm) and left (mean EPy = 11.6 ± 2.9 mm) targets.

Results for each of the three target positions with respect to EP AE precision are shown in Figure 6. As observed in this figure, precision differed between reaches to V (black bars) and P targets (white bars) ($F(2, 22) = 6.995, p = 0.006$), as well as across target positions ($F(2, 22) = 12.387, p = 0.001$). Analysis also revealed a significant target modality by target position interaction ($F(4, 44) = 3.909, p = 0.018$). Based on post hoc analysis, subjects were more precise in estimating the V targets compared to the P targets when the target was presented in the peripheral positions (Left target: $p = 0.05$, Right target: $p = 0.291$, which while not significant displays the same trend as the Left target), whereas they were more precise in estimating the P center target compared to the V center target ($p = 0.019$).

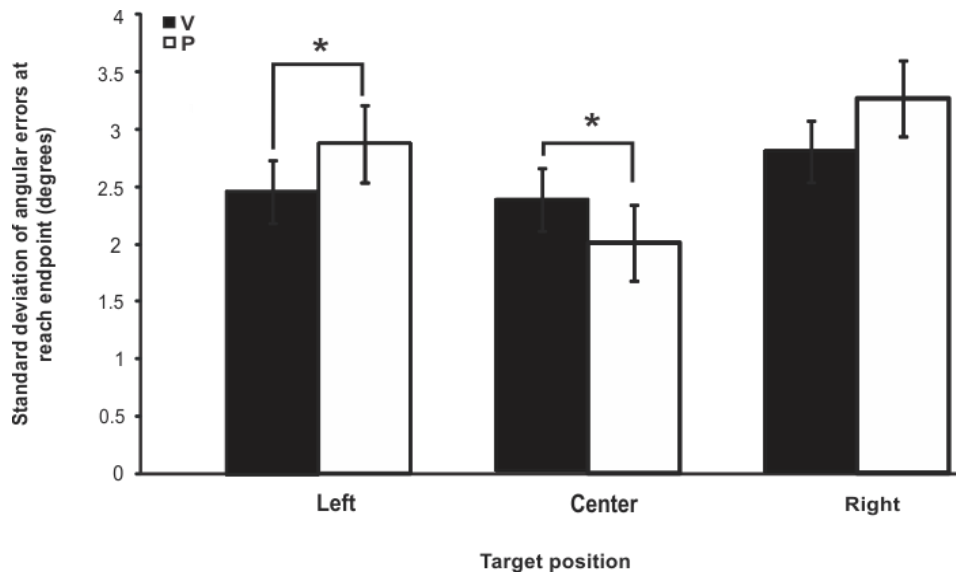


Figure 6. Variance of angular errors - unimodal conditions.

Variance of angular errors at reach endpoints for reaches to visual (V: black bars) and proprioceptive targets (P: white bars), when subjects reached to the left, center and right targets. Reaches to visual targets were more precise at peripheral targets, whereas proprioceptive reaches were more precise when reaching to the center target. Error bars reflect standard errors of the mean.

We also studied whether changing the visual delay condition influenced the precision of estimating target positions. A 5 (visual delay condition) x 2 (target modality) x 3 (target position) RM ANOVA showed that neither the precision of endpoint errors (EPx precision: ($F(4, 44) = 0.95, p = 0.435$), EPy precision: ($F(4, 44) = 2.085, p = 0.122$)) nor the precision of angular errors at reach endpoint ($F(4, 44) = 1.818, p = 0.142$), or peak velocity ($F(4, 44) = 2.906, p = 0.073$)) differed between the 5 delay conditions. Thus, subjects reached with similar levels of precision when reaching to online (actual) visual targets and remembered visual targets. That is, the variance in estimation of visual target position did not change across visual delay conditions. Likewise, the precision in estimating P targets did not vary between blocks (all p 's were > 0.05).

iv. Reaching performance during VP reaches

In accordance with the theory of optimal integration, we hypothesized that when subjects reached to VP targets, they would reach to a position between their V and P estimates. Figure 7A represents data from all subjects reaching to V, P, and VP targets at the three target locations. As shown in Figure 7A, VP endpoints tended to fall between the distributions of V and P endpoints rather than within one distribution or the other (VP endpoints are illustrated by the grey shapes in Figure 7A). The average distance between the mean V and VP endpoint positions was 16.2 mm, and was 12.5 mm between the mean P and VP endpoint positions. As demonstrated in Figure 7B, horizontal errors on VP reaches (grey bars) differed from the unimodal conditions and lay between the errors achieved on V and P trials ($F(2, 22) = 17.514, p < 0.001$). Statistical analysis revealed that this difference in EPx between bimodal reaches and unimodal reaches was only significantly different in reaches made to the center or to the right targets ($p < 0.05$). Likewise, errors in the vertical dimension for reaches to bimodal targets differed from the errors to unimodal targets ($F(2, 22) = 18.312, p < 0.001$) and differed significantly from both P and V estimates in reaches made towards the left and center target positions ($p < 0.05$) (Figure 7C).

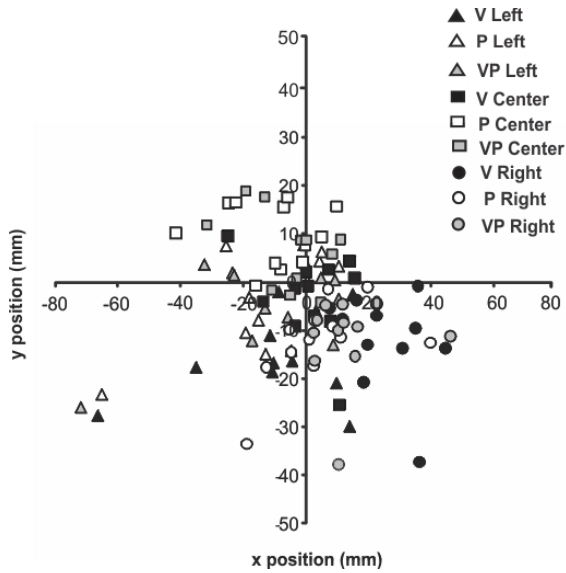
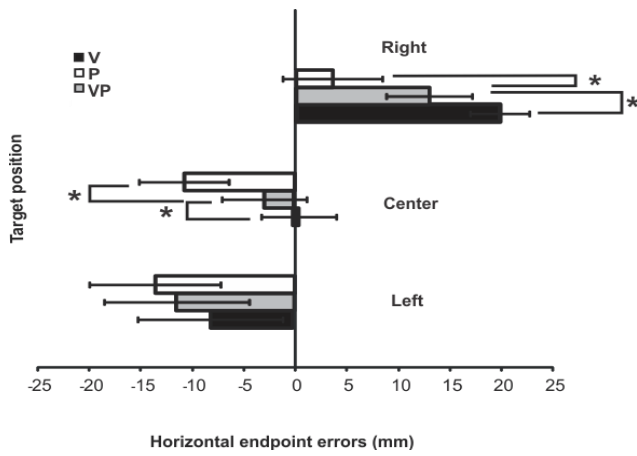
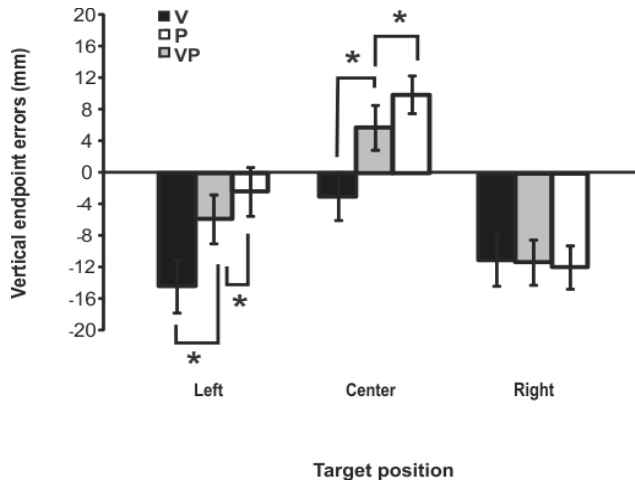
A**B****C**

Figure 7. Endpoint positions - bimodal vs. unimodal conditions.

A: Endpoint positions for reaches to visual (V: black symbols), proprioceptive targets (P: white symbols), and visual + proprioceptive targets (VP: grey symbols) when subjects reached to the left target (triangles), center target (squares) and right target (circles). Final positions of the reaching hand differed depending on target modality. VP endpoints tended to fall between the distributions of V endpoints and P endpoints rather than within one distribution or the other. Mean (B) horizontal and (C) vertical endpoint position errors for reaches to visual (V: black bars), proprioceptive targets (P: white bars) and visual + proprioceptive targets (VP: grey bars), when subjects reached to the left, center and right targets. Error bars reflect standard errors of the mean.

To further examine our first hypothesis of optimal sensory integration, we compared the EP AE for bimodal versus unimodal reaches, across the three target locations. Analysis of EP AE showed a main effect of target modality ($F(2, 22) = 16.35, p < 0.001$), target position ($F(2, 22) = 9.24, p = 0.008$), and target modality by target position interaction ($F(4, 44) = 15.915, p < 0.001$). According to post hoc analysis, the difference in errors between bimodal (grey bars in Figure 8) reaches and unimodal reaches (white and black bars in Figure 8) was significant when reaches were directed to the center or right target positions ($p < 0.05$), but not in reaches made to the left target position ($p > 0.05$).

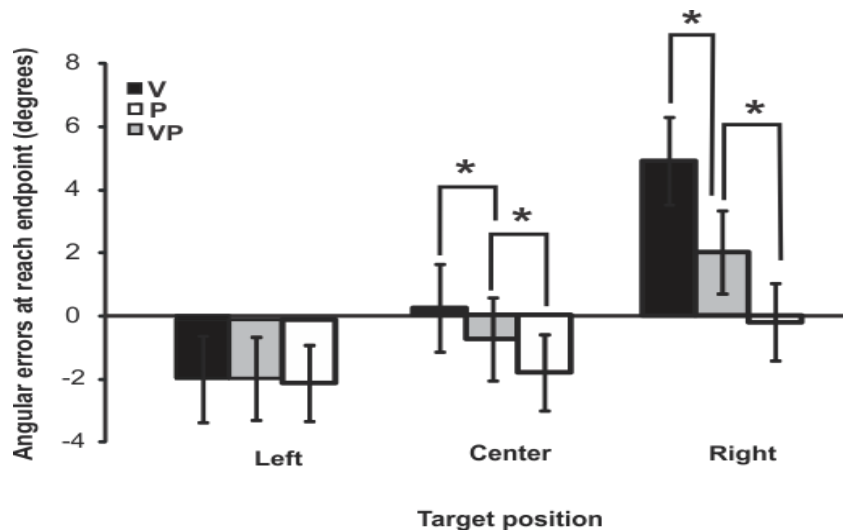


Figure 8. Angular errors - bimodal vs. unimodal conditions

Mean angular errors at reach endpoints (EP AE) for reaches to visual (V: black bars), proprioceptive targets (P: white bars) and visual + proprioceptive targets (VP: grey bars), when subjects reached to the left, center and right targets. Error bars reflect standard errors of the mean.

Additionally, we investigated how manipulating the timing of visual information would affect the bias of the bimodal estimates. Statistical analyses revealed that visual delay conditions had no affect on reaches to VP targets with respect to EP (EPx ($F(4, 44) = .0087, p = 0.952$),

and EPy ($F(4, 44) = 1.789, p = 0.17$) or EP AE ($F(4, 44) = 0.069, p = 0.974$). As well, analysis indicated that the factor of visual delay condition did not interact significantly with target modality, target position, or the interaction between these two factors (i.e., $p > 0.05$ for all interactions). Table 3 provides the mean and standard deviation (SD) of EPx, EPy, and EP AE errors for each target modality in each visual delay condition collapsed across target positions.

