2012

Manual asymmetries in the kinematics of reach-to-grasp actions

Flindall, Jason W.

Lethbridge, Alta. : University of Lethbridge, Dept. of Kinesiology and Physical Education, c2012

MANUAL ASYMMETRIES IN THE KINEMATICS OF REACH-TO-GRASP ACTIONS

JASON FLINDALL
Bachelor of Science (Biology), Dalhousie University, 2008

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

MASTER OF SCIENCE

Department of Kinesiology and Physical Education
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

DEDICATION

For Dorothy and Don, who

would have enjoyed this.

ABSTRACT

The purpose of this thesis was to investigate manual asymmetries in the reach-to-grasp movement based on two hypotheses: 1) manual asymmetries are resultant from asymmetries in the dorsal vision-for-action system; and 2) manual asymmetries are contingent on task difficulty. Participants grasped glasses of water under different visual-feedback conditions. Demand was manipulated by varying the level of the water contained in the glass. Hand asymmetries of the reach-to-grasp movement were studied through kinematic analyses. Visual feedback availability and task demand affected all kinematic measures. Manual asymmetries were found in peak velocity, movement time, and variability of maximum grip aperture. Consistent with reach-to-point literature, reach-to-grasp actions were faster and more accurate when performed with the right hand and when guided by the dorsal vision-for-action system. The results of the thesis provide support for a theory of left-hemisphere specialization for the visual control of actions.

ACKNOWLEDGEMENTS

There are many people to whom I owe a debt of gratitude for their help in producing this thesis. I would like to thank my supervisor, Dr. Claudia Gonzalez, who brought me in as her student and helped me at every stage of the process. Her insight, expertise, and friendship have been invaluable.

None of the work presented in the following pages would have been possible without the help of my colleagues. Dr. Jon Doan, who (along with Dr. Gonzalez) designed Experiment 1; David Sessford, who was not only my tech support specialist, but also a great friend; Dr. Natalie de Bruin-Nutley, who helped me navigate life as a grad student; Shane Hudson, who helped with data collection and always lent an ear; and finally my lab mates, Kayla Stone, Devon Bryant, Nicole Netelenbos, and Kelly Mills, who made the Brain in Action lab a fun place to spend my days.

I would like to thank my committee members, Dr. Lesley Brown, Dr. Jon Doan, and Dr. Robbin Gibb for their feedback and support.

I am grateful to the University of Lethbridge Graduate Student Association, the QE II Scholarship committee, and the Natural Sciences and Research Engineering Council (NSERC) for funding my degree.

Special thanks go to Brenda Nixon, who not only keeps the Kinesiology Department from imploding, but is also a good friend.

Finally, I would like to thank my family. My parents, Stephen and Laurie, who always supported and encouraged me, emotionally and financially, to follow my heart. My brothers, Aaron and Scott, and my sisters, Joanne and Ange, who were always ready to help me unwind and talk about nothing. My best friend, Jara, who has put up with my geekiness for years, I couldn’t have done this without her. From the bottom of my heart: Thank You.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
A	Amplitude
aIPS	Anterior Intraparietal Sulcus
D	Depth
DPt	Deceleration Phase Duration
ES	Extra-striate Region
fMRI	Functional Magnetic Resonance Imaging
H	Height
ID	Index of Difficulty
IRED	Infra-red LED
LED	Light Emitting Diode
LGN	Lateral Geniculate Nucleus
MGA	Maximum Grip Aperture
MGAt	Time of Maximum Grip Aperture
MT	Movement Time
Pn	Pulvinar Nucleus
PV	Peak Velocity
RT	Reaction Time
SC	Superior Colliculus
SPOC	Superior Parieto-occipital Cortex
V1	Primary Visual Cortex (aka Striate Cortex)
vMGA	Variability of Maximum Grip Aperture
W	Width

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 1: Introduction and Literature Review

Introduction

Visuomotor actions can be defined as the sequence of body movements that begin with a visually perceived stimulus and intent to interact with that stimulus, and result in the correct sequence of motor actions to accurately execute that intent. In other words, they are motor actions driven by visual stimuli. Consider picking an apple from a tree. In order to perform this task, you must first perceive and recognize the apple as an edible object, ripe for picking. The location of the apple must be explicit within your own frame of reference, so that a motor plan can be formed that will ultimately result in you plucking the apple from where it hangs. Knowing where the apple is in allocentric terms (i.e., world centered terms, or with reference to the apple's immediate environment) is not nearly as important as knowing where the apple is in egocentric terms (i.e., with reference to you, the actor). That the apple is hanging high above the ground and near the end of a branch is immaterial for visuomotor actions; it is more relevant to know that the apple is just above your head, in front of you, and slightly to your left. With such egocentric location information, you may form a motor plan that normally results in a smooth, accurate reach, with well-timed and appropriately scaled hand shaping leading to the grasp of the apple. The grasp is followed by a smooth transport to the basket. Visuomotor actions may involve the use of tools (i.e., "praxis"), or, as in the example above, they may be performed with an empty hand. They may be as simple as pointing at a visual stimulus, or as complex as intercepting a rapidly moving target. The human visual system has adapted to recognize and evaluate innumerable stimuli, and can aid in the production of a nearly infinite combination of motor responses.

All input to the human visual system begins at the retina. Light entering the eye causes cells on the retina to fire, producing electrical signals that are relayed to the occipital cortex via the optic nerve (Kolb & Whishaw, 2006). Visual signals cross to the contralateral hemisphere at the optic chiasm, such that input from the right visual hemifield is initially processed in the left hemisphere, and input from the left visual hemifield is processed in the right hemisphere. While visual information is processed initially in the striate region of the occipital cortex (area V1, a.k.a. the primary visual cortex), visual processing goes beyond the striate cortex, into other visual areas, including the temporal and parietal lobes. These visual processing regions are specialized for different aspects of the visual field. Blindness, rather than being absolute, is often described in limited terms; patients may experience colour blindness, motion blindness, pattern blindness, or light blindness, among many other types of partial blindness. Such forms of blindness do not always coincide, and blindness in one aspect often does not necessarily affect perception in the other aspects of vision. For example, a person suffering from facial blindness might have perfect vision in terms of edge detection or colour perception. The fact that such selective blindness can be present without damage to the eye implies that different features of the visual scene are processed differently in the brain, and that it is damage to these specialized processing regions that result in selective blindness (Kolb & Whishaw, 2006). Thus, vision processing in humans is not serial; instead, multiple systems are acting in parallel to bring us our visual representation of the world.

Two Visual Systems

Schneider's Model – Two Visual Systems for Orientation and Perception

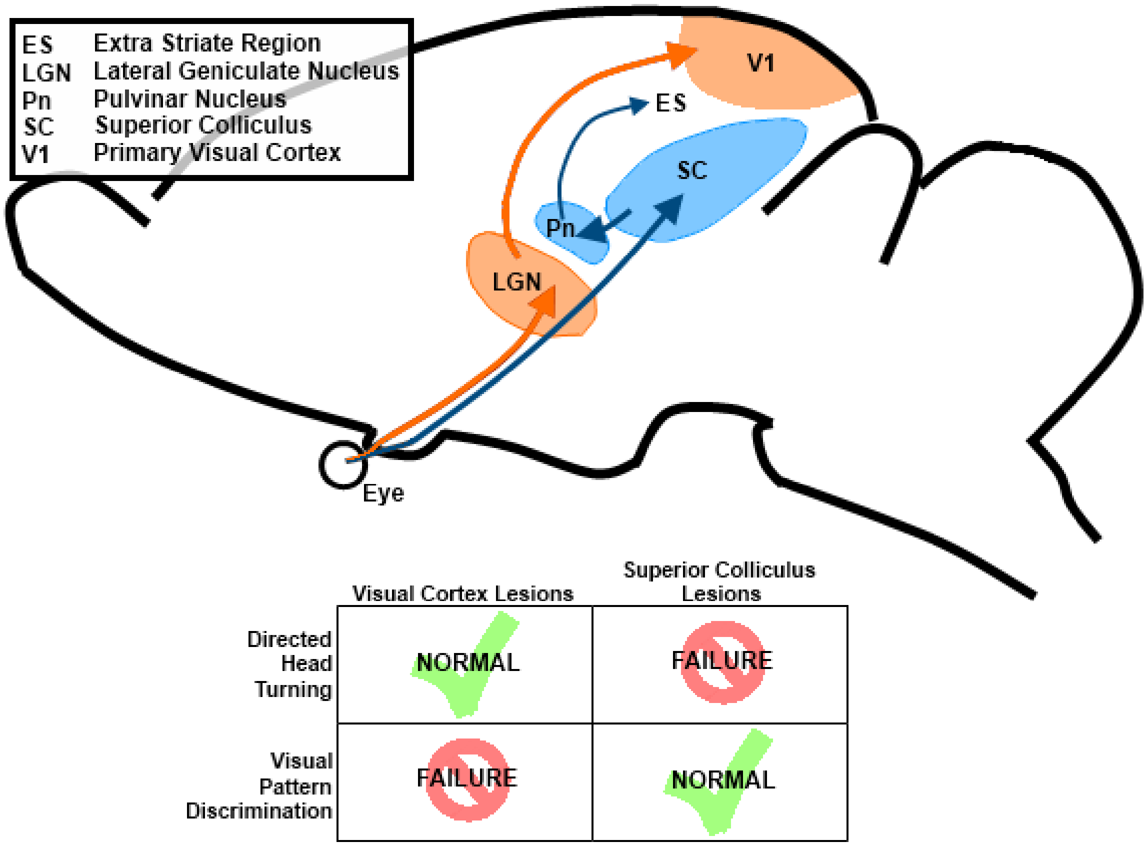
The idea of different systems processing visual information was first put forth by Schneider (Schneider, 1967; Schneider, 1969). By using hamsters, Schneider (1967) differentiated visual streams for spatial orientation and pattern discrimination. To do this he took advantage of the normal, nearly insatiable appetite hamsters have for sunflower seeds. If a researcher presents a seed near the hamster's head, then the hamster will orient itself toward that seed before taking it and storing it in its cheek pouches. If the hamster is totally blind (i.e., if the hamster has no eyes), then the seed must first touch its whiskers before the hamster will orient toward it. Following up on findings involving other animals (Flourens, 1847), Schneider (1967) observed that after complete bilateral ablations of the superior colliculi (which lies outside of the primary visual pathway from the retina to visual cortex), hamsters behaved as if they were completely blind when presented with seeds. Rather than orienting towards food presented in their visual field, they would not react until the seed touched their whiskers. That is, the hamsters relied on touch and olfaction (rather than vision) to find food, even though their primary visual pathway remained intact. He also noticed that the freezing response (the response-adaptation to a fear stimulus) could be triggered in these ablated animals by quick overhead movements – movement they could only sense visually. Thus, they were not blind in the global sense, but rather simply unable to orient toward visually presented objects.

Meanwhile, Schneider (1967) had a second group of hamsters to whom he had applied visual cortex lesions. This second group of hamsters would still orient themselves toward presented food; in fact, informal observations showed no neurological deficits whatsoever. In other animals (e.g., cats, dogs, and monkeys), this type of lesion normally resulted in "pattern blindness," an inability to discriminate between visual patterns (Kluver, 1942). In order to test for pattern recognition deficits, Schneider (1967) trained both groups of hamsters in a behavioural task.

In this task, a thirsty hamster was placed in a starting area from which two corridors extended. At the end of each corridor was a hinged door. One of the doors was perpetually locked, while behind the other was a drink of water. The doors were marked with cards, designed to test for discrimination ability. Black or white cards, vertically- or horizontally-striped cards, and speckled or striped cards were used. If the hamster pushed on the locked door (regardless of whether or not it inspected it), the researchers recorded the trial as an error. Normal hamsters learn quickly to discriminate between the doors; they may inspect both doors, but they only try to open the door marked with the pattern labelling it as unlocked. Hamsters with superior colliculi lesions also learn to discriminate between the patterns; Schneider (1967) observed some early white/black discrimination problems in some hamsters, but these difficulties did not persist in later trials. Hamsters that had experienced visual cortex lesions could not discriminate between patterns on the cards; they performed no better than chance on the door choice task.

With these experiments, Schneider dissociated two distinct mechanisms for visual processing: first, the superior colliculi was found to be critical for locating and orienting toward novel stimuli; and second, the visual cortex is critical for pattern discrimination. Ablating one of these areas did not affect the function of the other, thus the two systems were dissociated both anatomically and functionally. The first system begins at the retina and connects through the superior colliculus in the tectum of the midbrain to the pulvinar nucleus in the thalamus, which in turn provides input to extrastriatal cortices (Fig. 1). Because of this route, it is called the tectopulvinar system. The second pathway is called the geniculostriate pathway because it connects the retina to the striate cortex by way of the lateral geniculate nucleus of the thalamus (Fig. 1). This second pathway has become the dominant pathway in primates (including man), and has taken over the spatial function of the tectopulvinar pathway. The tectopulvinar system has in turn become responsible for orienting the gaze toward visual stimuli, particularly light in the periphery (Zihl & von Cramon, 1979).

In primates, the geniculostriate pathway feeds two visual streams, as identified by Mishkin and Ungerleider (1982) a decade later.



	Visual Cortex Lesions	Superior Colliculus Lesions
Directed Head Turning	NORMAL ✓	FAILURE
Visual Pattern Discrimination	FAILURE	NORMAL ✓

Figure 1 - Tectopulvinar (blue) and geniculostriate (orange) pathways in a rodent brain. Adapted from (Schneider, 1967). Insert: results of lesion studies showing double dissociation of the two pathways.

Mishkin's Model – Two Cortical Pathways for Object and Spatial Vision

In primates, the tectopulvinar pathway is functionally less relied upon than the geniculostriate system (Mishkin & Ungerleider, 1982; Mishkin, Ungerleider, & Macko, 1983). By studying primates, Mortimer Mishkin identified two extrastriatal visual streams arising from the geniculostriate system.

Mishkin knew from previous studies in which the visual cortex of the monkey was first described (Chow, 1951; Ettlinger & Wegener, 1958) that the visual system in monkeys extends beyond the striate cortex, into the parietal and temporal lobes. The extent of these cortical visual areas was unknown, however, except in broad and often contradictory terms (Iwai & Mishkin, 1969). In his attempts to delineate the visual system, Mishkin realized that the extra striate visual areas could be separated not only anatomically, but functionally as well.

Mishkin performed lesions on two groups of Macaque monkeys. The first group received lesions in the inferior temporal cortex (Iwai & Mishkin, 1969), and the second received lesions in the parieto-preoccipital cortex (Mishkin & Ungerleider, 1982). He tested both groups' post-operative visual abilities using modified versions of the Wisconsin General Test[1] (Fig. 2).

The first test he used was a pattern discrimination task. The food wells were marked with two interchangeable placards. The positive card (a black plus sign on a white background) marked the well containing a food reward, while a negative card (a black outline of a square on a white background) marked an empty well. A monkey is said to have learned this task when it

---

[1] The Wisconsin General Testing apparatus is a cage facing two (or more) food wells. These wells are separated from the cage by a removable opaque screen. The researcher places food in one of the wells, which the monkey can access once the screen is removed. The researcher marks one of the wells somehow, and the monkey must figure out which well contains food based on the manner in which the researcher has marked the wells.

correctly chooses the positively marked well in 90 of 100 consecutive trials. Normal monkeys are able to learn this task quickly, in less than 200 trials. The first group of monkeys (those with inferior temporal cortex lesions) have a very difficult time learning this task, and after 1000+ trials are still unable to distinguish between the patterns on the placards. The monkeys with parieto-preoccipital lesions, however, have no difficulty distinguishing between the cards, and learn the task as quickly as healthy, non- ablated monkeys (Fig. 2).

The second task was a landmark discrimination task, in which the well containing food is marked by the presence of a blank cylinder. During the first trials, the cylinder is touching the well containing food, but as the monkey learns, the cylinder is moved further and further away. In the later trials, the cylinder is 5 cm from the well containing food, and 20 cm from the empty well. A monkey has learned this task when he correctly chooses the well 5 cm from the cylinder in 90 of 100 consecutive trials. Again, normal monkeys learn this task quickly, in less than 200 trials. Monkeys with inferior temporal cortex lesions also have little difficulty learning this trial, and are not significantly impaired compared to controls. The parieto-preoccipitally ablated monkeys, however, were significantly impaired in their learning of this task, and after 800+ trials were still unable to consistently pick the correct well (Fig. 2).

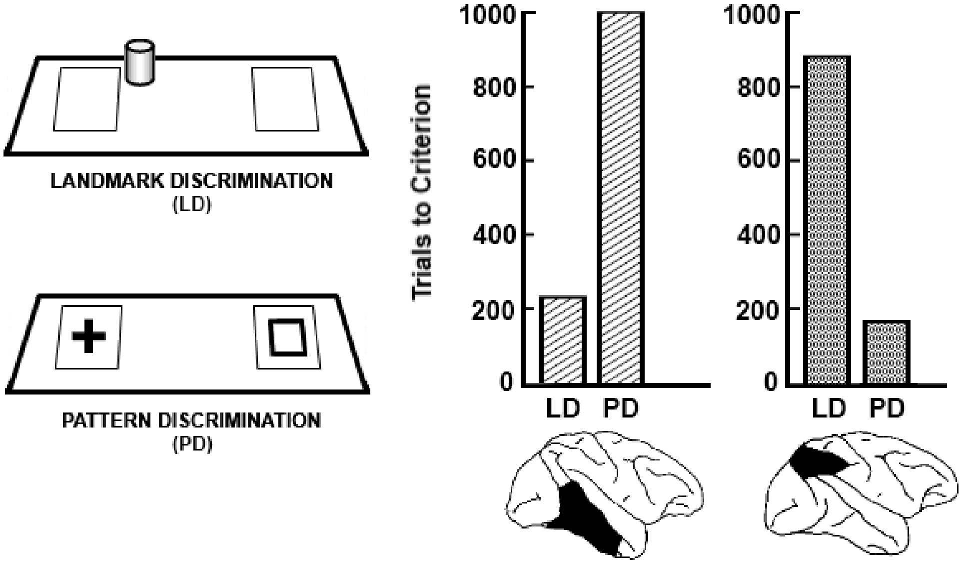


Figure 2 – Results of the Wisconsin General Tests run by Iwai and Mishkin (1969) and Mishkin and Ungerleider (1982). Parieto-preoccipital lesions result in an inability to learn a landmark discrimination task, but no deficits in learning a pattern discrimination task. Inferior temporal lesions result in difficulties learning a pattern discrimination task, but do not affect aptitude for learning a landmark discrimination task. (Modified from Iwai and Mishkin (1969) and Mishkin and Ungerleider (1982)).

Using these two tasks, Mishkin identified two visual streams arising from the primary visual cortex; a ventral stream (which begins in V1 and connects through V2, V3 and V4 before running ventrally into the inferior temporal cortex), which enables the visual identification of objects, and a dorsal stream (starting in the striate cortex and running through V2 into the posterior parietal lobe) which allows for the visual localization of objects. This was the first time these two functions were attributed to streams with a common striate cortex origin, rather than from systems diverging in the midbrain. Because of their functional roles in vision, Mishkin et al. referred to these pathways as the ventral 'what' pathway, and the dorsal 'where' pathway (Mishkin, Ungerleider, & Macko, 1983).

Goodale and Milner’s Model – Separate Visual Pathways for Perception and Action

Goodale and Milner (1992) proposed some modifications to Mishkin’s two cortical pathways theory. First, they corrected the origins of both the dorsal and ventral systems. Where Mishkin et al. (1983) said that the two streams first diverged in the primary visual cortex, Goodale and Milner pointed out that the distinction actually begins as early as the optic nerve (Fig. 3).

One type of retinal ganglion cell, known as P-cells, terminates exclusively in the parvocellular layers of the LGN (layers 3, 4, 5 and 6), while another type of ganglion cell, M-cells, feed into the magnocellular layers of the LGN (layers 1 and 2). The parvocellular layers are typically associated with the ventral stream, as they respond primarily to colour and changes in fine detail and feed into area V4 (which in turn provides primary input to the ventral stream). The M-cells respond to motion and are very good at edge detection. This, combined with their fast response rates relative to P-cells, mean that they are ideally suited for dorsal stream processing (which, in order to accurately represent movement, requires constant and up-to-date input from the visual field). Indeed, M-cells innervate area MT (middle temporal area), which provides major visual input to the dorsal stream.

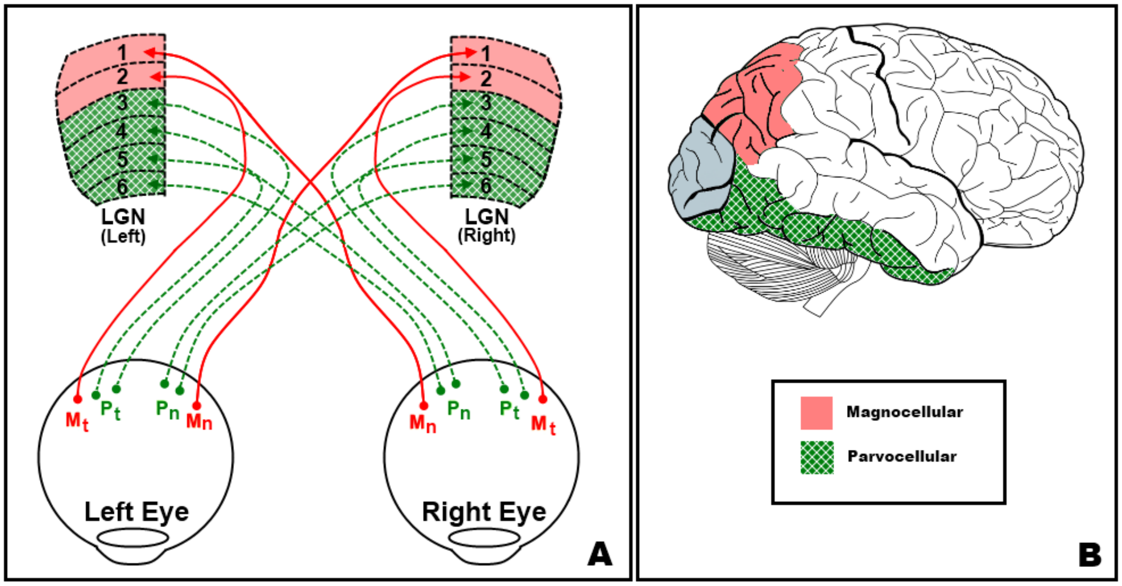


Figure 3 - *A*: Magnocellular (solid) and parvocellular (hatched) pathways showing output from the retina to their respective layers of the lateral geniculate nuclei. Adapted from Meissirel et al. (1997). *B*: Primary magnocellular (solid) and parvocellular (hatched) output to dorsal and ventral regions, respectively. Adapted from (Wikimedia Foundation, Inc., 2012)

Second, contrary to Mishkin's original model, the two streams are not completely separate and independent. The magnocellular and parvocellular layers are not exclusively dorsal and ventral, as there is some parvocellular input to area MT and some magnocellular input to V4 in the parietal lobe. Even after the divergence in the striate cortex, the dorsal stream has reciprocal connections to the ventral stream through superior temporal vision areas, as well as through the middle temporal sensory areas (Boussaoud, Ungerleider, & Desimone, 1990). Goodale and Milner (1992) noted this complex interaction between the dorsal and ventral streams and suggested that it makes more sense to focus on the output requirements of the two streams than on the characteristics of their input. That is, researchers should not worry so much about where information travels downstream from V1, and focus instead on what each terminal area is responsible for processing (Goodale & Milner, 1992). This perspective makes sense when looking at the visual streams from an evolutionary viewpoint as well as one for simplicity's sake. Along evolutionary lines, it is reasonable to assume that highly selective processing regions would have evolved to fit the various uses for vision (Goodale, 1988). For example, primary selective pressures surrounding the search for food and the avoidance of predators likely shaped the dorsal stream 'vision-for-action' functions, which do not require conscious perception to be effective (Milner & Goodale, 2007). The ventral stream's 'vision-for-perception' allows for more complex planning, communication, and recall, which in turn allows for more adaptive and complex behaviours. Because of this complexity, it likely did not mature until a more recent time in our evolutionary history (Goodale, Kroliczak, & Westwood, 2005).

In addition to these anatomical distinctions, Goodale and Milner also summarised more than 20 years of double-dissociation studies[2] supporting and shaping the two visual streams theory. They noted that patients with damage to the ventral stream often have difficulties recognizing or describing visual stimuli, whereas dorsal stream damage may lead to complications with object interaction.

Goodale and Milner describe several case studies differentiating disorders resulting from damage to the visual streams. Patients suffering from visual form agnosia, a disorder which follows ventral stream damage, cannot recognize shape, size, or orientation of objects, be they real or drawn (Kolb & Whishaw, 2006). Despite their impairment, some such patients can still guide and preshape their hands to perform remarkably accurate grasping motions to real targets. Patient D.F. (Milner, et al., 1991) suffered from bilateral lesions to the lateral occipital region, critically damaging her ventral stream functions but leaving her dorsal stream function

---

[2] In neuroscience, dissociation studies are experiments designed to establish which brain regions control which functions. By showing that lesions to a region A will negatively affect function X, but not function Y, scientists can show with some certainty that region A is critical for function X, but irrelevant to function Y. Double-dissociation studies take this one step further by finding region B, lesions to which will disrupt function Y, leaving function X unaffected. Double-dissociation studies require both specific behavioural tests, and highly localised lesions to be considered convincing.

unharmed. When asked to perform certain behavioural tasks, she could not differentiate between two wooden blocks presented in front of her, performing no better than chance when asked which block was larger or smaller. Similarly, when asked to estimate the size of a block with her fingers, her estimations bore no relation to the actual size of the block and were extremely variable between trials. When D.F. was asked to reach out and pick up the same blocks, however, her hand accurately shaped to the same grips observed in healthy individuals. Her grip sizes scaled to the size of the target to which she was reaching. When given rotated stimuli, she could not verbally or manually describe their orientation, but when asked to reach for one she turned her hand to correctly accommodate its orientation from the very start of the reach (Goodale, Milner, Jakobson, & Carey, 1991).