Table 3. Breakdown of trials completed in each testing block by Group Two.

V indicates reaches to visual targets, P reaches to proprioceptive targets and VP reaches to visual + proprioceptive targets. L.T., C.T. and R.T. correspond to the left, center and right targets respectively. In Block 1 (B1) all subjects completed 10 reaches to each of the different targets for each sensory modality under the full vision (FV) no-delay condition. In Block 2 through 5, subjects completed reaches to the V and VP targets under different delay conditions (0 second delay: D0; 1 second delay: D1; 2 second delay: D2 and 5 second delay: D5). Specifically, subjects completed 2-3 reaches per delay condition per block per target.

Visual Delay	Variables	V	P	VP
FV	EPx	6.1 mm (± 23.1 mm)	-5.1 mm (± 18.3 mm)	-1.5 mm (± 21.1 mm)
	EPy	-5.3 mm (± 12.9 mm)	4.2 mm (± 10.8 mm)	0.5 mm (± 11.9 mm)
	EP AE	1.1° ($\pm 4.5^\circ$)	-1.1° ($\pm 3.2^\circ$)	-0.3° ($\pm 3.8^\circ$)
D0	EPx	7.0 mm (± 23.6 mm)	-7.7 mm (± 17.3 mm)	-0.6 mm (± 20.3 mm)
	EPy	-2.5 mm (± 11.2 mm)	8.6 mm (± 11.0 mm)	4.6 mm (± 10.7 mm)
	EP AE	1.2° ($\pm 4.4^\circ$)	-1.6° ($\pm 3.2^\circ$)	-0.2° ($\pm 3.6^\circ$)
D1	EPx	7.6 mm (± 24.1 mm)	-5.7 mm (± 22.8 mm)	-0.6 mm (± 24.1 mm)
	EPy	-10.4 mm (± 12.1 mm)	4.5 mm (± 12.2 mm)	0.9 mm (± 10.5 mm)
	EP AE	1.2° ($\pm 4.7^\circ$)	-1.2° ($\pm 4.0^\circ$)	-0.2° ($\pm 4.3^\circ$)
D2	EPx	5.9 mm (± 22.5 mm)	-7.1 mm (± 21.7 mm)	-0.9 mm (± 20.6 mm)
	EPy	-9.2 mm (± 11.6 mm)	5.8 mm (± 13.2 mm)	0.2 mm (± 12.4 mm)
	EP AE	0.9° ($\pm 4.7^\circ$)	-1.6° ($\pm 4.0^\circ$)	-0.3° ($\pm 3.9^\circ$)
D5	EPx	4.4 mm (± 20.0 mm)	-6.5 mm (± 17.9 mm)	-0.2 mm (± 17.9 mm)
	EPy	-15.1 mm (± 13.5 mm)	7.7 mm (± 10.3 mm)	-2.1 mm (± 11.8 mm)
	EP AE	0.9° ($\pm 4.5^\circ$)	-1.3° ($\pm 3.1^\circ$)	-0.1° ($\pm 3.4^\circ$)

v. Reaching precision in VP reaches

To determine whether reaches to VP targets were more precise than reaches to V and P targets, we computed and compared the variance in pointing to VP targets versus V or P targets. According to the second tenant of sensory integration theories, we hypothesized that the variance for the bimodal estimates would be smaller than that for unimodal estimates. Overall, with respect to precision in the horizontal axis, subjects were more precise in localizing VP targets (mean EPx = 11.5 ± 3.8 mm) compared to V (mean EPx = 12.1 ± 3.2 mm) or P (mean EPx = 13.7 ± 4.2 mm) targets ($F(2, 22) = 8.345, p = 0.003$). However, post hoc analysis revealed that the difference in precision between bimodal and unimodal estimates was only significant between VP and P targets in reaches directed towards peripheral targets (Left target: $p = 0.005$, and Right target: $p = 0.035$). With respect to precision in the vertical axis, analysis revealed a main effect of target position ($F(2, 22) = 7.715, p = 0.006$); reaches made to the right target position (mean EPy = 13.2 ± 3.4 mm) were less precise compared with reaches directed to the center (mean EPy = 11.9 ± 3.1 mm) and left (mean EPy = 11.6 ± 2.9 mm) target positions. However, analysis showed no significant effect of target modality ($F(2, 22) = 3.020, p = 0.087$) on precision in the vertical dimension.

Analysis revealed a significant effect of target modality ($F(2, 22) = 6.995, p = 0.006$), target position ($F(2, 22) = 12.387, p = 0.001$), and a significant target modality by target position interaction ($F(4, 44) = 3.909, p = 0.018$) with respect to EP AE precision. As shown in Figure 9, the variance in reaches to VP targets (grey bars, mean AE = $2.3^\circ \pm 0.7^\circ$) was less than the variance in reaching to V (black bars, mean AE = $2.5^\circ \pm 0.6^\circ$) or P targets (white bars, mean AE = $2.7^\circ \pm 0.8^\circ$). Post hoc analysis showed that subjects were more precise in reaching to a left VP

target compared to a left P target and more precise in reaching to a center VP target compared to a center V target. Precision did not vary across the three target modalities at the right target.

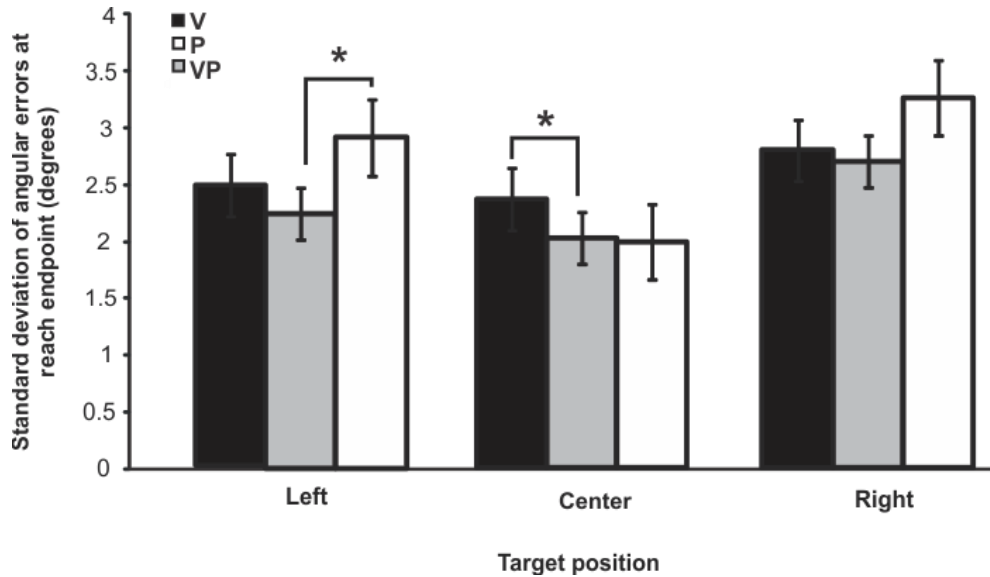


Figure 9. Variance of angular errors - bimodal vs. unimodal conditions.

Variance of angular errors at reach endpoints for reaches to visual (V: black bars), proprioceptive (P: white bars) and visual + proprioceptive targets (VP), when subjects reached to the left, center and right targets. Subjects were more precise in reaching to a left VP target compared to a left P target and more precise in reaching to a center VP target compared to a center V target. Error bars reflect standard errors of the mean.

On the other hand, the factor of visual delay condition did not interact significantly with target modality, target position, or the interaction between these two factors with respect to EPx and EPy (i.e., $p > 0.05$ for all interactions). Also, analysis revealed that visual delay condition had no effect on EP AE. Table 4 provides the mean and standard deviation (SD) of EPx, EPy, and EP AE precision for reaches to each target modality in each visual delay condition collapsed, across target positions.

Table 4. EPx, EPy, and EP AE errors.

Mean (and SD) of EPx, EPy, and EP AE errors for each target modality in each visual delay condition (full vision: FV; 0 second delay: D0; 1 second delay: D1; 2 second delay: D2 and 5 second delay: D5), collapsed across target positions.

Visual Delay	Variables	V	P	VP
FV	EPx	11.4 mm (± 5.5 mm)	12.3 mm (± 7.5 mm)	10.9 mm (± 4.4 mm)
	EPy	10.9 mm (± 4.7 mm)	11.6 mm (± 4.1 mm)	11.4 mm (± 5.2 mm)
	EP AE	2.3° (± 0.9 °)	2.4° (± 1.4 °)	2.2° (± 0.9 °)
D0	EPx	11.1 mm (± 3.5 mm)	14.6 mm (± 7.0 mm)	10.6 mm (± 4.4 mm)
	EPy	12.6 mm (± 4.9 mm)	10.7 mm (± 4.5 mm)	11.1 mm (± 4.4 mm)
	EP AE	2.2° (± 0.6 °)	2.8° (± 1.4 °)	1.9° (± 0.8 °)
D1	EPx	12.7 mm (± 7.3 mm)	13.4 mm (± 6.9 mm)	11.1 mm (± 4.8 mm)
	EPy	13.3 mm (± 5.4 mm)	12.6 mm (± 4.8 mm)	11.8 mm (± 4.7 mm)
	EP AE	2.8° (± 2.1 °)	2.7° (± 1.5 °)	2.2° (± 0.9 °)
D2	EPx	13.2 mm (± 4.9 mm)	14.8 mm (± 6.6 mm)	11.7 mm (± 6.2 mm)
	EPy	13.6 mm (± 6.1 mm)	11.8 mm (± 4.3 mm)	11.7 mm (± 5.4 mm)
	EP AE	2.7° (± 1.2 °)	2.9° (± 1.3 °)	2.4° (± 1.2 °)
D5	EPx	12.2 mm (± 6.0 mm)	13.4 mm (± 7.6 mm)	12.9 mm (± 7.5 mm)
	EPy	14.4 mm (± 4.5 mm)	12.2 mm (± 4.5 mm)	13.1 mm (± 4.1 mm)
	EP AE	2.6° (± 1.2 °)	2.7° (± 1.4 °)	2.8° (± 1.7 °)

To further examine the variability between reaches to unimodal and bimodal targets, we fit 95% confidence interval ellipses to each subject's data (i.e., to reaches completed to a given target (V, P or VP) at a specific target position in each visual delay block) and compared the area of these ellipses between bimodal and unimodal conditions. Although analysis revealed no main

effect of target modality on ellipse area ($F(2, 22) = 3.489, p = 0.062$), the area of the ellipses for reaches completed to VP targets tended to be smaller (mean area = $1631.4 \pm 974.1 \text{ mm}^2$), than reaches to V (mean area = $1893.9 \pm 818.6 \text{ mm}^2$) and P targets (mean area = $1912.7 \pm 1083.7 \text{ mm}^2$). On the other hand, analysis showed a significant effect of target position ($F(2, 22) = 11.058, p = 0.006$), such that subjects were more variable when reaching to the right target (mean area = $2311.6 \pm 1399.2 \text{ mm}^2$) compared to the left (mean area = $1655.5 \pm 809.5 \text{ mm}^2$) or center targets (mean area = $1470.8 \pm 658.5 \text{ mm}^2$). There was no significant effect of visual delay ($F(4, 44) = 1.930, p = 0.144$), and all interactions involving the factor of visual delay were not significant (all p 's > 0.05).

In summary, collapsed across visual delay blocks, biases (or errors) to VP targets lay between biases to V and P targets and the VP reaches were less variable than V and P reaches. This pattern of performance did not seem to change when visual information was delayed. However, errors increased in the vertical dimension when reaching to V targets with increasing visual delays.

vi. Sensory reweighting

Having established that subject integrated visual and proprioceptive cues, we next looked to determine if the brain reweighted the sensory cues, in response to changes in the availability of visual information, i.e., to determine if the brain can reweight sensory cues, we calculated the weight of vision (W_v) for every VP reach. Specifically, for each VP reach, we determined the mean endpoint positions of the 4 V and 4 P reaches that occurred closest in time and then compared these mean V and P positions to the mean position of 3 VP trials (the VP trial of interest, as well as the closest VP trial before and after the one of interest). With this method, we

were able to study the progression of reweighting on a trial-by-trial basis within a block of trials with a similar visual delay.

Given that we did not see any change in variance in reaches across the different delay conditions, if sensory cues are being integrated according to optimal integration accounts, we should not see any change in sensory reweighting. As shown in Figure 10, this is what we found. Specifically, subjects weighted visual information to a similar extent across all blocks of trials. In accordance with this observation, analysis revealed no significant difference between visual delay conditions on the weight assigned to vision in the resultant direction ($F(4, 44) = 0.849$, $p = 0.459$) (black bars), horizontal direction (W_{vx}) ($F(4, 44) = 1.534$, $p = 0.225$) (grey bars), or vertical direction (W_{vy}) ($F(4, 44) = 2.322$, $p = 0.102$) (white bars). Similar results were obtained even when weights were calculated for each target and hence accounting for different error biases between targets (i.e., all p 's > 0.05).

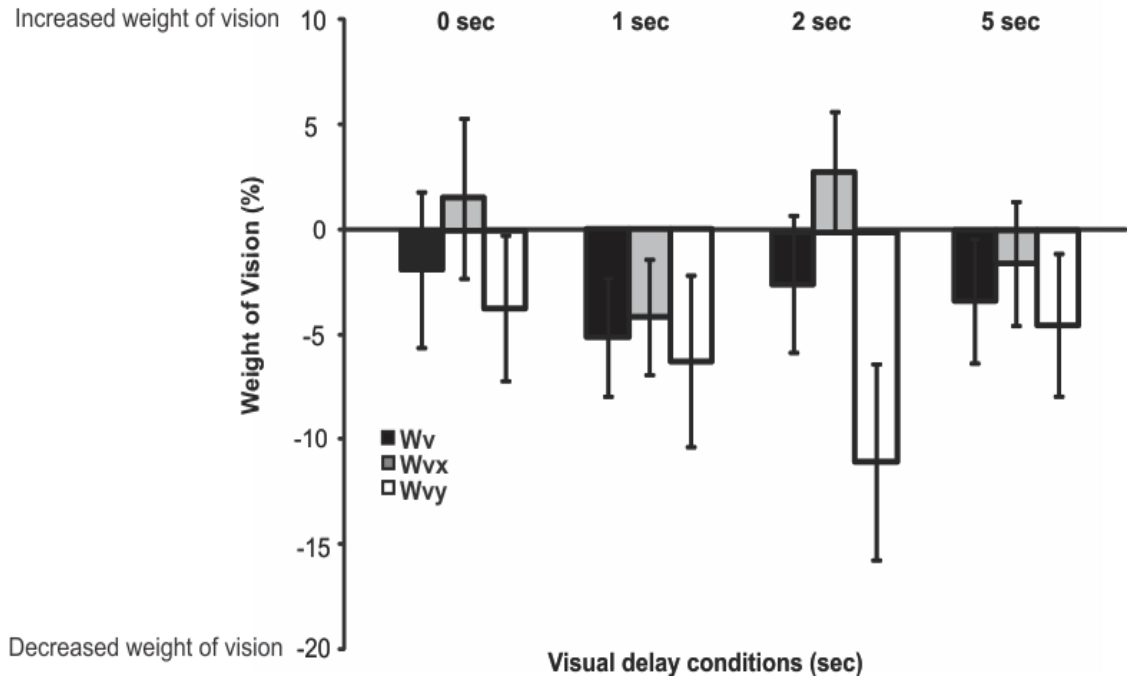


Figure 10. Weight of vision.

Weight assigned to vision in the resultant (W_v - black bars), horizontal (W_{vx} - grey bars) and vertical (W_{vy} - white bars) directions under the various delay conditions (0 second delay: D0; 1 second delay: D1; 2 second delay: D2 and 5 second delay: D5) compared to the weight assigned to vision in the full vision (FV) block of trials. Error bars reflect standard errors of the mean.

2. Additional Analysis

Similar to subjects in group one, those in Group Two completed one block of trials under the full vision condition. In the remaining 4 blocks of trials, trials for the other 4 visual delay conditions (D0, D1, D2, and D5) were intermixed.

We noticed a similar trend in final reach positions as exhibited by subjects in Group One. First, the overall distance between the V and P reaches was 34 mm and subjects reached to different locations when reaching to a V versus P target (Figure 12). Specifically, subjects reached more to the right of and undershot the target when reaching to a V target (illustrated by black shapes in Figure 11) compared to a P target (illustrated by white shapes in Figure 11).

Second, VP final positions (illustrated by grey shapes in Figure 11) tended to lie between the V and P endpoints rather than within the distributions of one or the other endpoints (illustrated by grey shapes in Figure 11). According to analysis of EP AE, there was a main effect of target modality ($F(2, 22) = 46.473, p < 0.001$), target position ($F(2, 22) = 13.172, p = 0.002$), and significant target modality by target position interaction ($F(4, 44) = 13.885, p < 0.001$). Post hoc analysis revealed that the difference between V (white bars) and P (black bars) reaches was significant in reaches made to the center and right targets ($p < 0.001$) (Figure 12), while the difference in bias between bimodal reaches (grey bars) and unimodal reaches was significant only in reaches directed to the right target position ($p < 0.05$) (Figure 12).

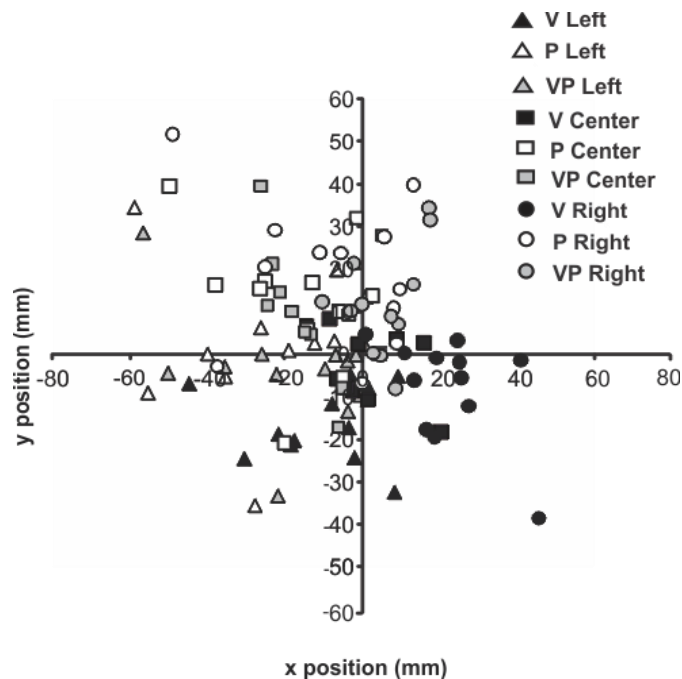


Figure 11. Endpoint positions - Group Two.

Endpoint positions for reaches to visual (V: black symbols), proprioceptive targets (P: white symbols), and visual + proprioceptive targets (VP: grey symbols) when subjects reached to the left target (triangles), center target (squares) and right target (circles). Final positions of the reaching hand differed depending on target modality. VP endpoints tended to fall between the distributions of V endpoints and P endpoints rather than within one distribution or the other.

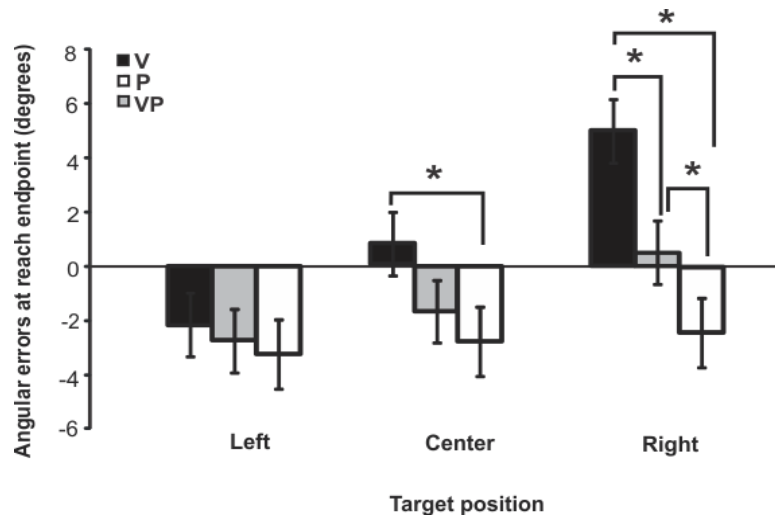


Figure 12. Angular errors - Group Two.

Mean angular errors at reach endpoints (EP AE) for reaches to visual (V: black bars), proprioceptive targets (P: white bars) and visual + proprioceptive targets (VP: grey bars), when subjects reached to the left, center and right targets. Error bars reflect standard errors of the mean.

Also, we compared EP AE precision between V, P and VP reaches (Figure 13). Again, we noticed a trend that was similar to Group One; i.e., variance was smaller on VP reaches (mean EP AE precision = $2.9^{\circ} \pm 0.7^{\circ}$) than reaches to V (black bars) (mean EP AE AE precision = $3.0^{\circ} \pm 0.6^{\circ}$) and P targets (white bars) (mean EP AE precision = $3.3^{\circ} \pm 1.2^{\circ}$). However, statistical analysis did not reveal a main effect of target modality ($F(2, 22) = 1.326, p = 0.281$). Analysis did reveal a main effect of target position ($F(2, 22) = 25.467, p < .001$), such that reaches to the center target (mean EP AE precision = $2.6^{\circ} \pm 0.7^{\circ}$) were more precise compared to reaches to the left (mean EP AE precision = $3.1^{\circ} \pm 0.7^{\circ}$) and right (mean EP AE precision = $3.5^{\circ} \pm 0.9^{\circ}$) targets. There was no significant target modality by target position interaction ($F(4, 44) = 2.577, p = 0.066$).

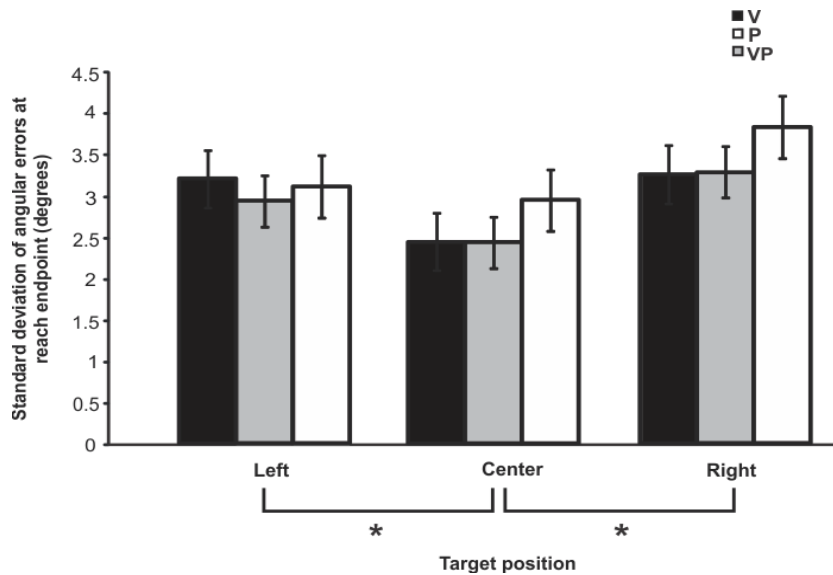


Figure 13. Variance of angular errors - Group Two.