Patient D.F. provided the first clear evidence that dorsal stream vision is completely unconscious. Unlike ventral stream vision, we are not cognizant of any of the visual information output from the posterior parietal cortex. Studies involving saccades (i.e., quick, ballistic eye movements (Purves, et al., 2012)) can show how the dorsal stream is active unconsciously in healthy individuals. Saccades only last a few hundredths of a second, during which time we are effectively blind; the brain selectively blocks visual processing during eye movements, such that we never perceive the motion of our own eyes (Dodge, 1900). By using target-shifting studies (where a reached-for target is moved slightly the instant a participant saccades), researchers have shown that even though participants are completely unaware that the target has moved, they still expertly adjust their reach to accommodate the change (Goodale, Pelisson, & Prablanc, 1986). Thus the ventral stream, which is blind during the saccade, is unable to process the movement of the target (and presumably attributes the shift as a relic of the saccade itself). The dorsal stream ‘recognizes’ the shift and adjusts its representation, which the motor system uses to change the path of the hand accordingly.

Visual disorders may also arise from damage to the dorsal stream. Patient V.K. suffered from bilateral parietal lobe damage causing a “profound disorder of spatial attention, gaze, and visually-guided grasping” (Jakobson, Archibald, Carey, & Goodale, 1991). Because the damage to her cortex was localised to her dorsal stream (leaving her ventral stream functions intact), she was able to effortlessly recognize line drawings of common objects, and name the objects themselves when presented, but was unable to pick up those same real objects. When reaching for small rectangular blocks of different sizes, she showed no grip aperture scaling from trial to trial, and her grasping showed far more grip aperture corrections than are typically present in a healthy individual’s movements. This patient’s disability demonstrates the dorsal stream’s function. Where her symptoms might appear to be purely motor, they in fact arise from dorsal stream lesions, underlining this region’s importance in processing information required for visuomotor actions.

Patients D.F. and V.K. were instrumental in showing that, contrary to what Mishkin, Ungerleider and Macko (1983) suggested, the dorsal stream is not limited to processing an object’s location; it also processes object size, shape, and orientation. It would seem that the primary function of the dorsal stream is to provide the motor system with visual information strictly tailored to guide behaviour (Goodale & Milner, 1992). Where Mishkin and Ungerleider (1982) refer to the ventral and dorsal streams as the ‘what’ and ‘where’ streams, Goodale and Milner modified this, referring to them as the ‘what’ and ‘how’ streams, respectively (Fig. 4).

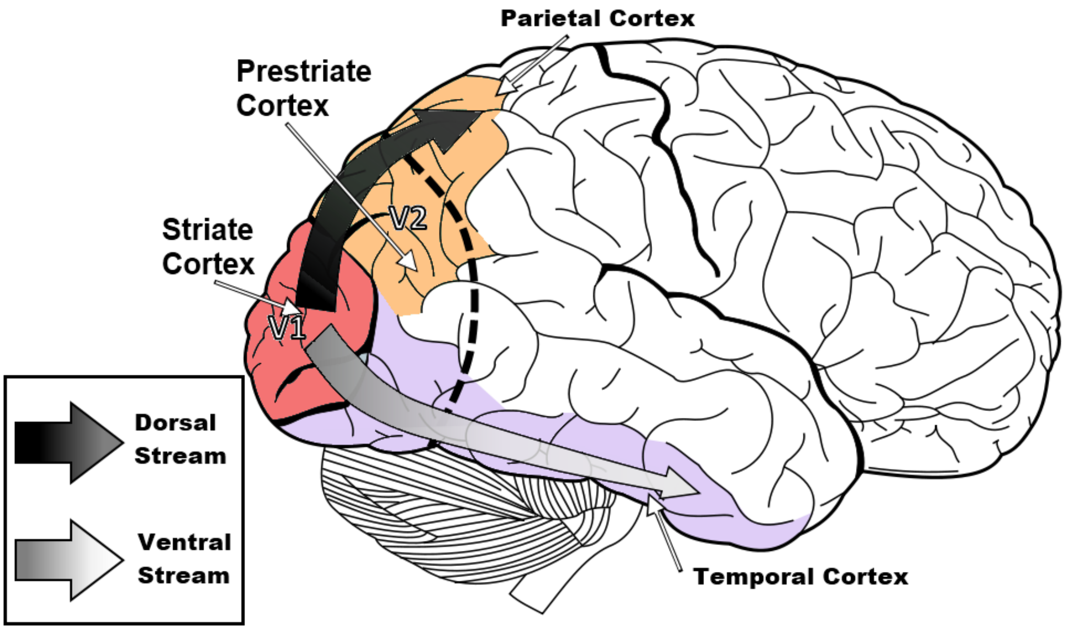


Figure 4 - The ventral ('what') and dorsal ('how') pathways as described by Goodale and Milner (1992). Adapted from Wikimedia Foundation, Inc., (2012)

The ventral stream is what we picture when we think of "vision"; its output is what we can consciously see and describe. This stream creates a mental interpretation of the world around us. Colour, relative size, texture, and shape are all processed in this region (Zeki, 1978). When we view an object, we create a mental representation of that object, and this representation is at least semi-permanent, becoming what we commonly refer to as memory. Because memories allow us to recognize the same object during subsequent viewings, the representation needs to be constant such that recognition can occur across different lighting conditions, from different angles, and from varying distances. Consider that an object viewed up close will occupy more space on the retinal field than the same object viewed from far away: if size inferred via retinal image information were recorded in the memory trace, it might make those two traces unrecognizable as representing the same object. Thus relative size (size in relation to nearby objects) becomes more important for recognizing objects, and absolute size and location are necessarily neglected. It is this ignorance that enables us to identify objects we see on television or computer screens – such images lack real 3-dimensional properties, but we can infer size based on our knowledge of other objects. Unfortunately, such inferences are not always reliable, further illustrating that our ventral stream is ill-suited for determining true size (Fig. 5). Regardless of its accuracy in discerning actual size, the ventral stream and temporal lobe are critical for both the formation and retention of memories (Goodale, Kroliczak, & Westwood, 2005; Mishkin, Ungerleider, & Macko, 1983).

Figure 5 - Ventral stream processing allows us to infer object size via perspective. Our inferences can be tricked, however, with the introduction of objects which do not conform to our expectations. In the above example, artists Theo Tveterås and Lars Marcus Ve use a giant coin to make common objects appear miniature when photographed. [Published in Scientific American (Size Illusions Trick the Brain, 2012)].

The dorsal stream processes visual input for the purpose of action, thus it is often referred to as the visuomotor system. This visual input is processed in a purely egocentric frame of reference, one where relative size is ignored in favour of absolute size, and position relative to nearby objects is eschewed for position relative to the body. In contrast with the ventral stream, the dorsal stream does not analyze location *with respect to* nearby objects, as an egocentric frame of reference is necessary for accurate motor plans. Tthe dorsal stream does not *ignore* nearby objects, however, when perceiving a target object; on the contrary, it constantly accounts for such objects as potential obstacles (or aids) to avoid (or use) when reaching and grasping (Striemer, Chapman, & Goodale, 2009). Finally, contrary to the ventral stream, the dorsal stream does not form permanent memories. Its representation is updated continuously, retaining information for less than 2 seconds (Hu, Eagleson, & Goodale, 1999). Our environments, including our presence within them, are rarely static, and as such any memories the dorsal stream could form would be useless as far as interaction is concerned. As a result, representations formed by the dorsal stream are in real-time, with real metrics, and in egocentric frames of reference (Heath & Binsted, 2007; Milner & Goodale, 2007). The two most common examples of actions produced via dorsal stream processing are reaching and grasping; they are described in the following section.

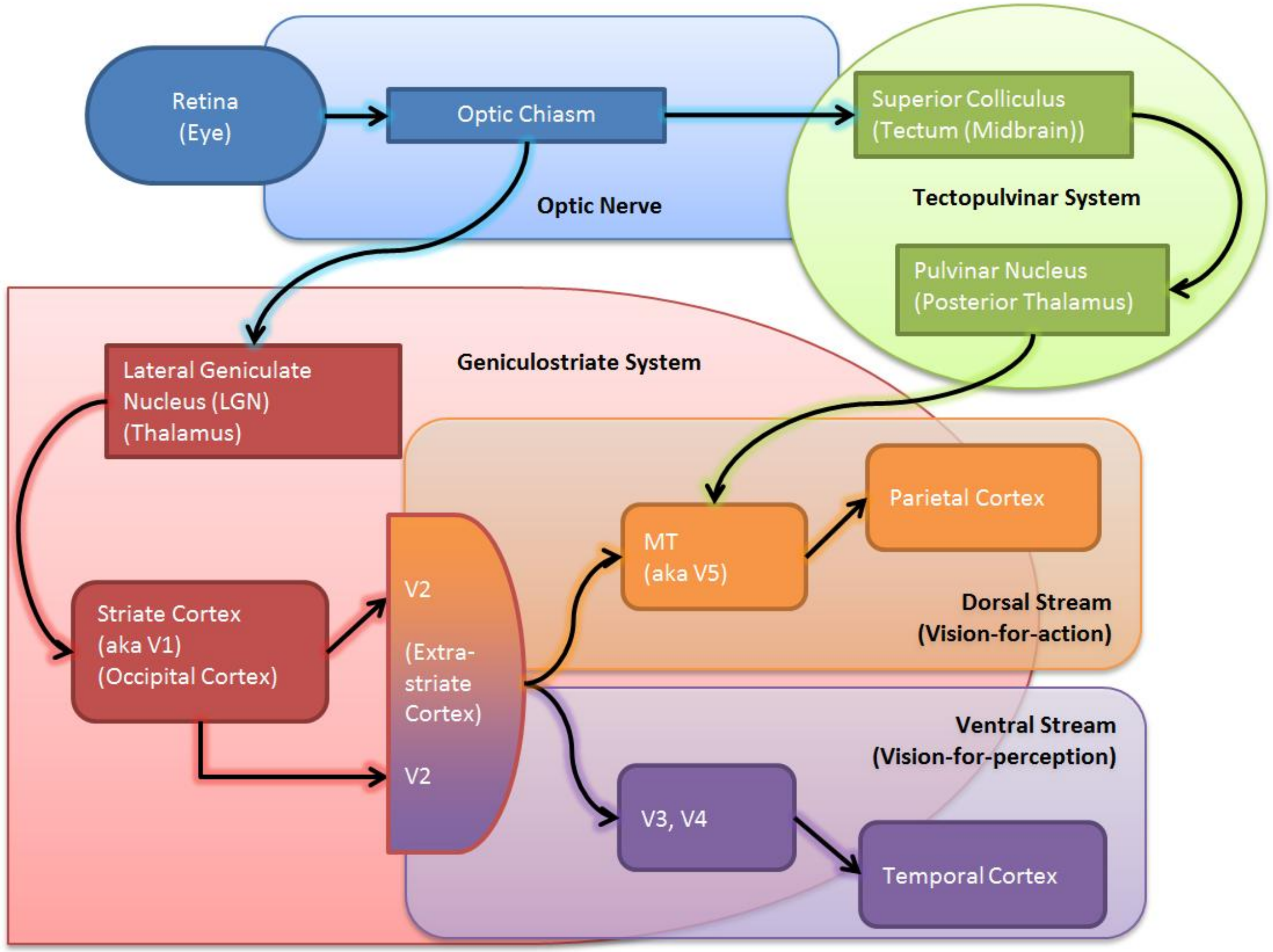


Figure 6 - Flow chart of the human visual system. Tectopulvinar and geniculostriate systems are labelled, as are the dorsal and ventral streams within the geniculostriate system. Sizes of structure boxes are not representative of their actual sizes.

The Visuomotor System

Almost 25 years ago, Jeannerod stated that prehension can be divided into two parts: a reaching component, and a grasping component (Jeannerod, 1986a). He based this conjecture on several observations. First, sensory systems do not detect objects; rather, they detect features of an object, and use those features to build a coherent representation of that object. With regards to prehension, such features can be split into two groups. ‘Intrinsic’ object features (such as size, shape, and colour) each activate a specific visual mechanism; that is, the visual neurones that respond to colour differences will not be the same neurones that fire in response to size differences, and vice versa. Intrinsic characteristics are objective properties of the object itself; they form the object’s identity. On the other hand, ‘extrinsic’ object characteristics are subjective, and exist entirely within a behavioural context. These are characteristics like orientation, and distance with respect to the observer. Jeannerod postulated that the extrinsic characteristics will drive the reaching component, and intrinsic characteristics will drive the grasping component of prehension.