Variance of angular errors at reach endpoints for reaches to visual (V: black bars), proprioceptive (P: white bars) and visual + proprioceptive targets (VP), when subjects reached to the left, center and right targets. Subjects were more precise in reaching to the center target compared to left and right targets. Error bars reflect standard errors of the mean.

Similar to Group One, EP AE errors and variability did not change across the visual delay conditions (EP AE errors: $F(4, 44) = 1.580, p = 0.225$), EP AE variability: $F(4, 44) = 0.649, p = 0.540$), as well, visual delay condition did not interact significantly with target modality and/or target position (i.e., $p > 0.05$ for all interactions). That is, in Group Two, subjects' reaching bias and reaching precision did not change as a function of visual delay condition. Thus, as with Group One, we did not expect sensory reweighting to change over the blocks of trials.

To examine sensory reweighting, we compared subjects' reaching performance on VP reaches in the control block (i.e., FV) to their performance on the remaining blocks of trials in which various visual delays were introduced. In general, when examining the weight subjects assigned to vision in the resultant direction, we found a main effect of visual delay ($F(4, 44) = 3.245, p = 0.04$), such that subjects assigned more weight to vision in the last block of trials

compared to the first block of trials (44% vs. 33%). Analysis of the weight assigned to vision in the horizontal and vertical directions did not reveal an influence of visual delay (horizontal W_v : $F(4, 44) = 2.581, p = 0.083$ and vertical W_v : $F(4, 44) = 1.031, p = 0.402$).

Thus, subjects did change their reliance on visual information across the testing session in the resultant direction. This is in contrast to Group One, who demonstrated no change in the weight assigned to vision.

V. Discussion

In this project, we investigated whether the brain is able to adjust how it weights sensory information when manipulating the availability of a visual cue. Two groups of subjects reached to visual (V), proprioceptive (P) and visual + proprioceptive (VP) targets. Subjects in the first group (Group One) reached to targets when the visual delay was the same across all V and VP reaches within a given block of trials. For subjects in Group Two, reaches were completed under full vision conditions in block one, while for the remaining 4 blocks of trials, the 4 other visual delay conditions (0 (D0), 1 (D1), 2 (D2), and 5 (D5) seconds delay) were randomly interleaved within a block. To determine the sensory cue that subjects weighted the most, we determined reach endpoint positions in V and P trials and compared them to VP endpoint positions. Results were consistent across the two groups of subjects. First, subjects reached to different locations when reaching to a V versus P target, such that they pointed to the right of and underestimated the target position in V reaches, while pointing to the left and overestimating the target position in P reaches. Second, results indicated that subjects combined visual and proprioceptive cues in accordance with the maximum-likelihood estimation (MLE) model when reaching to VP targets. In particular, subjects' endpoint positions in VP reaches tended to lie between the V and P endpoints rather than overlap with one or the other endpoint distributions and results indicated that subjects' reaching variability for VP targets was smaller than their variability when reaching to unimodal targets. Finally, subjects' reaching errors to visual targets increased with longer visual delays (in particular in the vertical direction). However, there was no change in reach variability with longer delays and subjects did not reweight visual information across testing blocks as the availability of visual information was manipulated. Thus, a change in reaching

environment and corresponding change in visual environment is not sufficient to cause the brain to reweight how it processes sensory information.

1. *Reaches differed across target positions*

We found that movement time was dependent on the location of the target, regardless of target modality, with reaches to the right target being completed faster than reaches to the left or center targets. This result is in accordance with previous findings demonstrating that movements to a target that is contralateral to the reaching hand (in our experiment the left target position) tend to take a significantly longer time to complete in comparison to movements directed to a target that is on the same side of the body or ipsilateral to the reaching hand (in our experiment the right target position) (Prablanc, Echallier, Komilis, & Jeannerod, 1979; Fisk & Goodale, 1985; Carson, Goodman, Chua, & Elliott, 1993). One interpretation of this difference between movements made to either side of body midline (i.e. ipsilateral vs. contralateral reaches) is that the ipsilateral target is processed in the same hemisphere as the motor, premotor and somatosensory cortices with direct connections to the reaching hand. Thus, faster movements to ipsilateral targets could be attributed to the more efficient transmission of target and/or reaching limb information within a hemisphere versus having to transmit information between hemispheres (Hodges, Lyons, Cockell, Reed, Elliot, 1997; Velay, Benoit-Dubrocard, 1999; Adamo & Martin, 2009; Adamo, Scotland, & Martin, 2012). However, Gordon *et al.* (1994) and Carey *et al.* (1996) suggested that biomechanical factors could lead to this temporal advantage for movements into ipsilateral versus contralateral space. Specifically, they argue that movements in which the hand path direction is perpendicular to the long axis of the upper arm (i.e., horizontal flexion of the upper arm, with some flexion of the forearm) have higher inertial loads that could account for higher movement durations to contralateral targets compared to

ipsilateral targets in which movements are completed in general with hand paths that are parallel to the long axis of the upper arm (i.e., horizontal extension of the forearm).

While subjects were faster to complete ipsilateral reaches in the current study, we also found that in general subjects were less precise when reaching to the right target compared to the left or center targets, demonstrating a speed accuracy trade-off (Fitts' Law; Woodworth, 1899; Fitts, 1954; Fitts & Peterson, 1964). Moreover, when we fitted 95% confidence interval ellipses to each subject's data (i.e. all reaches completed to a specific target modality at a given target position within a block of trials), we found a significant effect of target position, such that the scatter of subjects' endpoints were more variable when reaching to the right target compared to the left or center targets. These results are in accordance with Fitts' law, which indicates that greater variability is associated with faster movements (Woodworth, 1899; Fitts, 1954; Fitts & Peterson, 1964).

2. *Reaches differed across target modalities*

Our results indicate that reaches to V and P targets were biased in different directions. Specifically, subjects reached to the left of and overshot the proprioceptive target (mean EPx = -6.4 mm, mean EPy = 6.1 mm), whereas they reached to the right of and undershot the visual target (mean EPx = 6.2 mm, mean EPy = -8.5 mm). In other words, the same target position was estimated differently when it was cued by visual versus proprioceptive cues. Previous research has shown that visual and proprioceptive estimates are not necessarily aligned, even when they indicate the same target position or target property (van Beers *et al.*, 1998, 1999, & 2002; Smeets *et al.* 2006; Block & Bastian, 2010; Reuschel *et al.*, 2010). This misalignment between estimates may be due to how one codes the target position (i.e., the reference frame(s) used). Generally, to define the location of an object (or target) in space, we describe where it is in relation to either a

body part or a location in the environment. In reaching, information about a target location may be derived from different sources of information and hence coded in different reference frames. That is, visual and proprioceptive information might be expressed in different coordinate systems (Soechting & Flanders, 1989; van Beers *et al.*, 1996, 1999, & 2002; Sober & Sabes, 2005). While visual localization relies on extrinsic coordinates (i.e., using a reference frame external to the body), proprioceptive localization relies on intrinsic coordinates (i.e., using a reference frame internal to the body, such as joint angles). Transforming these different coordinates into a target position to reach to it may then give rise to different reaching errors.

In addition to the differences in reaching biases between unimodal targets (V vs. P targets), it has been shown that precision estimates differ between sensory cues depending on movement direction (van Beers *et al.*, 1998, 1999, & 2002). Specifically, van Beers and colleagues (1998, 1999, & 2002) have demonstrated that one is more precise in localizing proprioceptive targets when they are located in the radial direction (perpendicular to the shoulders) compared to the azimuthal/horizontal direction (parallel to the shoulders). In contrast, when reaching to targets in the azimuthal direction, one is more precise when reaching to visual versus proprioceptive targets. In accordance with these findings, we found that subjects were more precise when reaching to the V target when it was presented at the peripheral target locations and more precise in estimating the P target when it was located at center. Thus, our findings further indicate that proprioception is a more reliable source of information when reaching to a target at body midline compared to peripheral targets, while vision is a more reliable source of information for localizing peripheral compared to midline targets.

3. *Performance on VP trials / Sensory Integration*

The maximum-likelihood estimation (MLE) model (Ernst & Banks, 2002; Ernst & Bulthoff, 2004) for sensory integration assumes that noise in each unimodal estimate follows a Gaussian distribution and that these noise distributions are mutually independent from each other. The MLE model then predicts that these independent unimodal estimates (in our case: visual and proprioceptive estimates of target location) are combined in a linear fashion to form a coherent estimate of the target's location. Moreover, these cues are optimally combined (or weighted), such that the weight of a single sensory cue is proportionally to the cue's relative reliability; i.e. a more reliable estimate is assigned a higher weight, such that the variance of the final multimodal estimate is minimal. In accordance with the MLE model, we hypothesized that: (1) the location that subjects reached to on bimodal trials would lie between the unimodal estimates and, (2) the variance of bimodal estimates would be smaller than that of unimodal estimates (van Beers *et al.*, 1996 & 1999, Ernst & Bulthoff, 2004; Helbig & Ernst 2007; Block & Bastian, 2010; Reuschel *et al.*, 2010).

In support of the MLE model, Block and Bastian (2010) found that reaches to VP targets tended to fall between the distributions of V and P endpoints rather than overlap with one of the distributions. Moreover, van Beers and colleagues (1996), who investigated the integration of visual and proprioceptive information during target localization by asking subjects to match the position of visual, proprioceptive, or visual + proprioceptive targets with their index finger, have shown a decrease in variance under bimodal conditions compared to unimodal conditions. Interestingly, recent work by Monaco *et al.* (2010) also suggests that the addition of proprioceptive to visual information not only leads to sensory integration such that one's variance is reduced, but also leads to smaller errors overall.

In addition to visual and proprioceptive target information being integrated in accordance with the MLE model during targeted reaching, research suggests that these cues are integrated in an optimal manner for perceptual judgments and that sensory integration can extend beyond visual and proprioceptive cues to include other sensory modalities. For example, Reuschel *et al.* (2010) have shown that perceptual judgments regarding the type of angle formed by two consecutive trajectories (i.e., acute or obtuse), were influenced by visual and proprioceptive cues such that the bimodal bias differed from each unimodal bias and lay between the unimodal biases. Moreover, Reuschel *et al.* (2010) found that while their subjects underestimated angular trajectories in the proprioceptive condition and overestimated angular trajectories in the visual condition, they showed a nearly unbiased perception in the visual + proprioceptive condition. In addition to visual-proprioreceptive integration, sensory cues have been shown to be combined during such tasks as audiovisual localization (Ghahramani *et al.*, 1997), and visual-haptic object size and shape discrimination (Ernst & Banks, 2002; Helbig & Ernst, 2007). Together, these studies provide convincing evidence that the brain integrates available sensory signals so as to reduce the uncertainty of their estimates and increase the robustness of the multimodal percept.

Similar to these previous results, our findings agree with the MLE model, as we found that errors on bimodal trials lay between the unimodal biases and significantly differed from both unimodal estimates. We further noticed higher variance when reaching to visual or proprioceptive targets compared to when reaching to visual + proprioceptive targets (although this was not significant for subjects in Group Two).

These results together with previous findings from optimal integration accounts urge one to wonder which brain areas are responsible for multisensory integration. The past decade has witnessed an increasing number of studies that have investigated the neural basis of multisensory

integration. Traditionally, it was assumed that information processing in the primary sensory areas was modality specific, and integrated only after transmission to higher brain areas (i.e. association cortices). Conversely, recent studies provide evidence that multisensory interactions can occur even at the lowest levels of the cortical processing hierarchy (e.g. Malholm *et al.*, 2002, Foxe *et al.*, 2002; Pekkola *et al.*, 2005; Martuzzi *et al.*, 2007). Moreover, the growing body of evidence from recent neuroimaging studies in healthy humans suggests a set of cortical regions (such as the lateral occipital cortex (Amedi *et al.*, 2001; James *et al.*, 2002; Naumer *et al.*, 2010), posterior (Saito *et al.*, 2003) and anterior (Grefkes *et al.*, 2002) intraparietal sulcus (IPS) and subcortical structures (such as the left putamen, left thalamus, and right cerebellum (Gentile *et al.*, 2011)) that are activated by multiple sensory cues (e.g., spatially coincident tactile and visual stimuli). However, it remains unclear whether these brain areas integrate multisensory input in a statistically optimal manner in accordance with the MLE.

4. *Manipulation of Visual Information*

The primary purpose of this research was to investigate the ability of the brain to reweight sensory information. In particular, we studied whether manipulating the time that a visual cue was available for prior to movement initiation would alter how sensory information was integrated. Moreover, we examined the time course of this sensory reweighting by having subjects reach to targets under different visual delays.

Generally, the accuracy with which goal-directed movements are executed depends substantially on the availability of (accurate) visual information (Soechting & Flanders, 1989; Berkinblit *et al.*, 1995). When visual information regarding target position is not available during movement execution, typical results reveal a decrease in movement accuracy and an increase in movement variability, indicating that the visual information about the movement environment

can only be stored for a restricted period of time (Elliott & Madalena, 1987; Goodale & Milner, 1992). For example, when Berkinblint *et al.* (1995) examined accuracy in reaches to a visual target 1 second after vision of the target was occluded, they found relatively large three dimensional reach errors with an average of 9.16 cm. This average error decreased significantly to 2.78 cm when subjects performed reaches with vision of the target available. Other studies that have examined the role of vision in target localization have compared a full-vision (FV) condition to a condition in which visual information regarding target position was eliminated immediately upon movement initiation (no vision 0 second delay condition) and a condition in which a brief delay time was introduced between target occlusion and response cueing. Using this type of paradigm, Elliott and Madalena (1987) found no significant difference in pointing error between the full vision (total error 4.8 mm) and no vision 0 second delay conditions (total error = 6.8 mm). However, their subjects exhibited a twofold increase (total error = 9.8 mm) in pointing error after only 2 seconds of visual occlusion prior to movement onset, with no further increases in errors when reaches were initiated after 5 or 10 seconds of visual occlusion. Based on these results, they suggested that the accurate visual representation of the movement environment is available to subjects for a brief period of time (< 2 s) following visual occlusion to guide goal-directed movements in the absence of direct visual input. More recently, there has been some debate as to the time course of the decay of visual information, as some have suggested that even very brief delays can have dramatic effects (Westwood *et al.* 2001 & 2003; Heath *et al.* 2004). For example, Westwood, Roy, and Heath (2001 & 2003) reported greater errors in reaches to targets in a no vision 0 second delay condition (i.e. occluding vision with the onset of the reaching response, mean error = 15.6 mm approximately) than errors in a full vision condition (average error = 8 mm approximately). Moreover, they noticed that the error greatly

increased with delay of 500, 1000, 1500 or 2000 ms of visual occlusion prior to the reach, with similar errors associated with all delay conditions (i.e. from 500-2000 ms, average error = 30 mm approximately). In addition to changes in reaching errors or biases, reaching movements to remembered visual targets (i.e. delayed reaching) have also been shown to be more variable than movements to visual targets. For example, Health Westwood (2003) found that reaches under a 0 second delay condition were associated with greater endpoint variability than reaches under the FV condition. Additionally, while variability in the 2 and 5 second delay conditions did not differ from each other, they were more variable compared to the 0 second delay reaches. Similarly, Westwood *et al.* (2003) showed that endpoint variability was smaller under FV conditions (variable error = 10 mm approximately), increased when the delay was 0 seconds (variable error = 12 mm approximately) and increased again when the delay was 500 ms (variable error = 13.8 mm approximately) and 2,000 ms (variable errors = 16.2 mm approximately). Based on these results, it has been proposed (Elliott & Madalena, 1987; Goodale & Milner, 1992; Westwood *et al.*, 2001 & 2003) that visually guided and delayed reaching movements are governed by two distinct modes of visuomotor processing, and that the transition between online visual information to a stored representation occurs quickly (< 500 ms). Further evidence for two distinct modes of visual processing (or two visual streams) comes from the performance of neurological patients in delayed reaching paradigms (Goodale & Milner, 1992; Goodale, Jakobson, & Keillor, 1994; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999). For example, Goodale *et al.* (1994) found that patient D.F. who was diagnosed with visual form agnosia, and thus had no perceptual awareness of the size of the target object, had normal visually guided grasping abilities. On the other hand, when a 2 second delay was introduced between visual object occlusion and response cueing, D.F. showed a

noticeable inability to grasp objects; i.e., the requirement of remembering an object even briefly disturbed her visuomotor scaling. Moreover Milner *et al.* (1999) reported that, in contrast to neurologically intact subjects, patient A.T., who suffered from optic ataxic, reached more accurately to targets in delayed reaching conditions compared to visually guided conditions. These cases suggest the existence of two independent visual streams responsible for visually guided and delayed movement control. In other words, the online visuomotor system (Goodale and Milner's dorsal stream, 1992) is involved in the control of reaching movements when the target remains visible. On the other hand, when the visual target is occluded, the motor system accesses a representation of the target that has been stored by a second visual system (Goodale and Milner's ventral stream, 1992). Therefore, changes in movement performance that occur immediately following target occlusion could be due to a rapid transition between online and perception-based modes of movement control.

In our study we found an increase in reaching errors with visual delay. Specifically, we found that subjects were less accurate and did not reach as far in the 5 second delay condition compared to the remaining four blocks of trials. This decrease in accuracy with a longer delay is in agreement with previous results. However, in contrast to previous findings, we did not find a significant decrease in reaching precision with increases in visual delay.

In contrast to visual information, proprioception has been shown to remain a reliable source of information when the visual environment is kept constant (Desmurget *et al.*, 2000; Chapman *et al.*, 2001). While early studies argued that reaching accuracy is prone to degradation over time when subjects rely exclusively on proprioception to estimate the location of his or her hand in space (Paillard & Brouchon 1968; Craske & Crawshaw 1975; Wann & Ibrahim 1992), more recent work has found similar levels of accuracy when reaching to

proprioceptive targets under delay and no-delay conditions. In fact, Desmurget *et al.* (2000) showed that one's accuracy in localizing the unseen hand was similar regardless of whether reaches were completed immediately after the positioning of the target hand or after a 10 second delay. As well, Chapman *et al.* (2001) illustrated that subjects' reaching accuracy did not change over delays of 1, 2, or 10 seconds when subjects reached to the remembered position of their hand. In our research, we did not implement a delay period between positioning the proprioceptive target and initiating the reaching response as there was no way to differentiate between some of the delay conditions (i.e., the on-line and delay 0 condition). Thus, all proprioceptive reaches were cued with the go-signal 500 ms after the hand was positioned and the hand was maintained at the target position for all trials (i.e. they were online reaches). Thus as expected, we found that neither accuracy nor precision in localizing proprioceptive target locations varied between blocks of trials (Desmurget *et al.*, 2000; Chapman *et al.*, 2001; Monaco *et al.*, 2010; Jones, Fiehler, & Henriques, 2012). These results suggest that even if it is not calibrated with vision, proprioceptive cues reliably indicate target position when the visual representation of the movement environment is kept constant.

With respect to reaches to bimodal targets, we found that manipulating the availability of visual information did not influence reaching errors or precision when localizing VP targets. Moreover, when we compared the area of 95% confidence interval ellipses across visual delay conditions, there was no significant effect of visual delay. Taken together, these data suggest that, regardless of visual delay condition, (1) bimodal biases differed from unimodal biases and lay between unimodal estimates, (2) and bimodal estimates were less variable than unimodal estimates.

5. *Sensory Reweighting*

Recent results indicate that one can change the way the brain integrates sensory information. In other words, there are certain cues that may lead to one reweighting his or her reliance on one sensory modality more than another when estimating the position of a target location (Block & Bastian, 2010). Such cues include instructions to aim to one modality rather than the other and changing the target's salience. In this research, we further sought the circumstances under which one can learn to reweight sensory information. In particular, we were interested in examining whether the timing of a sensory cue's availability would change how sensory information is integrated.

Our data showed no change in variance in reaches across the different delay conditions. If sensory cues are being integrated according to optimal integration accounts, i.e., the more reliable sensory cues (i.e. more precise/less variable information) are assigned a higher weight, we should not see any change in sensory reweighting across blocks of trials since the reliability (i.e. precision/variability) of sensory cues did not change with the manipulation of visual information. In general this is what we found. Group One employed the same sensory weighting strategy across all blocks of trials. Group Two did employ a different weighting strategy in their last block of trials such that vision was weighted more in that block compared to the full vision block. This is somewhat surprising, as visual information was not available for this fifth block of trials and if anything we would expect the weight of vision to decrease. Perhaps interleaving different visual delays within a block of trial caused subjects to pay more attention to visual cues and hence by the end of the experiment this lead to sensory reweighting. Thus, manipulating the visual environment was not enough to change subjects' weighting strategy. This is probably due to the fact that there was no change in reaching variance, further

indicating that sensory information is integrated in accordance with the reliability of a sensory cue.

References

- Adamo, D., & Martin, B. (2009). Position sense asymmetry. *Exp Brain Res*, *192*, 87-95.
- Adamo, D., Scotland, S., & Martin, B.J. (2012). Asymmetry in grasp force matching and sense of effort. *Exp Brain Res*, *217*(2), 273-85.
- Berkinblit, M., Fookson, O., Smetanin, B., Adamovich, S., & Poizner, H. (1995). The interaction of visual and proprioceptive inputs in pointing to actual and remembered targets. *Exp Brain Res*, *107*, 326-330.
- Block, H., & Bastian, A. (2010). Sensory reweighting in targeted reaching: Effects of conscious effort, error history, and target salience. *Journal of Neurophysiology*, *103*, 206-217.
- Block, H., & Bastian, A. (2011). Sensory weighting and realignment: independent compensatory processes. *J Neurophysiol*, *106*, 59-70.
- Block, H., & Bastian, A. (2012). Cerebellar involvement in motor but not sensory adaptation. *Neuropsychologia* (in press).
- Carey, D., & Hargreaves, E. (1996). Reaching to ipsilateral or contralateral targets: within-hemisphere visuomotor processing cannot explain hemispacial differences in motor control. *Exp Brain Res*, *112*, 496-504.
- Carson, R., Goodman, D., Chua, R., & Elliott, D. (1993). Asymmetries in the regulation of visually guided aiming. *J Motor Behav*, *25* (1), 21-32.
- Chapman, C., Heath, M., Westwood, D., & Roy, E. (2001). Memory for kinesthetically defined target location: evidence for manual asymmetries. *Brain Cogn*, *46*(1-2), 62-66.
- Craske, B., & Crawshaw, M. (1975). Shifts in kinesthesia through time and after active passive movement. *Perceptual and Motor Skills*, *40*, 755-761.
- Desmurget, M., Vindras, P., Gréa, H., Viviani, P., & Grafton, S. (2000). Proprioception does not quickly drift during visual occlusion. *Exp Brain Res*, *134*, 363-377.
- Elliott, D., & Madalena, J. (1987). The influence of premovement visual information on manual aiming. *The Quarterly Journal of Experimental Psychology*, *39* (A), 541-559.
- Ernst, M., Banks, M., & Bulthoff, H. (2000). Touch can change visual slant perception. *Nat Neurosci*, *3*, 69-73.
- Ernst, M., & Banks, M. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*, 429-433.