Evidence for this reaching/grasping division comes from several sources. First, infants develop a rudimentary reaching movement as young as one week (von Hofsten, 1982), while grasping behaviour does not develop until 4 to 5 months later (Halverson, 1931; Sacrey, 2012). This discrete development implies a functional distinction between the reaching and grasping systems. Second, animal experiments show that monkeys have a similar developmental pattern wherein reaching accuracy develops sooner than grasping accuracy, and that by ablating cortical area 4 (Brodman’s area, within the primary motor cortex) in infancy, researchers could arrest the development of grasping movements through adulthood without interfering with the animal’s ability to reach (Passingham, Perry, & Wilkinson, 1978). Third, split-brain studies show that if you have a split-brain monkey reach for a moving target while vision is restricted to one eye, he can do so accurately, and intercept the target with either hand. However, during the same motion, the split-brain monkey is unable to accurately grasp the target with the hand ipsilateral to the unrestricted eye (i.e., block vision to the left eye, and the right hand can no longer grasp; block the right eye’s vision, and the left hand can no longer grasp) (Trevarthen, 1968). This implies that the reaching aspect of prehension is unaffected by the split, but the grasping component of prehension is governed by visuomotor systems independent to each hand (Brinkman & Kuypers, 1973). Finally, fMRI studies show selective activation in the anterior intraparietal sulcus (aIPS) when participants grasp a target (Binkofski, et al., 1998; Frey, Vinton, Norlund, & Grafton, 2005), and selective activation of the superior parieto-occipital cortex (SPOC) when determining if an object is within reach (Gallivan, Cavina-Pratesi, & Culham, 2009).

Reaching

Reaching, the act of stretching one's arm with the intent of touching or pointing at an object at some distance from the body, is a visuomotor behaviour found in many species. The kinematics[3] of the reaching motion in humans have been studied since the latter part of the 19th century. Woodworth (1899) notably divided the reaching movement into two phases; an initial impulse phase, and a current control phase. The initial impulse phase is ballistic, and planned in advance of movement initiation, where the current control phase is later in the movement (after peak velocity has been reached) and is under visual control (Elliott, Binsted, & Heath, 1999). It is during the current control phase that reaches decelerate, and any necessary corrections to the original movement plan are made (Elliott, Binsted, & Heath, 1999). Numerous studies have shown that the kinematic measurements of the reach (i.e., reaction time (RT), movement time (MT), peak velocity (PV), time of peak velocity (PVt), and deceleration phase duration (DPt)) are affected by both intrinsic and extrinsic target characteristics, and that these kinematics are also influenced by the visual feedback availability of the reaching hand, the limb, and the target, throughout the reaching movement.

Fitts' Law

Woodworth (1899) also studied the effects of speed on end-point accuracy of unimanual aiming movements, and found that an increase in speed precipitated a decrease in accuracy. In 1954, this relationship was quantified by Fitts, who determined that movement time can be predicted by the difficulty (accuracy requirement and distance to be travelled) of a movement (Fitts, 1954). This relationship, which has since come to be known as Fitts' Law, is governed by the following equation:

---

[3] Kinematics are features describing the motion of objects, without reference to either mass or the forces that cause those movements.

$$\mathrm{MT} = a + b(\mathrm{ID})$$

where *a* is the latency (reaction time) of the movement, and ID is the Index of Difficulty. ID is determined by:

$$\mathrm{ID} = \log_2(\frac{2A}{W})$$

where A is the amplitude of the movement, and W is the width (size) of the target.

As the size of the target decreases (i.e., accuracy requirement increases) or the amplitude of the movement increases, movement time (MT) will increase in direct relation to an experimentally determined constant, b. This effect on movement time has been reproduced in numerous studies (Elliott, et al., 1993; Goodale, 1988; Langolf, Chaffin, & Foulke, 1976; Mackenzie, Marteniuk, Dugas, Liske, & Eickmeier, 1987; Soechting, 1984; Vaughan, Barany, & Rios, 2012; Winstein, Grafton, & Pohl, 1997). The foundation of Fitts' law is thought to be a product of the requirements of increased motor planning while increasing task difficulty and maintaining accuracy (Winstein, Grafton, & Pohl, 1997); however, the movement time increase is usually due to a disproportionate increase in the duration of Woodworth's current control phase, when the hand is decelerating toward the target (Langolf, Chaffin, & Foulke, 1976; Mackenzie, Marteniuk, Dugas, Liske, & Eickmeier, 1987; Soechting, 1984). Therefore it is more likely that Fitts' law is less a consequence of planning, and more a requirement for corrective sub-movements following the inaccuracy of initial movements (Crossman & Goodeve, 1983; Keele, 1968; for review, see Vaughan, Barany, & Rios, 2012).

Interestingly, Fitts' law uses both an intrinsic (target width) parameter and an extrinsic (movement amplitude) parameter to account for changes in movement time. Where Jeannerod said that reaching was driven by extrinsic parameters alone, researchers have examined many cases where reaching kinematics have been affected by changes in both intrinsic and extrinsic target characteristics.

Effects of Intrinsic And Extrinsic Target Characteristics

In addition to affecting movement time, research shows that intrinsic and extrinsic object features affect other kinematic measures of the reach. In particular, the effects of object size and distance (intrinsic and extrinsic characteristics, respectively) on the kinematics of the reach movement are well known.

With respect to object size, some studies have shown that reaches directed toward a small target will achieve a lower peak velocity, sooner, than those reaches directed toward a large target (Heath, Hodges, Chua, & Elliott, 1998), even after accounting for changes in movement amplitude to maintain an equivalent index of difficulty (Winstein, Grafton, & Pohl, 1997). Target size may also affect movement time, but it is unclear exactly how: Jeannerod found no effect of target size on movement time in his original studies (Jeannerod, 1984; 1986a; 1986b), but some studies report longer deceleration phase durations associated with smaller targets (Kudoh, Hattori, Numata, & Maruyama, 1997), while others report that both peak velocity and movement time increase with *increasing* target size (Jakobson & Goodale, 1991).

The distance to the target also affects more than just movement time. Absent changes in target width, larger movement amplitudes normally result in higher peak velocities (Winstein, Grafton, & Pohl, 1997), but if the reach requires moving your hand toward your body (i.e., into near space), then the peak velocity of your reach will actually be higher than if you were to reach for a target the same distance away from your hand in the opposite direction (Heath & Binsted, 2007). In the same sense, reaches directed toward far targets are more variable (less consistent) and produce more errors (less accurate) than those directed toward targets in near space (Heath & Binsted, 2007; Roy & Elliott, 1989).

Effects of Vision Availability

In addition to intrinsic and extrinsic target characteristics, studies have found that vision availability has a profound effect on the kinematics of the reach. The dorsal stream, being unable to form memories, will only be engaged when vision is available. If vision is removed (that is to say, the reach is directed toward a remembered target), then the reach will be governed entirely by the ventral stream.

In an early study, Les Carlton investigated the influence of vision on the accuracy of an aiming movement (Carlton, 1981). In this study, he asked participants to point at a nearby target with a hand-held stylus as accurately as possible while maintaining a movement time of 330 ms (± 30 ms). Participants completed this task in both full-vision and no-vision conditions. When participants completed this task blind, their mean error rates were 3x higher than when they completed the task with full vision. This demonstrated that pointing movements completed with full visual feedback of the hand and limb are more accurate than those completed from memory.

More recently, Westwood, Heath, and Roy (2001) tested the influence of vision on the kinematics of the reach. Participants were asked to point to various targets in the mid-sagittal plane, at amplitudes ranging from 20 to 40 cm. The participants pointed within three types of visual feedback condition: a closed-loop condition, where full visual feedback was available during the entire planning and reaching phases of the movement; an open-loop condition, where vision was occluded at the onset of the movement, limiting the potential influence of visual feedback during the reach; and delay conditions, where vision was occluded 500-2000 ms prior to movement initiation, leaving the reach to be performed entirely from memory. All conditions began with a 2 second viewing period. In addition to the effects of extrinsic target parameters (which were consistent with previous studies), the investigators found that visual feedback influenced reach kinematics. Closed-loop reaches had lower peak velocities (PVs) and longer movement times (MTs) than open-loop reaches, though this difference was slight, and borderline non-significant. The speed increase seen in open-loop reaches translated into significantly less accurate end-point positions, suggesting that rather than open-loop reaches being performed more quickly, closed-loop reaches may in fact slow down to make better use of visual feedback during the reach. Delayed reaches, initiated after visual information in the dorsal stream had decayed, had the longest MTs, slowest PVs, and lowest accuracy of all visual conditions, regardless of the length of the delay period. Westwood et al. concluded that visually-guided and delayed reaching are governed by two distinct modes of visuomotor processing. Specifically, closed-loop reaches take advantage of ongoing visual feedback and are governed by dorsal stream processes, and delayed reaches are memory-driven, guided by ventral stream processes. The switch between these processes happens very quickly, in as little as 500 ms, perhaps even less (Westwood, Heath, & Roy, 2001).

In sum, reaches without dorsal stream input are more prone to error (Jakobson & Goodale, 1991; Westwood, 1899), have longer movement times, lower peak velocities, and longer deceleration phase durations (Heath & Binsted, 2007; Elliott, et al., 1993; Roy & Elliott, 1989) than reaches completed under conditions allowing full visual feedback.

Reaching – Hemispheric Asymmetries

In addition to intrinsic and extrinsic target characteristics and vision availability, researchers have found that hand selection may also have a significant effect on reach kinematics. Many studies have demonstrated that right handed people perform reaches more quickly (shorter MTs), with higher peak velocities, and with greater end-point accuracy[4] when using their dominant hands (Elliott & Chua, 1996; Elliott, et al., 1993; Fisk & Goodale, 1985; Roy & Elliott, 1989). Despite these right hand advantages in aiming movements, a large number of studies have shown that right handed people tend to have quicker reaction times (RTs) when pointing with their left, non-dominant hands (Boulinguez, Nougier, & Velay, 2001a; Carson, Chua, Elliott, & Goodman, 1990; Carson, Goodman, Chua, & Elliott, 1993; Elliott, et al., 1993; Velay, Daffaure, Raphael, & Benoit-Dubrocard, 2001; for review, see Grouios, 2006). This left hand RT advantage exists for left handers as well (Boulinguez, Velay, & Nougier, 2001b), and also applies to other motor actions, such as finger-tapping (Annett & Annett, 1979).[5]

The root of these asymmetries is unclear, though they are generally assumed to be effects due to hemispheric specialization; i.e., absent of any biomechanical asymmetries, right hand advantages for accuracy and movement time and left hand advantages for reaction time must originate in the brain. The nature of this hemispheric asymmetry is contentious, and several theories exist which attempt an explanation.

---

[4] Unless the movement is made very slowly (Woodworth, 1899).

[5] The left hand reaction time advantage is not necessarily universal, as studies exist which report no reaction time difference between hands (Vaughan, Barany, & Rios, 2012), or even a right hand RT advantage (Goodale, 1988). Overall, the majority of prehension literature supports the theory of a left hand/right hemisphere advantage for movement planning (Grouios, 2006).

One theory is that the right hand simply enjoys more directed attention than the left hand, at least during the process of reaching and aiming (Roy & Elliott, 1986). It has been demonstrated that right-handed participants completing bimanual tasks in the laboratory generally favour an attentional bias on their right hands (Honda, 1982; Riek, Tresilian, Mon-Williams, Coppard, & Carson, 2003; Roy & Elliott, 1986; 1989; Rushworth, Krams, & Passingham, 2011; for review, see Grouios, 2006). Unfortunately, this theory predicts quicker reaction times in right-handed aiming movements, and as such fails to explain the left-hand advantage in RT discussed above.

Another theory is that the right-hand motor advantage stems from a left-hemisphere visual processing advantage; specifically, that the right hand/left hemisphere system is better able to process visual feedback of the ongoing movement, and is able to integrate this information more efficiently into online corrections (Flowers, 1975; Roy, Kalbfleisch, & Elliott, 1994). In support of this theory, studies have shown that when a target is shifted during a reaching movement it is reacquired more quickly by the right hand than the left hand, regardless of the direction of shift (Elliott, Lyons, Chua, Goodman, & Carson, 1995). Conversely, such perturbations are more quickly identified when they occur in left visual space, which speaks against a left-hemisphere visual advantage. Also, because it has been shown that the right hand movement advantage persists absent of vision of the moving limb (Roy & Elliott, 1986; 1989), this hypothesis cannot solely and entirely explain the right hand movement advantage.

A third theory states that the left hemisphere enjoys an advantage in timing complex sequences of muscle contractions, resulting in a more consistent and efficient ability to program and execute aiming movements; i.e., the sequence of muscle contractions required to initiate, accelerate, and decelerate the limb towards a target is more easily accomplished in a left-hemisphere-driven movement (Boulinguez, Nougier, & Velay, 2001a). This theory is supported by a large body of research showing that the observed right-hand advantages in aiming accuracy and speed are mostly due to more efficient control and execution of small trajectory adjustments as the hand approaches the target (Mieschke, Elliott, Helsen, Carson, & Coull, 2001). This theory also allows for the left hand reaction time advantage discussed earlier, as, despite having a slower reaction time, right-handed aiming movements are completed more quickly than left-handed ones. This effect is owing to the right hand displaying quicker and more efficient deceleration when approaching a target. This theory is also compatible with right-hand advantages in finger-tapping (Annett & Annett, 1979; Peters, 1980), and right-side advantages in producing complex sequences of movements (Goodale, 1988; Todor & Smiley, 1985).

How then can we account for the left hand reaction time advantage? Some researchers present results suggesting that it may be due to an increased ability of the right hemisphere to establish target location in situations of spatial complexity (Chua, Carson, Goodman, & Elliott, 1992). As such, the right hemisphere may be able to assess requirements of (and be able to initiate) left handed aiming movements more quickly than the left hemisphere. This is consistent with the right-hand movement advantage, as the studies cited above demonstrate right hand advantages in movement execution, not initiation. This theory predicts that spatially ambiguous targets should lead to increased left-hand RT advantages (Elliott et al., 1993). To test this prediction, Elliott et al. performed two studies investigating the effects of spatial uncertainty on reaching kinematics. In the first study, participants pointed to either a small dot (no spatial uncertainty) or the center of increasingly large circles (2-6 cm diameter); the thought being that while the right hand is more accurate in targeted aiming studies, perhaps this accuracy advantage will decrease or disappear in cases of increasing spatial uncertainty. The second study was a speeded aiming task in which participants were asked to point to one of two targets, which they inferred to be at the center of circles (6 cm diameter) located 12° to the left or right of the midline. In this experiment, participants had no knowledge of what their target would be prior to an auditory 'go' signal, to which they responded as quickly as possible. They reasoned that the spatial complexity of finding the target quickly would recruit the right-hemisphere more than a simple aiming task (Elliott et al., 1993), and maximize the RT advantage for the left hand.

The results of the first study showed a right hand movement advantage consistent with the results of previous aiming studies; the right hand had quicker movement times and fewer errors than the left hand, even in the case of spatially inferred targets. In the second experiment, however, while results still showed a right hand movement time and accuracy advantage, a left hand reaction time advantage appeared that was not present in the first experiment. The fact that this RT advantage only appeared after the visuospatial processing system was sufficiently stressed implies right-hemisphere superiority in either deriving the movement goal based on spatial environmental cues, or in planning the specific movement derived from those cues. These results are consistent with the theory of left-hemisphere superiority in timing and executing visuomotor movements, and right-hemisphere superiority in spatial analysis (Cohen, 1973; Goodale, 1990).

Unfortunately, this theory fails to explain the left hand RT advantage found in simple aiming tasks, when the target is specified well in advance of movement (Carson, Chua, Goodman, Byblow, & Elliott, 1995). One theory that is consistent with both these results and those of Elliott et al.'s study (1993) states that the right hemisphere is involved in the early stages of movement planning, both in determining target location and in some final preparation before movement initiation (Mieschke, Elliott, Helsen, Carson, & Coull, 2001). To test this, Mieschke et al. (2001) conducted an experiment in which knowledge of the target was varied independently of the response requirements. Mieshke et al. (2001) split their participants into two groups. All participants were pre-cued as to the direction (left/right), amplitude (near/far), or location (direction and amplitude) of the target, but one group was required to make a pointing movement toward the target, while the second group was required to simply lift their finger when the target appeared. If spatial uncertainty is intrinsic to the left hand initiation advantage, then both groups should display a left hand RT advantage. If the movement preparation hypothesis is true, however, then left hand reaction time advantages should only appear in the first group. Mieschke et al. (2001) found that a left hand reaction time advantage was present only when a pointing movement was required. If a participant was required to respond with a simple finger lift, he/she actually reacted more quickly with the right hand, regardless of target location or pre-cueing condition. These results support the theory that left hand RT advantage stems from right hemisphere superiority in the planning of movement, rather than any spatial or attentional advantage.

In sum, results from numerous studies have shown kinematic differences in reaching depending on the hand used. These results are complex; there are many variables that influence reach kinematics, and many examples of mixed or contradictory results, often from the same research team. Overall, the sum of these studies suggest that movement time and accuracy advantages for the right hand stem from a left hemisphere specialization for the timing and execution of visuomotor movements, and not a selective advantage in processing visual feedback. The left hand reaction advantage in reaching movements might also arise from a right hemisphere specialization for the planning of visuomotor movements, rather than a right hemisphere advantage in processing spatial complexities.

Reach-to-Grasp

As reviewed above, Jeannerod was the first to describe prehension as being a superimposition of the independent – yet coordinated – reaching and grasping actions (Jeannerod, 1984). The grasp can be defined as the sum of the wrist, hand and finger movements in which the fingers envelop a targeted object, in order that the object may be manipulated or otherwise interacted with. The grasp can be described in its own kinematic terms, which are influenced primarily by intrinsic target qualities (Jeannerod, 1984).

Early studies on grip formation (Jeannerod, 1984, 1986b; Wing & Fraser, 1983) showed that in a normal grasping movement, the fingers will extend beyond the actual size of the target object, reaching a peak before beginning to flex around the target as the reach brings the fingers within range of contact. This peak, dubbed Maximum Grip Aperture (MGA), scales linearly with the size of the target (Jeannerod, 1984, 1986b). The time of MGA (MGAt) has been linked temporally to the kinematics of the reach, and under simple, unstressed conditions (e.g., full visual feedback, unambiguous target, un-speeded response), occurs after approximately 70% of the reach has been completed (Connolly & Goodale, 1999; Jeannerod, 1984; Kudoh et al., 1997)[6]. The variability of MGA (vMGA) is a measurement of the inter-trial differences between

---

[6] Studies vary on the exact timing of maximum grip aperture; one such study places the time of MGA (MGAt) in a range, dependent on both the size and shape of the object to be grasped. MGAt may be as early as 50% (Schettino, Adamovich, & Poizner, 2003) or as late as 80% (Santello & Soechting, 1998) of MT, depending on the size and complexity of the grasp's target, as well as on visual feedback availability. Generally, however, studies have placed MGAt at approximately 65-75% of MT (Connolly & Goodale, 1999; Jeannerod, 1984; Kudoh et al., 1997; Wallace & Weeks, 1988).

MGAs; it is sometimes considered a measurement of uncertainty or perceptual and/or motor inconsistency (i.e., accuracy) in the formation of the grasp.

Despite the fact that the grasp can be defined and described independent of the reach, it is difficult if not impossible to separate the two experimentally: how do you grasp something without first reaching for it? Aside from highly controlled studies investigating catching (Polman, Whiting, & Savelsbergh, 1996; van der Kamp, Savelsbergh, & Smeets, 1997), virtually all studies that analyze grasp kinematics (including all those referenced in the following section) use a reach-to-grasp experimental task. In the course of using reach-to-grasp tasks, investigators have found that both intrinsic and extrinsic parameters will affect grasp kinematics. Numerous studies exist showing that the kinematic measurements of the grasp (MGA, MGAt, and vMGA) are affected by both intrinsic and extrinsic target characteristics, and that these kinematics are also influenced by visual feedback.

Effects of Intrinsic and Extrinsic Target Characteristics

The target itself is the greatest determinant of grasp kinematics. As already mentioned, MGA scales linearly with the size of the object to be grasped (Jeannerod, 1984; 1986a; Paulignan, Frak, Toni, & Jeannerod, 1997; Kudoh et al., 1997; Santello, Flanders, & Soechting, 2002). MGAt is also affected by target size, with larger objects producing grasps in which MGAt occurs later in the reach (Connolly & Goodale, 1999; Holmes, Mulla, Binsted, & Heath, 2011; Jakobson & Goodale, 1991; Paulignan et al., 1997).

Grasp kinematics may also influence reach kinematics, as demonstrated by Castiello, Bennett and Stelmach (1993a). In this study, researchers asked participants to reach and grasp two objects simultaneously; one hand was to grasp an object with a full-handed grip, the other hand using a precision grip. They found that in the bilateral movement, movement times and MGAs of both hands were identical. When tested independently, however, precision grips had longer movement times and longer deceleration periods than full-handed grips, regardless of which hand was used (Castiello, Bennett, & Stelmach, 1993a). These results not only show that a reach movement will slow to accommodate the precision requirements of the grasp – they also suggest that this effect will transfer between limbs during bimanual non-homologous reach-to-grasp movements. That is, in bilateral reach-to-grasp movements, the movement speed of the hand performing the simpler of the two grasps will slow to accommodate the precision requirements of the other hand (Castiello, Bennett, & Stelmach, 1993a).

Although the reaching and grasping components of the reach-to-grasp movement are programmed separately, there is evidence suggesting that factors that affect the kinematics of the reach (i.e., distance and visual feedback availability) may also affect the kinematics of the grasp. When instructed to perform reaches quickly, participants react with larger, more variable MGAs (Mon-Williams & Bingham, 2011; Wing, Turton, & Fraser, 1986). Some studies report that longer reaches (i.e., those of increased amplitude) are associated with larger MGAs (Chieffi & Gentilucci, 1993; Jakobson & Goodale, 1991; Kudoh et al., 1997), and that this effect occurs independently of changes in actual target size. This finding is contentious, however, as others report no effect of distance on MGA (Jeannerod, 1984), or even the opposite effect, wherein MGA is larger for shorter reaches than it is for longer reaches (Paulignan et al., 1997).

Another factor affecting the reach-to-grasp movement is target fragility. Marteniuk et al. (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987) looked at kinematic differences between reach-to-grasp motions directed at a tennis ball versus those directed at a light bulb. The tennis ball and the light bulb shared the same physical dimensions, and only differed in the fact that one would be perceived as fragile. They found that grasps directed toward the light bulb were associated with longer movement times; this was due to increased time spent in the deceleration phase, as they found no difference in either peak velocity or time of peak velocity between reaches directed toward the two targets. Savelsbergh et al. (Savelsbergh, Steenbergen, & van der Kamp, 1996) followed up on this study by looking at the grasp kinematics (in addition to those of the reach) when participants were asked to grasp either transparent or black tubes. The participants reported the transparent tubes gave an impression of fragility, while the black tubes were perceived as sturdy. They found that, consistent with Marteniuk et al. (1987), the increased perception of fragility coincided with longer movement times, and participants spent more time decelerating toward the targets they perceived as fragile. While participants closed their fingers more slowly around the fragile targets, the researchers found no effect of perceived fragility on MGA. While it may seem that fragility is an intrinsic quality of a target, fragility can vary independently of the dimensions of the target, and is a factor whose extent is largely determined by subjective perception and previous experience, rather than by objective target parameters. As such, these studies may serve as a demonstration of the interaction between dorsal and ventral streams. Subjective perception (a ventral stream function) may influence the kinematics of the reach-to-grasp movement produced by dorsal stream input.

Effects of Vision Availability

In addition to affecting the kinematics of the reach, visual feedback also affects the kinematics of the grasp. Wing, Turton, and Fraser (1986) performed a study in which participants were asked to grasp a target cylinder with their eyes closed. Half of all participants tested knocked the cylinder over on at least one trial, demonstrating a decrease in accuracy compared to visually-guided reaches. The researchers also found that memory-guided reaches produced larger, more variable MGAs than reaches guided by visual feedback. These results are consistent with those of other researchers, who found that MGA gets systematically larger, but still scales with target size when visual feedback is restricted (Jakobson & Goodale, 1991; Jeannerod, 1984). Later studies have found that the effect of vision on MGA is contingent upon visual feedback of the target, but not the moving hand and limb. In open-loop reach-to-grasp movements, where visual feedback regarding the hand and limb is restricted at movement onset, MGA occurs later (Connolly & Goodale, 1999) but is no larger than it is in closed-loop reach-to-grasp movements. Thus, MGA is not affected by visual feedback as long as visual contact with the target is maintained (Connolly & Goodale, 1999; Hu, Eagleson, & Goodale, 1999). If, however, the grasp is performed after a delay, and the reach-to-grasp movement is performed entirely from memory, then MGA increases significantly (Hu, Eagleson, & Goodale, 1999), especially if the target object is made to appear larger by placing it next to a smaller object (Hu & Goodale, 2000). These last two studies show that memory-guided grasping (which uses ventral stream processing) produces movements with larger, more variable MGAs compared to movements produced under the dorsal stream's guidance. Hu and Goodale (2000) also showed that grasps produced from memory are influenced by our visual perception of size, rather than an object's actual size.

The studies discussed above have shown that the kinematic measurements of the grasp (MGA, MGAt, and vMGA) are affected by both intrinsic and extrinsic target characteristics, and that these kinematics are again influenced by visual feedback.