- Ernst, M., & Bulthoff, H. (2004). Merging the senses into robust percept. *Trends in Cognitive Sciences*, 8(4), 162-169.
- Fisk, J., & Goodale, M. (1985). The organization of eye and limb movements during unrestricted reaching to targets in ipsilateral and contralateral space. *Exp Brain Res*, 60, 159-178.
- Fitts, P. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, 47, 381-391.
- Fitts, P., & Peterson, J. (1964). Information capacity of discrete motor responses. *Journal of Experimental Psychology*, 67 (2), 103-112.
- Ghahramani, Z., Wolpert, D., & Jordan, M. (1997). Computational models for sensorimotor integration. In: *Self-organization, computational maps and motor control*. North Holland: Morasso PG, Sanguineti V. Amsterdam.
- Goodale, M., & Milner, A. (1992). Separate visual pathways for perception and action. *Trends Neurosci*, 15(1), 20-25.
- Goodale, M., Jakobson, L., & Keillor, J. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, 32, 1159-1178.
- Goodale, M., Westwood, D., & Milner, A. (2004). Two distinct modes of control for object-directed action. *Prog Brain Res*, 144, 131-144.
- Gordon, J., Gilhardi, M., Cooper, S., & Ghez, C. (1994). Accuracy of planar reaching movements. II. Systematic errors resulting from inertial anisotropy. *Exp Brain Res*, 99, 112-130.
- Helbig, H., & Ernst, M. (2007). Optimal integration of shape information from vision and touch. *Exp Brain Res*, 179, 595-606.
- Heath, M., Westwood, D., & Binsted, G. (2004). The control of memory-guided reaching movements in peripersonal space. *Mot Control*, 8, 76-106.
- Hodges, N., Lyons, J., Cockell, D., Reed, A., & Elliot, D. (1997). Dand, space, and attentional asymmetries in goal-directed manual aiming. *Cortex*, 33, 251-269.
- Jones, S., Cressman, E., & Henriques, D. (2009). Proprioceptive localization of the left and right hands. *Exp Brain Res*, 204(3), 373-383.
- Jones, S., Fiehler, K., & Henriques, D. (2010). Proprioceptive acuity varies with task, hand target, and when memory is used. *Haptics: Generating and perceiving tangible sensations*, 321-326.

- Jones, S., Fiehler, K., & Henriques, D. (2012). A task-dependent effect of memory and hand-target on proprioceptive location. *Neuropsychologia* (in press).
- Lovelace, E. (1989). Vision and Kinesthesia in accuracy of hand movement. *Perceptual and Motor Skills*, 68, 707-714.
- Milner, A., Paulignan, Y., Dijkerman, H., Michel, F., & Jeannerod, M. (1999). A paradoxical improvement of misreaching in optic ataxia: new evidence for two separate neural systems for visual localization. *Pro Biol Sci*, 266, 2225-2229.
- Monaco, S., Kroliczak, G., Quinlan, D., Fattori, P., Galletti, C., Goddalle, M., & Culham, J. (2010). Contribution of visual and proprioceptive information to the precision of reaching movements. *Exp Brain Res*, 202, 15-32.
- Mon-Williams, M., Wann, J., Jenkinson, M., & rushton, K. (1997). Synaesthesia in the normal limb. *Proc Biol Sci*, 264(1384), 1007-1010.
- Paillard, J., Brouchon, M. (1968). Active and passive movements in the calibration of position sense. In: *The neuropsychology of spatially oriented behavior* (Freedman SJ, ed), pp 37-55. Homewood, IL: Dorsey.
- Prablanc, C., Echallier, J., Komilis, E., & Jeannerod, M. (1979). Optimal response of the eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. *Biological Cybernetics*, 35,113-124.
- Reuschel, J., Drewing, K., Henriques, D., Rosler, F., & Fiehler, K. (2010). Optimal integration of visual and proprioceptive movement information for the perception of trajectory geometry. *Exp Brain Res*, 201, 853-862.
- Rossetti, Y. (1998). Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Conscious Cogn*, 7, 520-558.
- Sarlegna, F., & Sainburg, R. (2007). The effect of target modality on visual and proprioceptive contributions to the control of movement distance. *Exp Brain Res*, 176, 267-280.
- Sober S., & Sabes, P. (2005). Flexible strategies for sensory integration during motor planning. *Nature Neuroscience*, 8(4), 490-497.
- Soechting, J., & Flanders, M. (1989). Sensorimotor representations for pointing to targets in three-dimensional space. *Journal of Neurophysiology*, 62(2), 582-594.
- van Beers, R., Sitting, A., & van Der Gon, D. (1996). How humans combine simultaneous proprioceptive and visual position information. *Exp Brain Res*, 111, 253-261.

- van Beers, R., Sittig, A., & van Der Gon, J. (1998). The precision of proprioceptive position sense. *Exp Brain Res*, *122*, 367-377.
- van Beers, R., Sittig, A., & van Der Gon, D. (1999). Integration of proprioceptive and visual position-information: An experimentally supported model. *Journal of Neurophysiology*, *81*, 1355-1364.
- van Beers, R., Wolpert, D., & Haggard, P. (2002). When feeling is more important than seeing in sensorimotor adaptation. *Curr Biol*, *12*, 834-837.
- Velay, J., & Benoit-Dubrocard, S. (1999). Hemispheric asymmetry and interhemispheric transfer in reaching programming. *Neuropsychologia*, *37*, 895-903.
- Wann, J., & Ibrahim, S. (1992). Does limb proprioception drift ? *Exp Brain Res*, *91*, 162-166.
- Warren, D., & Schmitt, T. (1978). On the plasticity of visual-proprioceptive bias Effects. *J Exp Psychol Hum Percept Perform*, *4*(2), 302-10.
- Westwood, D., Health, M., & Roy, E. (2001). The accuracy of reaching movements in brief delay conditions. *Canadian Journal of Experimental Psychology*, *55*(4), 304-310.
- Westwood, D., & Goodale, M. (2003). Perceptual illusion and the realtime control of action. *Spat Vis*, *16*, 243-254.
- Westwood, D., Roy, E., & Health, M. (2003). No evidence for accurate visuomotor memory: systematic and variable error in memory-guided reaching. *Journal of Motor Behavior*, *35*(2), 127-133.
- Woodworth, R. (1899). The accuracy of voluntary movement. *Psychol. Monogr.*, *3* (3), 1-114.

Chapter Three: General Discussion and Conclusions

In this research project, we sought to examine whether the brain adjusts how it weights sensory information when the availability of a visual cue is manipulated. For the purpose of this study, subjects were divided into two groups. In Group One, subjects performed a reaching task to visual (V), proprioceptive (P), and visual + proprioceptive (VP) targets under different visual delay conditions and the visual delay condition was the same across all V and VP reaches within a given block of trials. In Group Two, subjects completed full vision condition trials like Group One for one block (control block), while for the remaining 4 blocks of trials, the 4 other visual delay conditions (0, 1, 2, and 5 seconds delay) were intermixed within a block. We analyzed endpoint positions completed to V and P targets and compared them to the VP endpoint positions to determine the sensory cue that subjects weighted the most. The two groups of subjects showed similar results. First, our data showed that subjects reached to different locations when reaching to a V versus P target. In particular, they pointed to the right and underestimated the target position in V reaches, while pointing to the left and overestimating the target position in P reaches. These findings provide further evidence that visual estimation and proprioceptive estimation of the same target position are not aligned, i.e., the position at which we feel our limb is not necessarily the same location at which we see it (van Beers *et al.*, 1998, 1999, & 2002; Smeets *et al.* 2006; Block & Bastian, 2010; Reuschel *et al.*, 2010). Second, consistent with recent research on reaches to bimodal VP targets (van Beers *et al.*, 1999; Block & Bastian, 2010; Reuschel *et al.*, 2010), we found that subjects' final reach positions in VP reaches tended to lie between the V and P endpoints rather than within one or the other endpoint distributions. Likewise, we found a trend that the variance for bimodal estimates was smaller than that for unimodal estimates. Thus in accordance with the maximum-likelihood estimation (MLE) model, we found that when both visual and proprioceptive information were available, the CNS

integrated both types of information in an optimal manner, in which the variance of the bimodal percept was smaller than the variances of either unimodal estimate (van Beers *et al.*, 1996, 1998, & 1999; Ghahramani *et al.*, 1997; Ernst & Banks, 2002; Helbig & Ernst, 2007; Reuschel *et al.*, 2010). Third, while subjects' reaching errors increased with longer visual delays, we did not find a similar increase in variance and no change in reweighting strategies across blocks of trials. Thus, this study further emphasizes that sensory cues are weighted based on their reliability in order to minimize the variance of bimodal estimates of target position in accordance with the MLE model.

In addition to the analysis reported in Chapter 2, we also examined whether subjects' sex influenced their reaching performance and hence reweighting strategies. Specifically, we examined the factor of sex on angular errors (both bias and precision) at the end of the movement (EP AE) and the weights assigned to vision by Group One in the resultant direction. Behavioural studies have suggested sex-related differences in reaching performance when it comes to accuracy. For example Hansen *et al.* (2007) examined performance of male and female subjects when the visual environment was perturbed using a prism. Specifically, subjects looked through a prism lens prior to movement initiation, and the prism was then removed at the beginning of or during the movement to a visual target. Results indicated that movement trajectories of females were significantly disturbed during prism presentation at movement initiation. However, female subjects efficiently attained the target when the prism was removed at movement initiation. In contrast, male subjects were more influenced by the visual information provided prior to movement initiation such that they attained the target even when the prism was presented early in their movement trajectories, and failed to attain the target even after the prism was removed at movement initiation. Moreover, Rohr (2006) found that males

and females engaged different strategies when completing a traditional Fitts reciprocal tapping task (i.e., subjects tapped two rectangular metal plates alternately with a stylus). Specifically, based on results, Rohr proposed that males preferentially adopt a strategy emphasizing speed, while females adopt a strategy emphasizing accuracy. In contrast to these results, we found no difference between male and female subjects with respect to reaching accuracy or precision even when the availability of a visual cue was manipulated. Moreover, we did not find any change in sensory reweighting. Specifically, regardless of subjects' sex, they weighted visual information to a similar extent across all blocks of trials, i.e. between sexes, analysis revealed no significant difference across visual delay conditions on the weight assigned to vision. Thus our results imply that one's sex does not influence how subjects weighted sensory information when estimating target positions.