Reach-to-Grasp – Hemispheric Asymmetries

As with reaching, researchers have conducted studies looking for hemispheric asymmetries in the reach-to-grasp movement. Grosskopf and Kuhtz-Buschbeck (2006) performed a study in which they searched for kinematic differences between prehensile movements performed with either the left or right hand. In this study, participants were asked to reach for, grasp, and remove a small peg from a hole into which it had been fit. After removing the target peg, they were tasked with fitting it into a similar hole a short distance away. Because they knew that visual feedback availability and speed of movement have both been shown to affect the pre-shaping of the hand, the researchers manipulated the speed at which the participants were asked to move (slow, normal, and fast), as well as the availability of visual feedback (vision or no-vision). In the full vision condition, they identified minor differences between the hands; specifically, the right hand achieved peak velocity sooner than the left hand, but only in the "slow" speed trials. In the "fast" trials, the right hand achieved a higher peak velocity than the left. Additionally, after grasping the target, the right hand moved more smoothly and more quickly to the insertion point. While this latter effect was observed in all speed conditions, all other kinematic measurements between hands were comparable, and no other significant differences were found.

The no-vision condition was identical in procedure to the vision condition, save that the lights in the room were extinguished as soon as the participant was told to begin the movement (i.e., while the participant could see the experimental set-up initially, they completed the reach-to-grasp and subsequent transport and placement in complete darkness). Without visual feedback of the ongoing movement, both hands demonstrated a larger maximum grip aperture on the way to the peg. Despite the right hand opening slightly sooner than the left hand, the maximum grip apertures each hand reached were not significantly different from one another. The smoothness with which the right hand moved with visual feedback also disappeared, meaning there were even fewer hand differences in this no-vision condition. Grosskopf and Kuhtz-Buschbeck (2006) concluded that, despite their manipulations, and excluding some very minor differences in the early grasp behaviour, the left and right hands are essentially the same when it comes to the kinematics of the grasp.

A different study restricted the initial view of the hand and arm in a series of reach-to-grasp tasks (for targets of different sizes), assuming that this restriction will stress differences in grip pre-shaping by removing any influence by the visual system (Tretriluxana, Gordon, & Winstein, 2008). The investigators found that, while both hands accurately scaled to the size of the target, the manner in which they scaled differed; the left hand scaling was visible in the "preparatory aperture," an inflection in the early grasp motion where the opening fingers slow slightly on their way to MGA. By contrast, though the right hand MGA did scale appropriately, there were no differences in the preparatory aperture linked to changes in target size. Once again, this study found no other manual asymmetries in the reach-to-grasp kinematics.

It is possible that hand differences do not become apparent until the task becomes demanding. To address this possibility, Gorniak et al. (2010) looked at how the actual forces exerted by the fingers on a grasped object vary with changes in fragility. By coupling the grasping of an easily collapsible object with a movement requirement, these researchers directly measured behavioural changes in response to fragility concerns. They found no kinematic differences between left and right handed movements, regardless of the fragility of the grasped object. This shows that when tasked with making fine manipulations to the amount of grip force produced, people are equally well at doing so with either hand.

The findings of the studies cited above are puzzling particularly for the unexpected nature of their results. Despite a vast amount of evidence suggesting a strong right hand preference for visuomotor actions (Annett, 1970; Bryden, Roy, & Mamolo, 2003; Gonzalez, Ganel, & Goodale, 2006; Gonzalez & Goodale, 2009; Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Stone, Bryant, & Gonzalez, In Press), studies have been unable to find consistent kinematic asymmetries between hands for reach-to-grasp movements. How then can we reconcile a prominent right hand preference with an absence of kinematic asymmetries in these same actions?

The Problem

The studies cited in the previous sections all searched for reach-to-point and reach-to-grasp asymmetries in different ways, and each met with different levels of success. The general consensus is that for reaching movements, manual asymmetries are prominent and easily identified, but aside from a preference to use our dominant hands, asymmetries in the reach-to-grasp motion are difficult to isolate. Why then should this preference exist if not for asymmetrical movements? It is possible that manual asymmetries in the reach-to-grasp movement will only become significant after task difficulty passes beyond some as-yet-undefined level.

Kinematics of the reach often influence the kinematics of the grasp, and vice versa; without investigating the kinematics of the reach and grasp in a single study, grasp asymmetries may remain undetectable. In order to maintain control in a laboratory setting, one would ideally manipulate a single dimension of the reach-to-grasp action (size, fragility, orientation, intent, grip type, or visual feedback) and measure any kinematic differences this change would produce. However, this places only one point of stress on the participant’s visuomotor system, which may be easily accommodated, in turn producing insignificant manual asymmetries. If, as in the reaching movement, manual asymmetries appear only when the task is sufficiently difficult (Woodworth, 1899), then perhaps the next course of action will be to stress the reach-to-grasp visuomotor system via several parameters simultaneously. By changing the availability of visual feedback (vision vs. reduced vision, or absent vision entirely), and the demands of the task (reducing the size or increasing the fragility of the target, or reducing the speed at which it can safely be moved) concurrently, one may be able to tease-out reach-to-grasp asymmetries that have proven elusive in the past.

The purpose of my thesis was to test the possibility that manual asymmetries in the reach-to-grasp action are 1) resultant from asymmetries in the dorsal vision-for-action system, and 2) significant only in a sufficiently difficult task. Two experiments were conducted and form the major part of this thesis, which was built around the following theory.

Theory

There are hemispheric asymmetries in the vision-for-action system.

Hypothesis and Predictions

Hypothesis I

Hemispheric asymmetries in the vision-for-action system can be documented by studying manual asymmetries in the kinematics of the reach-to-grasp movement.

Prediction: If there are hemispheric differences in the reach-to-grasp movement, we should be able to identify them by looking at reach variables such as reaction time (RT), movement time (MT), peak velocity (PV), and deceleration phase duration (DPt), as well as grasp kinematics such as maximum grip aperture (MGA), time of maximum grip aperture (MGAt), and variability of maximum grip aperture (vMGA).

Hypothesis II

Hemispheric differences in the vision-for-action system should be contingent upon visual feedback availability.

Prediction: If there are hemispheric differences in this system, these differences should only be apparent during conditions in which the dorsal stream is engaged. In other words, we should find kinematic asymmetries in visually-guided conditions (CLOSED- and OPEN-LOOP), but not in memory-guided conditions (DELAY).

Hypothesis III

Hemispheric differences in the vision-for-action system should be contingent upon task difficulty, with tasks requiring a higher degree of precision and/or skill exposing kinematic asymmetries favouring the right hand/left hemisphere visuomotor system.

Prediction: If there are hemispheric differences in this system, reach-to-grasp asymmetries should be more prominent (or, alternatively, only become significant) in grasps requiring a higher degree of precision. Right-handed reach-to-grasp actions should produce reaches with shorter MTs, higher PVs, and shorter DPts, and grasps with more accurate (i.e., smaller) and less variable MGAs than left-handed grasps, but only when the demands of the required task are high.

Experiments

To test these hypotheses, two experiments were conducted. Both experiments involved unimanual reach-to-grasp tasks. Participants were recruited from the undergraduate population at the University of Lethbridge in exchange for class credit.

Experiment 1

To test my first hypothesis, that hemispheric asymmetries can be documented by describing manual asymmetries in the reach-to-grasp movement, I asked that participants reach for, grasp, and take a sip from an ordinary glass of water (80 mm tall, 67 mm across at the mouth and base), using both their right and left hands in separate blocks. Using an Optotrak Certus camera and infrared LEDs placed on the wrist and fingertips, I was able to track the movement of their hand and wrist, and pull kinematic measures of the reach-to-grasp movement from the resulting data. To describe the reach component of the reach-to-grasp movement, I extracted and analyzed the following measurements from the IRED marker placed on the participant's wrist: reaction time (RT), movement time (MT), peak velocity (PV), time of peak velocity (PVt), and deceleration phase duration (DPt). To analyze the grasp component of the reach-to-grasp movement, I extracted and analyzed the following measurements from the IRED markers placed on the participant's fingertips: maximum grip aperture (MGA), time of maximum grip aperture (MGAt), and inter-trial variability of maximum grip aperture (vMGA).

To test my second hypothesis, that manual asymmetries are contingent upon visual feedback availability, I manipulated participants' vision using PLATO Liquid Crystal goggles. These goggles, which can change from fully transparent to opaque in 3 ms, allowed me to restrict each participant's vision with precise timing. There were three vision conditions in this experiment. The goggles remained opaque between trials. Each trial began with a 1-2 second period in which the goggles became transparent and the participant was allowed to view the target glass, and assess its position and properties. In the CLOSED-LOOP visual condition, vision was unrestricted throughout the duration of the reach-to-grasp motion. In the OPEN-LOOP condition, the participant's vision was blocked 100ms following the cue to begin reaching toward the glass. Finally, in the DELAY condition, vision was blocked 2 seconds before the cue to begin the reach.

To test my third hypothesis, that manual asymmetries are contingent upon task difficulty, I manipulated the demand requirements of the task by changing the fill level of the glass, as has been done by others (Doan, Whishaw, Pellis, Suchowersky, & Brown, 2006). A full glass of water cannot be moved as quickly as an empty glass, as there is a chance that a quick lateral acceleration will cause the water to “slosh” over the side of the glass. This risk drops with lower levels of water in the glass. There were two demand conditions in this experiment: a HIGH demand condition, in which the water level was ≤ 10 mm from the rim of the glass, and a LOW condition, in which the water level was ≤ 10 mm from the bottom of the glass. The Demand was varied between trials, and the participant did not know the level of water in the glass until the beginning of each trial.

Hand, Vision, and Demand were arranged in a 2 x 3 x 2 factorial design, resulting in 12 total conditions for analysis. The left and right-handed trials were presented in two blocks of 48 trials apiece (3x2 factorial design, 8 trials per condition). While this design allowed me to search for hand differences in multiple conditions, it also provided me with an opportunity to observe the previously unexplored interactions between vision and demand.

Experiment 2

The design for experiment 2 was identical to that of experiment 1, in that I manipulated hand, vision, and demand task parameters in order to discern manual asymmetries in the reach-to-grasp movement. For this experiment, however, I replaced the standard drinking glass with a taller, narrower, 60 ml (2 fluid oz.) shot glass (104 mm tall, 38 mm across at the mouth and base). By switching the larger glass out for the shot glass, I hoped to induce a larger over-opening of the MGA (Muelenbroek, Rosenbaum, & Vaughn, 2001) and a larger inter-trial variability of this same measurement (Tretriluxana, Gordon, & Winstein, 2008). I also hoped that a change to a more challenging target might also produce longer MTs, with associated increases in deceleration phase duration (Kudoh et al., 1997).

Chapter 2: Methods, Analysis, and Results

There are many examples of hemispheric asymmetries in the human brain. Language is dominantly represented in the left hemisphere (Damasio, 1984), as are visual and auditory discrimination of verbal cues (Bradshaw J. L., 1978). Judgements of non-verbal visual stimuli, such as brightness/colour discriminations, dot localizations, facial features, and judgements of curvature, depth, or orientation are accomplished more effectively by the right hemisphere (Bradshaw, 1978). It is controversial, however, whether or not there are manual asymmetries for reach-to-grasp actions. While many researchers have found a dominant hand superiority in reaching tasks (Goodale, 1988; Lenhard & Hoffmann, 2007; for review, see Grouios, 2006), studies have found no significant kinematic differences between hands in reach-to-grasp actions (Grosskopf & Kuhtz-Buschbeck, 2006; Smeets & Brenner, 2001) despite a marked preference to use the dominant hand for simple reach-to-grasp actions (Stone, Bryant, & Gonzalez, In Press). It is possible that, as with the reaching movement (Woodworth, 1899), manual asymmetries in the reach-to-grasp action are undetectable and/or insignificant unless the visuomotor system is stressed via a sufficiently difficult task.

Reach-to-grasp kinematics are affected by a number of intrinsic and extrinsic factors, one of which is perceived fragility (Marteniuk & MacKenzie, 1990; Marteniuk et al., 1987). Studies have shown that reach-to-grasp actions directed toward objects perceived as fragile have longer movement times and longer periods of deceleration than those directed toward objects perceived as stable (Marteniuk et al. 1987; Savelsbergh et al. 1996). The demand characteristics of many everyday graspable objects may vary considerably, even apart from those characteristics owing to their external dimensions or construction materials. The way in which we approach to pick up a cup of coffee would likely be different if the cup is full rather than empty, or if the coffee is hot versus cold. There are only a few studies investigating the effect of target demand on reach-to-grasp movements even though it may prove to be a significant source of variability in the reaching and grasping kinematics.

Studies exploring the effects of visual feedback on grasping kinematics have found mixed results. Some researchers have found that when constant visual feedback of both the hand and the target is available throughout the task (CLOSED-LOOP), maximum grip aperture (MGA) is more accurately scaled to object size, and PV is higher compared to those tasks performed with reduced (OPEN-LOOP) or absent (DELAY) visual feedback (Wing et al. 1986; Jakobson and Goodale 1991). Others find no difference between OPEN- and CLOSED-LOOP conditions (Connolly and Goodale 1999; Hu, Eagleson, and Goodale 1999). This dichotomy may be due to methodological differences, specifically those relating to task difficulty. The availability of visual feedback of the moving hand and limb varied from study to study, as did the target's size, mass, and location, suggesting that the interaction of these factors may crucially influence reach-to-grasp kinematics.

The purpose of our study was to assess the influence and interactions of vision and demand on kinematic performance of an ecologically valid reach-to-grasp task, performed with either the left or right hand. Participants were asked to take a sip from a glass of water in CLOSED-LOOP, OPEN-LOOP, and DELAY visual conditions, during both left- and right-handed reach-to-grasp actions. We introduced a within-subject demand factor into our design by manipulating the water level in the glass. We predicted that, should manual asymmetries exist, they would most likely be found in the HIGH demand condition. Using infra-red LEDs and a motion tracking system, we captured reaching displacement and grasping behaviour of the hand, wrist, and fingers, and subsequently compared reaction time, peak velocity, movement time, deceleration phase duration, maximum grip aperture, time of maximum grip aperture, and variability of maximum grip aperture between conditions.

Experiment 1: Methods

Participants

15 right-handed participants (8 female) took part in the experiment. Each participant gave informed consent in accordance with the local ethics review board. Each participant was tested individually.

Materials

3 infra-red diodes (IREDs) were placed on the participant's hand; 2 on the distal phalanges of thumb and index finger, slightly proximal with respect to the nails, and one on the wrist at the medial aspect of the styloid process of the radius (proximal and medial with respect to the anatomical-snuffbox) (Fig. 7 (insert)). An Optotrak Certus camera [*Northern Digital, Waterloo, ON, Canada*], positioned overhead, recorded IRED position during each trial at 200 Hz for 8 seconds. Visual conditions were controlled via PLATO Liquid-crystal glasses [*Translucent Technologies, Toronto, ON, Canada*], worn by the participant throughout the test. Visual conditions were planned and controlled using Superlab 2.0 [*Cedrus Corporation, San Pedro, CA, USA]*. Reach-to-grasp target was a cylindrical (but not tapered) water glass, 80 mm tall and 67 mm in diameter at the mouth and base.

Procedure

The water content of the target glass was altered to impose the demand on each trial. For the HIGH demand condition, the glass was filled to within 10 mm of the lip of the glass. In the LOW demand condition the water level was within 10 mm from the base of the glass.

Participants were seated in front of a table (W=107 cm, D=77 cm, H=67 cm) on which the target glass was placed at a viewing distance of approximately 60 cm. Before each trial, participants placed their hands in a ‘rest position’ by positioning the wrist and the lateral edge of the hand on the table with thumb and forefinger touching in such a way that all 3 markers were visible to the overhead camera (Fig. 7 (insert)).

Each trial began with the Plato goggles in a closed (opaque) state. When IRED recording began, the goggles opened (i.e., became transparent), allowing the participant to locate the target and plan their grasp. Participants were instructed to wait for an audible signal before reaching for and taking a sip from the glass as quickly and accurately as possible. Timing of the go signal varied with visual condition (Fig. 7). In the CLOSED-LOOP and OPEN-LOOP conditions, the go signal was given 1000 ms after the beginning of recording. The goggles remained open a further 4000 ms during the CLOSED-LOOP condition (giving the participant full vision throughout the duration of the reach and grasp). In the OPEN-LOOP condition the goggles closed 100 ms after go signal, so the movement was executed without vision, but with recent visual (i.e., dorsal stream) input. In the DELAY condition, the goggles opened for 2000 ms before closing, and then a 2000 ms delay period was observed before participants were given the go signal. In this condition the movement was executed without vision, and also entirely from memory as any input from the dorsal stream should have decayed by the time the signal to move was given. Each participant reached for the same glass for all trials. We varied Vision and Demand in a 3 x 2 factorial design, repeating each condition 8 times, resulting in 48 trials per hand (96 trials total). Trials were judged successful and included in statistical analysis if the participant: i) began from a proper resting state (fingertips together), ii) correctly waited for the go signal to begin, and iii) did not knock over or otherwise spill the glass. Conditions were presented in a pseudo-random order, in right and left hand blocks. Right/left hand starting order was randomly assigned and counter-balanced. To avoid a motor learning effect, the target glass was moved randomly between each trial on a 20 cm arc approximately 40 cm from the participant’s resting hand.

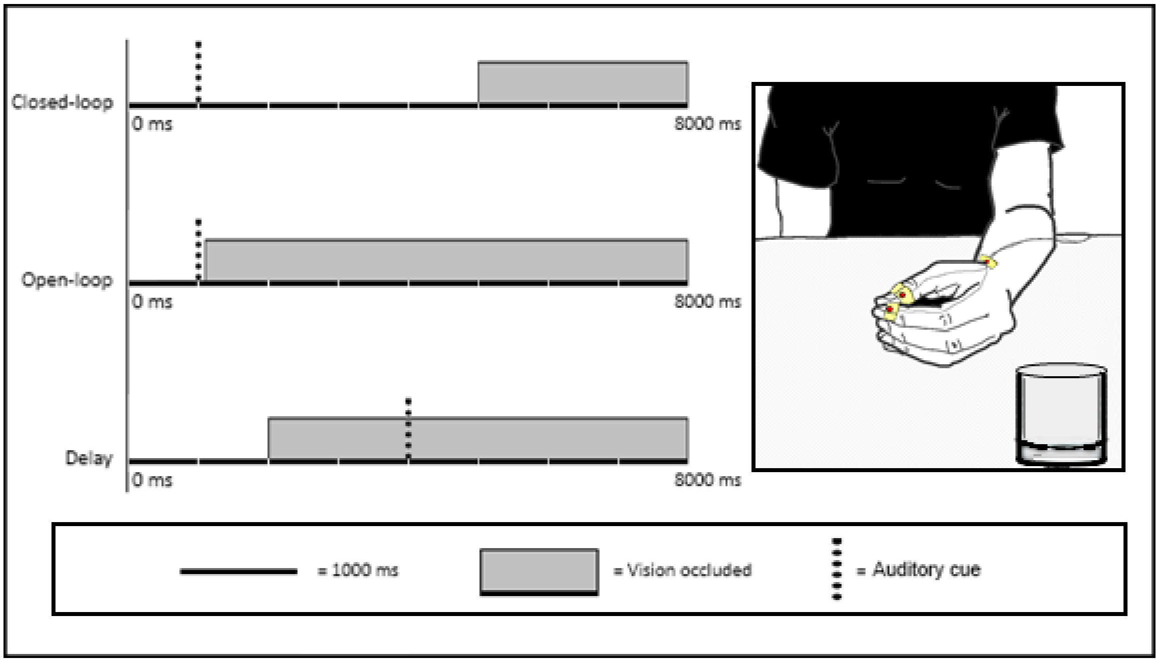


Figure 7 – Experimental Design. Timeline of visual conditions. Auditory cue was followed by movement onset in the direction of the target (Insert: resting position, showing typical IRED marker sites and sample placement of a target glass**.)**

Analyses

We determined kinematic parameters using finite differences in the two-step method[7]. All kinematic calculations were performed using Microsoft Excel 2007/2010, and statistical analyses were completed using PASW Statistics 18.0.0. An average of 8.8% of trials per participant (± 5.9%) were missing critical data or were considered failures, and as such were

---

[7] Using the two-step method, average speed at time *n* is calculated by by determining displacement between times *n-1* and *n+1*, and dividing that displacement by the elapsed time between those two points. The method can be expressed by the formula $v(n) = \frac{[p(n+1)-p(n-1)]}{2n}$, where v is velocity, p is position, and n is a single point in time. The accuracy of this method is limited by the collection frequency of the motion tracking system.

excluded from analysis. Any participant missing more than 20% of trial data for any reason was removed from analysis. The data from remaining trials were averaged across condition, and repeated measures ANOVAs were used on a variable by variable basis.

Reach Kinematics

Reaction time (RT) was defined as the time following the go signal at which a participant achieved a resultant equal to 5% of their peak velocity. Peak velocity (PV) was defined as the maximum speed the participant achieved during their reach towards the target. Because the target's location changed between trials, we calculated outgoing velocity as a resultant in absolute terms using a two-step model. Movement time (MT) was calculated as the difference between time of grasp contact[8] and RT, and represents the span during which the participant reached outward toward the target glass. Deceleration phase duration (DPt) was calculated as the time during which the participant was decelerating while still reaching outwards toward the target; it is reported as a percentage of movement time. We calculated this as the difference between the time of grasp contact minus time of PV, divided by total movement time.

Grasp Kinematics

Maximum grip aperture (MGA) was measured as the peak resultant distance achieved between the thumb and index finger IREDs prior to the time of grasp contact. In trials where the participant missed the target on their initial grasp attempt, the first MGA was used for analysis even if the second MGA was found to be larger; this ensured that only visually-influenced MGAs (as opposed to those with additional somatosensory feedback) were included in analysis. MGA values were corrected for IRED placement using the average of the ten smallest resting grip

---

[8] The time of grasp contact was defined as the point at which: i) the subject's outward speed dropped below .02 m/s, and ii) their corrected grip aperture plateaued at the approximate diameter of the target glass. Trials in which these two conditions were not synchronised to within 10 frames (±.05 seconds) were removed from analysis.

apertures recorded per participant per hand; we feel this correction factor allows us to control for slight variations in IRED placement between the hands as well as variations in hand size within participants[9]. Time of MGA (MGAt) is the time at which MGA was expressed, measured as a percentage of the movement time. Variability of MGA (vMGA) is the standard deviation of the MGAs achieved during the 8 trials of each vision/demand/hand grouping.

---

[9] Analyses were also conducted on uncorrected MGA data, which revealed main effects and interactions were still present.

Experiment 1: Results

Significant (or approaching significant) main effects and interactions are reported below. Results are reported as either reach or grasp kinematics, within each vision condition (CLOSED-LOOP, OPEN-LOOP, and DELAY). Means and standard errors of all measurements are reported in Table 1. ANOVA results (F-statistics and significance) are reported in Table 2.

Table 1 – Results of Experiment 1. Means and standard errors are reported for all reach and grasp kinematic measures.

			RT (ms)	PV (m/s)	MT (ms)	DPt (% MT)	MGA (mm)	MGAt (% MT)	vMGA (mm)
CLOSED-LOOP	LEFT	LOW	447 (29)	0.780 (0.04)	960 (39)	62.0 (0.7)	82.3 (2.1)	71.3 (1.4)	3.77 (0.4)
		HIGH	419 (21)	0.772 (0.04)	996 (39)	62.7 (0.7)	82.2 (2.1)	68.3 (1.6)	3.21 (0.4)
	RIGHT	LOW	454 (26)	0.792 (0.04)	913 (39)	62.6 (1.0)	83.9 (2.5)	68.0 (1.3)	2.40 (0.2)
		HIGH	430 (30)	0.787 (0.04)	979 (42)	63.5 (1.0)	83.4 (2.3)	67.0 (1.5)	2.76 (0.2)
OPEN-LOOP	LEFT	LOW	460 (26)	0.749 (0.05)	1146 (44)	68.0 (0.9)	90.4 (2.6)	60.1 (1.1)	4.11 (0.4)
		HIGH	452 (41)	0.721 (0.05)	1238 (56)	69.4 (0.8)	90.5 (2.7)	58.9 (1.0)	4.39 (0.5)
	RIGHT	LOW	431 (21)	0.737 (0.03)	1092 (56)	68.0 (1.0)	90.1 (2.7)	59.5 (0.9)	3.83 (0.5)
		HIGH	454 (24)	0.753 (0.04)	1200 (58)	70.8 (0.9)	89.8 (2.8)	57.9 (1.0)	3.32 (0.4)
DELAY	LEFT	LOW	374 (19)	0.660 (0.04)	1334 (48)	71.7 (1.1)	95.2 (2.9)	54.0 (1.5)	4.05 (0.6)
		HIGH	376 (17)	0.632 (0.03)	1427 (45)	73.5 (0.9)	93.5 (2.6)	52.2 (1.3)	3.42 (0.4)
	RIGHT	LOW	375 (12)	0.665 (0.03)	1289 (49)	72.3 (0.6)	94.1 (3.1)	54.7 (1.1)	3.56 (0.5)
		HIGH	379 (14)	0.651 (0.03)	1388 (53)	73.7 (0.8)	93.8 (3.3)	50.9 (1.3)	2.89 (0.3)

Table 2 – ANOVA results of Experiment 1. Significant results (*p*<.05) are marked with an asterisk (*). Borderline effects (.05<*p*<.1) are marked with a cross (†).