Finally, we had 5 subjects (three subjects from Group One and two subjects from Group Two) complete the tasks a second time under conditions in which we switched the hands. In particular, subjects reached with their non-dominant hand (i.e., left hand) and their right index finger indicated the position of the proprioceptive target. These five subjects completed the same 5 blocks of trials as performed by Group One. That is, within a given block of trials, the visual delay condition was the same across all V and VP reaches. For our two groups of subjects who reached with the right hand, we found that movement time differed based on the location of the target, regardless of target type, with reaches to the target ipsilateral to the reaching hand (i.e., right target) being completed faster than reaches to the target contralateral to the reaching hand (i.e., left target). Likewise, when subjects performed reaches using their left hand, we noticed a similar trend (but it was not significant). Specifically, movements to the right target contralateral to the hand being used tended to take a longer time to complete in comparison to

movements directed to the left ipsilateral target. These results are in agreement with previous findings showing facilitation in reaches made to ipsilateral targets (Prablanc *et al.*, 1979; Fisk & Goodale, 1985; Carson, Goodman, Chua, & Elliott, 1993), which has been attributed to (1) neurological factors (i.e., within-hemisphere versus between-hemispheres transmission of sensory information regarding target and reaching hand position (Hodges, Lyons, Cockell, Reed, & Elliot, 1997; Velay & Benoit-Dubrocard, 1999; Adamo & Martin, 2009; Adamo, Scotland, & Martin, 2012)), and (2) biomechanical factors (i.e., movements in which the hand path direction is perpendicular to the long axis of the upper arm have higher inertial loads that could account for longer movement durations than movements with hand paths that are parallel to the long axis of the upper arm (Gordon *et al.*, 1994; Carey *et al.*, 1996). While these subjects were faster to reach to the left target, they did not exhibit a speed accuracy trade-off as shown in the subjects that reached with their right hand. Specifically, for reaches made with the left hand, target position had no significant effect on the precision of endpoint position in the horizontal (EP_x) or vertical (EP_y) directions. We also found that neither biases nor precision of endpoint errors differed between the 5 visual delay conditions. Finally, with respect to reweighting of sensory information, we did not see any change in the weight that subjects assigned to vision across the blocks of trials when reaching with their left hand. Thus, regardless of the usage of dominant versus non-dominant hand, sensory cues were integrated according to optimal integration accounts.

In summary, this research provides further evidence that the brain optimally combines sensory information in a way that minimizes the uncertainty in one's estimation of a bimodal target position. To our knowledge we are the first to study whether manipulating the availability of visual information drives the brain to change how it weights visual and proprioceptive

information when reaching to a target. Although our results indicate that manipulating the visual environment was not enough to cause subjects to change their weighting strategy, given that subjects continued to reach with similar levels of precision across visual delay blocks suggests that sensory information was integrated in accordance with the reliability of a sensory cue.

The brain's capability to weight sensory modalities according to their variance provides insight into the behavioral flexibility in humans, and it worth further study. Specifically, determining what causes a sensory cue to be processed as more or less reliable could provide insight into how incoming sensory information is converted into an appropriate motor commands in the healthy brain. This then has important implications for people suffering from neurological disorders, as after we have an understanding of the normal mechanisms underlying sensory integration during goal directed actions, we can begin to design effective rehabilitation programs for individuals with damage to certain areas of the brain such as Parkinson's Disease and stroke patients. Recent studies have proposed that such patients may have problems integrating concurrent visual and proprioceptive information during movement and this could lead to motor impairments (i.e., difficulties in postural control and performing arm reaching movements; Almeida *et al.*, 2005; Bugnariu & Fung, 2010; Oliveira *et al.*, 2011; Scalha *et al.*, 2011).

References as Cited in Thesis

- Adamo, D., & Martin, B. (2009). Position sense asymmetry. *Exp Brain Res*, *192*, 87-95.
- Adamo, D., Scotland, S., & Martin, B.J. (2012). Asymmetry in grasp force matching and sense of effort. *Exp Brain Res*, *217*(2), 273-85.
- Almeida, Q., Frank, J., Roy, E., Jenkins, M., Spaulding, S., Patla, A., & Jog, M. (2005). An evaluation of sensorimotor integration during locomotion toward a target in Parkinson's disease. *Neuroscience*, *134*(1), 283-293.
- Andersen, R., Snyder, L., Bradley, D., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, *20*, 303-330.
- Aquilla, P., Sutton, S., & Yack, E. (2003). *Building bridges through sensory integration: Therapy for Children with autism and other pervasive developmental disorders*. Future Horizons:Texas.
- Batista, A., Buneo, C., Snyder, L., & Andersen, R. (1999). Reach plans in eye-centered coordinates. *285*, 257-260.
- Berkinblit, M., Fookson, O., Smetanin, B., Adamovich, S., & Poizner, H. (1995). The interaction of visual and proprioceptive inputs in pointing to actual and remembered targets. *Exp Brain Res*, *107*, 326-330.
- Bhatnagar, S. (2002). *Neuroscience for the study of communicative disorders*. (2nd edition). Philadelphia: Lippincott Williams & Wilkins.
- Block, H., & Bastian, A. (2010). Sensory reweighting in targeted reaching: Effects of conscious effort, error history, and target salience. *Journal of Neurophysiology*, *103*, 206-217.
- Block, H., & Bastian, A. (2011). Sensory weighting and realignment: independent compensatory processes. *J Neurophysiol*, *106*, 59-70.
- Block, H., & Bastian, A. (2012). Cerebellar involvement in motor but not sensory adaptation. *Neuropsychologia* (in press).
- Bremmer, F., Schlack, A., Shah, N., Zafiris, O., Kubischik, M., Hoffmann, K., Zilles, K., & Fink, G. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, *29*, 287-296.
- Bugnariu, N., & Fung, J. (2007). Aging and selective sensorimotor strategies in the regulation of upright balance. *Journal of NeuroEngineering and Rehabilitation*, *4* (19).

- Bugnariu, N., & Fung, J. (2010). Virtual environments and sensory integration: effects of aging and stroke. *Schedae*, 5, 59-76.
- Carey, D., & Hargreaves, E. (1996). Reaching to ipsilateral or contralateral targets: within-hemisphere visuomotor processing cannot explain hemispatial differences in motor control. *Exp Brain Res*, 112, 496-504.
- Carson, R., Goodman, D., Chua, R., & Elliott, D. (1993). Asymmetries in the regulation of visually guided aiming. *J Motor Behav*, 25 (1), 21-32.
- Chapman, C., Heath, M., Westwood, D., & Roy, E. (2001). Memory for kinesthetically defined target location: evidence for manual asymmetries. *Brain Cogn*, 46(1-2), 62-66.
- Cheatum, B., & Hammond, A. (2000). *Physical activities for improving children's learning and behavior: a guide to sensory motor development*. Champaign: Human Kinetics.
- Clark, S., & Riley, M. (2007). Multisensory information for postural control: sway-referencing gain shapes center of pressure variability and temporal dynamics. *Exp Brain Res*, 176, 299-310.
- Cohen, H. (1999). *Neuroscience for rehabilitation*. (2nd edition). Philadelphia: Lippincott Williams & Wilkins.
- Cohen, L., Celnik, P., Pascual-Leone, A., Corwell, B., Faiz, L., Dambrosia, J., Honda, M., Sadato, N., Gerloff, C., Catala, M., & Hallett, M. (1997). Functional relevance of cross-modal plasticity in blind humans. *Nature*, 389, 180-183.
- Colby, C., & Duhamel, JR. (1996). Spatial representations for action in parietal cortex. *Cognitive Brain Research*, 5, 105-115.
- Coon, D., & Mitterer, J. (2008). *Introduction to psychology: gateways to mind and behaviour*. (20th edition). Belmont: Cengage.
- Costantini, M., Urgesi, C., Galati, G., Romani, G., & Aglioti, S. (2011). Haptic perception and body representation in lateral and medial occipito-temporal cortices. *Neuropsychologia*, 49, 821-829.
- Craske, B., & Crawshaw, M. (1975). Shifts in kinesthesia through time and after active passive movement. *Perceptual and Motor Skills*, 40, 755-761.
- Crawford, D., Medendorp, W., & Marotta, J. (2004). Spatial transformations for eye-hand coordination. *J Neurophysical*, 92(1), 10-19.
- Desmurget, M., Vindras, P., Gréa, H., Viviani, P., & Grafton, S. (2000). Proprioception does not quickly drift during visual occlusion. *Exp Brain Res*, 134, 363-377.

- Elliot, D., & Madalena, J. (1987). The influence of premovement visual information on manual aiming. *The Quarterly Journal of Experimental Psychology*, 39 (A), 541-559.
- Ernst, M., Banks, M., & Bulthoff, H. (2000). Touch can change visual slant perception. *Nat Neurosci*, 3, 69-73.
- Ernst, M., & Banks, M. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, 415, 429-433.
- Ernst, M., & Bulthoff, H. (2004). Merging the senses into robust percept. *Trends in Cognitive Sciences*, 8(4), 162-169.
- Eysenck, M. (2001). *Principles of cognitive psychology*. (2nd edition). United Kingdom: Psychology Press Ltd.
- Fisk, J., & Goodale, M. (1985). The organization of eye and limb movements during unrestricted reaching to targets in ipsilateral and contralateral space. *Exp Brain Res*, 60, 159-178.
- Fitts, P. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, 47, 381-391.
- Fitts, P., & Peterson, J. (1964). Information capacity of discrete motor responses. *Journal of Experimental Psychology*, 67 (2), 103-112.
- Foxe, J., Wylie, G., Martinez, A., Schroeder, C., Javitt, D., Guilfoyle, D., Ritter, W., & Murray, M. (2002). Auditory-somatosensory multisensory processing in auditory association cortex: an fMRI study. *J Neurophysiol*, 88, 540-543.
- Gentile, G., Petkova, V., & Ehrsson, H. (2011). Integration of visual and tactile signals from the hand in the human brain: an fMRI study. *J Neurophysiol*, 105, 910-922.
- Ghahramani, Z., Wolpert, D., & Jordan, M. (1997). Computational models for sensorimotor integration. In: *Self-organization, computational maps and motor control*. North Holland: Morasso PG, Sanguineti V. Amsterdam.
- Glickstein, M. (1992). The cerebellum and motor learning. *Curr. Opin. Neurobiol.*, 2, 802-806.
- Glickstein, M. (1993). Motor skills but not cognitive tasks. *Trends Neurosci.*, 16, 450-451.
- Goble, D., Noble, B., & Brown, S. (2010). Where was my arm again? memory-based matching of proprioceptive targets is enhanced by increased target presentation time. *Neuroscience Letters*, 481, 54-58.
- Goodale, M., Jakobson, L., & Keillor, J. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, 32, 1159-1178.

- Goodale, M., & Milner, A. (1992). Separate visual pathways for perception and action. *Trends Neurosci*, 15(1), 20-25.
- Goodale, M., Westwood, D., & Milner, A. (2004). Two distinct modes of control for object-directed action. *Prog Brain Res*, 144, 131-144.
- Gordon, J., Gilhardi, M., Cooper, S., & Ghez, C. (1994). Accuracy of planar reaching movements. II. Systematic errors resulting from inertial anisotropy. *Exp Brain Res*, 99, 112-130.
- Graziano, M. (1999). Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proc. Natl. Acad. Sci. USA*, 96, 10418-10421.
- Granziano, M., Cook, D., & Taylor, C. (2000). Coding the location of the arm by sight. *Science*, 290, 1782-1786.
- Greenstein, B., & Greenstein, A. (2000). *Color atlas of neuroscience: neuroanatomy and neurophysiology*. Germany: Library of Congress.
- Grefkes, C., Weiss, H., Zilles, K., & Fink, R. (2002). Crossmodal processing of object features in human anterior intraparietal cortex: an fMRI study implies equivalencies between humans and monkeys. *Neuron*, 35, 173-184.
- Hansen, S., Elliott, D., & Tremblay, L. (2007). Gender differences in discrete action following visual perturbation. *Perception*, 36, 268-287.
- Helbig, H., & Ernst, M. (2007). Optimal integration of shape information from vision and touch. *Exp Brain Res*, 179, 595-606.
- Heath, M., Westwood, D., & Binsted, G. (2004). The control of memory-guided reaching movements in peripersonal space. *Mot Control*, 8, 76-106.
- Hodges, N., Lyons, J., Cockell, D., Reed, A., & Elliot, D. (1997). Dand, space, and attentional asymmetries in goal-directed manual aiming. *Cortex*, 33, 251-269.
- Horak, F., Hery, S., & Shumway-Cook, A. (1997). Postural perturbations: new insights for treatment of balance disorders. *Physical Therapy*, 77 (5), 517-533.
- Horak, F., Nashner, L., & Diener, H. (1990). Postural strategies associated with somatosensory and vestibular loss. *Exp Brain Res*, 82, 167-177.
- James, T., Humphrey, G., Gati, J., Servos, P., Menon, R., & Goodale, M. (2002), Haptic study of three-dimensional objects activates extrastriate visual areas. *Neuropsychologia*, 40, 1706-1714.

- Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements*. Oxford, UK: Clarendon Press.
- Jones, S., Cressman, E., & Henriques, D. (2009). Proprioceptive localization of the left and right hands. *Exp Brain Res*, 204(3), 373-383.
- Jones, S., Fiehler, K., & Henriques, D. (2010). Proprioceptive acuity varies with task, hand target, and when memory is used. *Lecture Notes in Computer Science*, 6192, 321-326.
- Jones, S., Fiehler, K., & Henriques, D. (2012). A task-dependent effect of memory and hand-target on proprioceptive location. *Neuropsychologia* (in press).
- Kalat, J. (2008). *Biological psychology*. (10th edition). Cengage: Belmont.
- Kandel, E., Schwartz, J., & Jessell, T. (2000). *Principles of neural science*. (4th edition). McGraw-Hill Professional: United States.
- Kauffman, T., Theoret, H., & Pascual-Leone, A. (2002). Braille character discrimination in blindfolded human subjects. *NeuroReport*, 13, 571-574.
- Koch, C. (2004). *The quest for consciousness: a neurobiological approach*. Colorado: Roberts and Company Publishers .
- Kröger, B., Kopp, S., & Lowit, A. (2009). A model for production, perception, and acquisition of actions in face-to-face communication. *Cogn Process*.
- Kuo, A. (2005). An optimal state estimation model of sensory integration in human postural balance. *J. Neural Eng*, S235-S249.
- Kurtz, L. (2006). *Visual perception problems in children with AD/HD, autism, and other learning disabilities: a guide for parents and professionals*. Jessica Kingsley Publishers: London.
- Lovelace, E. (1989). Vision and Kinesthesia in accuracy of hand movement. *Perceptual and Motor Skills*, 68, 707-714.
- Mahboobin, A., Loughlin, P., Redfen, M., & Sparto, P. (2005). Sensory reweighting in human postural control during moving-scene perturbations. *Exp Brain Res*, 167, 260-267.
- Martin, J. (2003). *Neuroanatomy: text and atlas*. (3rd edition). United States: McGraw-Hill Professional.
- Martuzzi, R., Murray, M., Michel, C., Thiran, JP., Maeder, P., Clarke, S., & Meuli, R. (2007). Multisensory interactions within human primary cortices revealed by BOLD dynamics. *Cerebral Cortex*, 17, 1672-1679.

- Milner, A., Paulignan, Y., Dijkerman, H., Michel, F., & Jeannerod, M. (1999). A paradoxical improvement of misreaching in optic ataxia: new evidence for two separate neural systems for visual localization. *Pro Biol Sci*, 266, 2225-2229.
- Monaco, S., Kroliczak, G., Quinlan, D., Fattori, P., Galletti, C., Goddalle, M., & Culham, J. (2010). Contribution of visual and proprioceptive information to the precision of reaching movements. *Exp Brain Res*, 202, 15-32.
- Molholm, S., Ritter, W., Murraray, M., Javitt, D., Schroeder, C., & Foxe, J. (2002). Multisensory auditory-visual interactions during early sensory processing in humans: a high-density electrical mapping study. *Brain Res Cogn Brain Res*, 14, 115-128.
- Moller, A. (2006). *Neural plasticity and disorders of the nervous system*. Champaign: Cambridge University Press.
- Mon-Williams, M., Wann, J., Jenkinson, M., & Rushton, K. (1997). Synaesthesia in the normal limb. *Proc Biol Sci*, 264(1384), 1007-1010.
- Naumer, M., Ratz, L., Yalachkov, Y., Polony, A., Doehrmann, O., van de Ven, V., Muller, N., Kaiser, J., & Hein, G. (2010). Visuohaptic convergence in a corticocerebellar network. *European Journal of Neuroscience*, 31, 1730-1736.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9, 97-113.
- Oliveira, C., Medeiros, I., Greters, M., Frota, N., Lucato, L., Scaff, M., & Conforto, A. (2011). Abnormal sensory integration affects balance control in hemiparetic patients within the first year after stroke. *Clinics (Sao Paulo)*, 66(12), 2043-2048.
- Paillard, J., Brouchon, M. (1968). Active and passive movements in the calibration of position sense. In: *The neuropsychology of spatially oriented behavior* (Freedman SJ, ed), pp 37-55. Homewood, IL: Dorsey.
- Peelen, M., & Downing, P. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, 8, 636-648.
- Pekkola, J., Ojanen, V., Autti, T., Jaaskelainen, I., Mottonen, R., Tarkiainen, A., Sams, M. (2005). Primary auditory cortex activation by visual speech: an fMRI study at 3 T. *Neuroreport*, 16, 125-128.
- Prablanc, C., Echallier, J., Komilis, E., & Jeannerod, M. (1979). Optimal response of the eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. *Biological Cybernetics*, 35, 113-124.

- Rohr, L. (2006). Upper and lower limb reciprocal tapping: evidence for gender biases. *Journal of Motor Behavior*, 38, 15-17.
- Rosdahl, C., & Kowalski, M. (2007). *Textbook of basic nursing*. (9th edition). Philadelphia: Lippincott Williams & Wilkins.
- Rossetti, Y. (1998). Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Conscious Cogn*, 7, 520-558.
- Sadato, N., Pascual-Leone, A., Grafman, J., Lbanez, V., Deiber, M.P., Dold, G., & Hallett, M. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. *Nature*, 380, 526-528.
- Saito, D., Okada, T., Morita, Y., Yonekura, Y., & Sadato, N. (2003). Tactile-visual cross-modal shape matching: a functional MRI study. *Cognitive Brain Research*, 17, 14-25.
- Sarlegna, F., & Sainburg, R. (2007). The effect of target modality on visual and proprioceptive contributions to the control of movement distance. *Exp Brain Res*, 176, 267-280.
- Sathian, K., Zangaladze, A., Hoffman, M., & Grafton, T. (1997). Feeling with the mind's eye. *NeuroReport*, 8, 3877-3881.
- Scalha, B., Miyasaki, E., Lima, N., & Borges, G. (2011). Correlations between motor and sensory functions in upper limb chronic hemiparetics after stroke. *Arq Neuropsiquiatr*, 69(4), 624-629.
- Scheiman, M. (2002). *Understanding and managing vision deficits: a guide for occupational therapists*. (9th edition). Thorofare: Slack Incorporated.
- Serwe, S., Kording, K., & Trommershauser, J. (2011). Visual-haptic cue integration with spatial and temporal disparity during pointing movements. *Exp Brain Res*, 210, 67-80.
- Smeets, J., Van Den Dobbelen, J., De Grave, D., van Beers, R., & Brenner, E. (2006). Sensory integration does not lead to sensory calibration. *Proc Natl Acad Sci USA*, 103 (49), 18781-18786.
- Sober, S., & Sabes, P. (2003). Multisensory integration during motor planning. *Journal of Neuroscience*, 23(18), 6982-6992.
- Sober S., & Sabes, P. (2005). Flexible strategies for sensory integration during motor planning. *Nature Neuroscience*, 8(4), 490-497.
- Soderquist, D. (2002). *Sensory processes*. California: Sagw Publications Inc.
- Soechting, J., & Flanders, M. (1989). Sensorimotor representations for pointing to targets in three-dimensional space. *Journal of Neurophysiology*, 62(2), 582-594.

- Squatrito, S., Raffi, M., Maioli, M., & Battaglia-Mayer, A. (2001). Visual motion responses of neurons in the caudal area PE of macaque monkeys. *The Journal of Neuroscience*, *21*(4), 1-5.
- Starr, C., & Mcmillan, B. (2008). *Human Biology*. (8th edition). USA: Cengage Learning.
- Tideiksaar, R. (1997). *Falling in old age*. (2nd ed.). New York: Springer Publishing Company.
- Valentinuzzi, M. (1980). *The organs of equilibrium and orientation as a control system*. Amsterdam: Harwood Academic Publishers.
- van Beers, R., Sittig, A., & van Der Gon, D. (1996). How humans combine simultaneous proprioceptive and visual position information. *Exp Brain Res*, *111*, 253-261.
- van Beers, R., Sittig, A., & van Der Gon, J. (1998). The precision of proprioceptive position sense. *Exp Brain Res*, *122*, 367-377.
- van Beers, R., Sittig, A., & van Der Gon, D. (1999). Integration of proprioceptive and visual position-information: An experimentally supported model. *Journal of Neurophysiology*, *81*, 1355-1364.
- van Beers, R., Wolpert, D., & Haggard, P. (2002). When feeling is more important than seeing in sensorimotor adaptation. *Curr Biol*, *12*, 834-837.
- van Boven, W., Hamilton, H., Kauffman, T., Keenan, P., & Pascual-Leone, A. (2000). Tactile spatial resolution in blind Braille readers. *Neurology*, *54*, 2230-2236.
- Velay, J., & Benoit-Dubrocard, S. (1999). Hemispheric asymmetry and interhemispheric transfer in reaching programming. *Neuropsychologia*, *37*, 895-903.
- Wann, J., & Ibrahim, S. (1992). Does limb proprioception drift? *Exp Brain Res*, *91*, 162-166.
- Warren, D., & Schmitt, T. (1978). On the plasticity of visual-proprioceptive bias Effects. *J Exp Psychol Hum Percept Perform*, *4*(2), 302-10.
- Westwood, D., Health, M., & Roy, E. (2001). The accuracy of reaching movements in brief delay conditions. *Canadian Journal of Experimental Psychology*, *55*(4), 304-310.
- Westwood, D., & Goodale, M. (2003). Perceptual illusion and the realtime control of action. *Spat Vis*, *16*, 243-254.
- Westwood, D., Roy, E., & Health, M. (2003). No evidence for accurate visuomotor memory: systematic and variable error in memory-guided reaching. *Journal of Motor Behavior*, *35*(2), 127-133.

Weinrich, M., & Wise, S. (1982). The premotor cortex of the monkey. *The Journal of Neuroscience*, 2, 1329-1345.

Woodworth, R. (1899). The accuracy of voluntary movement. *Psychol. Monogr.*, 3 (3), 1-114.

Appendix

Edinburgh Handedness Inventory¹

Name: _____

Date: _____

Please indicate with a check (✓) your preference in using your left or right hand in the following tasks.

Where the preference is so strong you would never use the other hand, unless absolutely forced to, put two checks (✓✓).

If you are indifferent, put one check in each column (✓|✓).

Some of the activities require both hands. In these cases, the part of the task or object for which hand preference is wanted is indicated in parentheses.

Task / Object	Left Hand	Right Hand
1. Writing		
2. Drawing		
3. Throwing		
4. Scissors		
5. Toothbrush		
6. Knife (without fork)		
7. Spoon		
8. Broom (upper hand)		
9. Striking a Match (match)		
10. Opening a Box (lid)		
Total checks:	LH =	RH =
Cumulative Total	CT = LH + RH =	
Difference	D = RH - LH =	
Result	R = (D / CT) × 100 =	
Interpretation: (Left Handed: R < -40) (Ambidextrous: -40 ≤ R ≤ +40) (Right Handed: R > +40)		

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