		RT	PV	MT	DPt	MGA	MGAt	vMGA
CLOSED-LOOP	Hand	0.15	0.43	3.85†	0.62	1.32	2.52	18.59*
	Demand	3.00	0.46	42.91*	6.30*	0.79	10.82*	0.16
	Hand X Demand	0.03	0.02	3.94	0.09	0.83	1.65	4.53*
OPEN-LOOP	Hand	0.34	0.26	2.96	0.95	0.17	0.52	3.96†
	Demand	0.24	0.33	47.64*	21.07*	0.16	4.00†	0.18
	Hand X Demand	0.89	6.11*	0.25	2.55	0.63	0.07	1.23
DELAY	Hand	0.03	0.48	4.59*	0.28	0.10	0.04	2.00
	Demand	0.12	3.61†	21.77*	13.88*	5.81*	16.66*	5.54*
	Hand X Demand	0.00	0.36	0.08	0.36	1.76	2.99	0.01

Closed-loop: Reach Kinematics

Effects of hand (Fig. 8) and demand (Fig. 9) are reported for the reach kinematics in the CLOSED-LOOP visual condition. No main effects of hand or interactions between Hand X Demand were found for RT, PV or DPt. A main effect of hand on MT nearly reached significance (F(1,14)=3.849, *p*=.070) (Fig. 8). When the right hand was used, reach-to-grasp movements were completed sooner (M=946, SE=40 ms) than when the left hand was used (M=978, SE=39 ms). A main effect of demand was observed on MT (F(1,14)=42.908, *p*<.001), and DPt (F(1,14)=6.304, *p*=.025) (Fig. 9). When reaching for a glass in the HIGH demand condition, reaches took longer to complete (M=988, SE=40 ms) than they did in the LOW demand condition (M=937, SE=38 ms). With respect to DPt, participants spent a significantly larger percentage of the reach decelerating in the HIGH demand condition (M=63.1, SE=0.8%) than in the LOW demand condition (M=62.3, SE=0.7%).

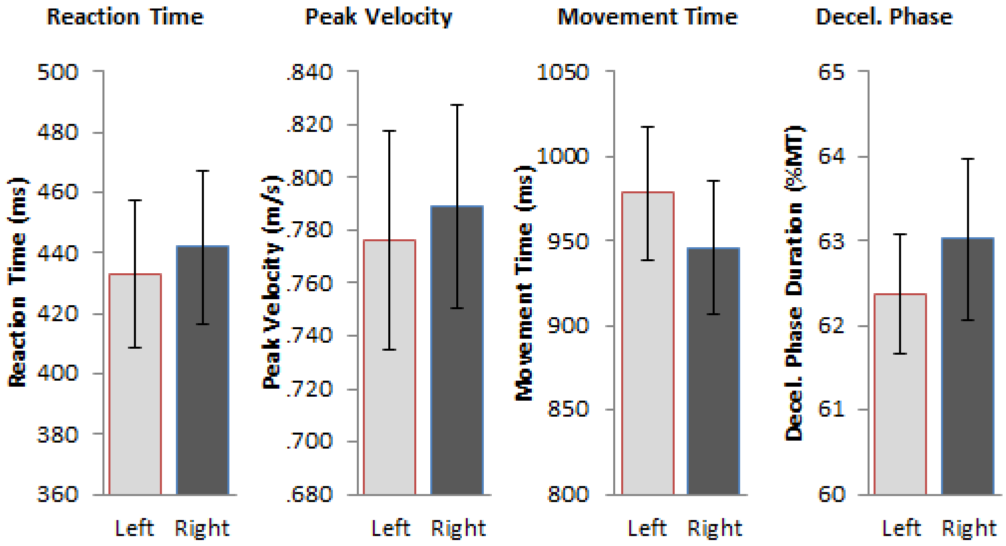


Figure 8 – Reach kinematics by Hand manipulation in the CLOSED-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean.

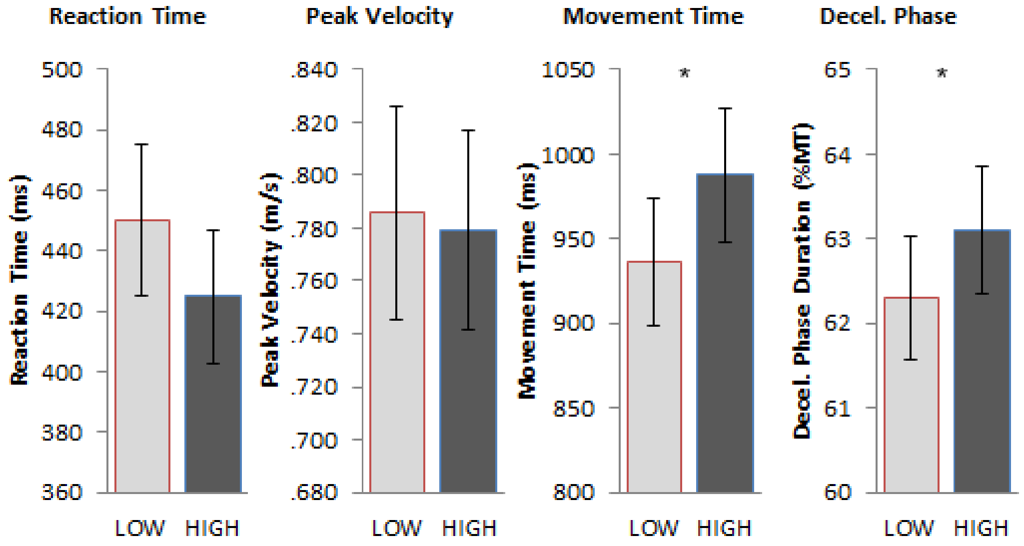


Figure 9 – Reach kinematics by Demand manipulation in the CLOSED-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean.

Closed-loop: Grasp Kinematics

Effects of hand (Fig. 10) and demand (Fig. 11) are reported for the grasp kinematics in the CLOSED-LOOP visual condition. No main effects of hand or demand or interaction between hand and demand were found in MGA. A main effect of hand was observed on vMGA, F(1,14)=18.588, *p*<.001) (Fig. 10). Specifically, when the right hand was used for the reach-to-grasp movement, participants were significantly less variable (M=2.58, SE=.21 mm) in producing their MGA than they were during left-handed movements (M=3.49, SE=.32 mm). A main effect of demand was found in MGAt, (F(1,14)=10.823, *p*=.005) (Fig. 11). MGAt occurred earlier in the grasp in the HIGH demand condition (M=67.6, SE=1.2%) than in the LOW demand condition (M=69.6, SE=1.2%). We also found a significant Hand X Demand interaction in vMGA (F(1,14)=4.531, *p*=.05) (Fig. 12). Reach-to-grasp movements completed with the left hand were significantly more variable than those completed with the right hand in the LOW demand condition (t(14)=4.397, *p*<.001) but not in the HIGH demand condition (p > 0.1).

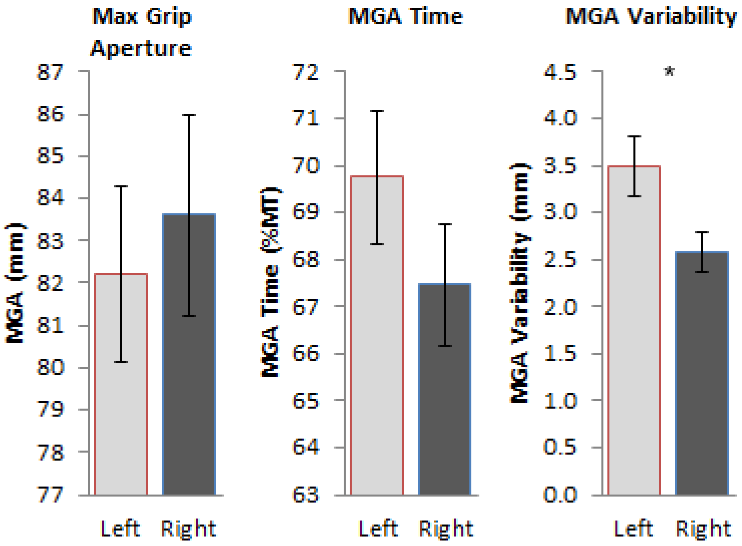


Figure 10 – Grasp kinematics by Hand manipulation in the CLOSED-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean.

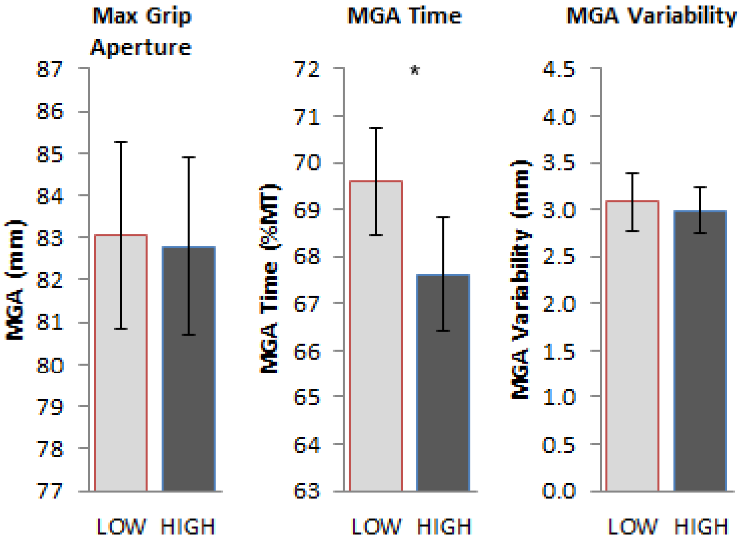


Figure 11 – Grasp kinematics by Demand manipulation in the CLOSED-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean.

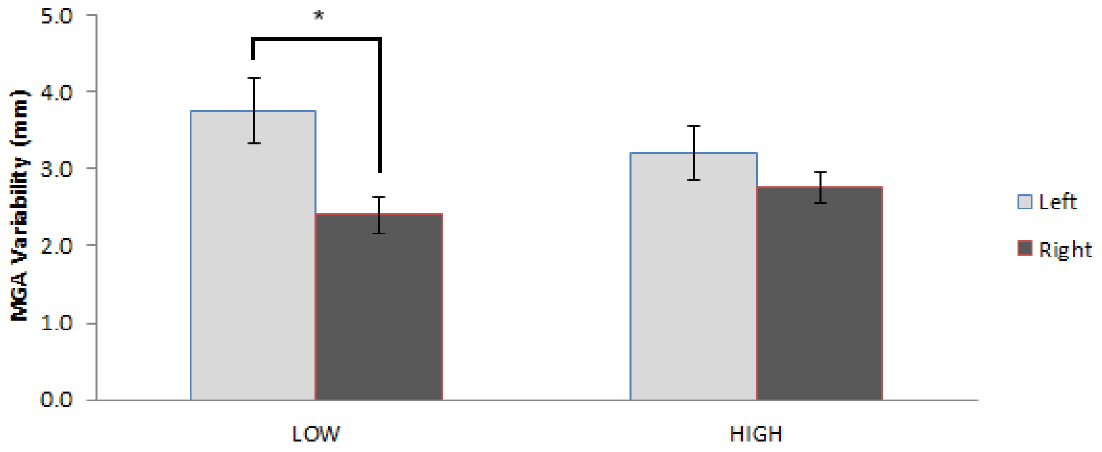


Figure 12 – Hand x Demand interaction on vMGA in the CLOSED-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean. Right hand reach-to-grasp movements are significantly less variable than are left hand reach-to-grasp movements in the LOW demand condition. In the HIGH demand condition, there is no significant variability difference between hands.

Open-loop: Reach Kinematics

Effects of hand (Fig. 13), demand (Fig. 14), and interactions (Fig. 15) are reported for the reach kinematics in the OPEN-LOOP visual condition. No main effects of hand or demand or interactions were found in RT. For PV a significant interaction of Hand X Demand was observed (F(1,14)=6.109, *p*=.027) (Fig. 15). Follow-up paired sample t-tests showed that participants reached significantly higher PVs in left-handed movements (t(14)=2.3; *p*<0.05) in the LOW demand condition (M=0.749, SE=.05 m/s) than in the HIGH demand condition (M=0.721, SE=.05 m/s)[10]. The same was not true for the right-handed movements (*p*>.2).

A significant effect of demand was found on MT (F(1,14)=47.638, *p*<.001) and DPt (F(1,14)=21.072, *p*<.001) (Fig. 14). When reaching for a glass in the HIGH demand condition, reaches took longer to complete (M=1219, SE=55 ms) than they did in the LOW demand condition (M=1119, SE=48 ms). Participants also spent a significantly larger percentage of the reach decelerating in the HIGH demand condition (M=70.1, SE=0.7%) than in the LOW demand condition (M=68.0, SE=0.9%).

---

[10] This difference was not significant following Bonferonni correction (revised alpha ≤ .025).

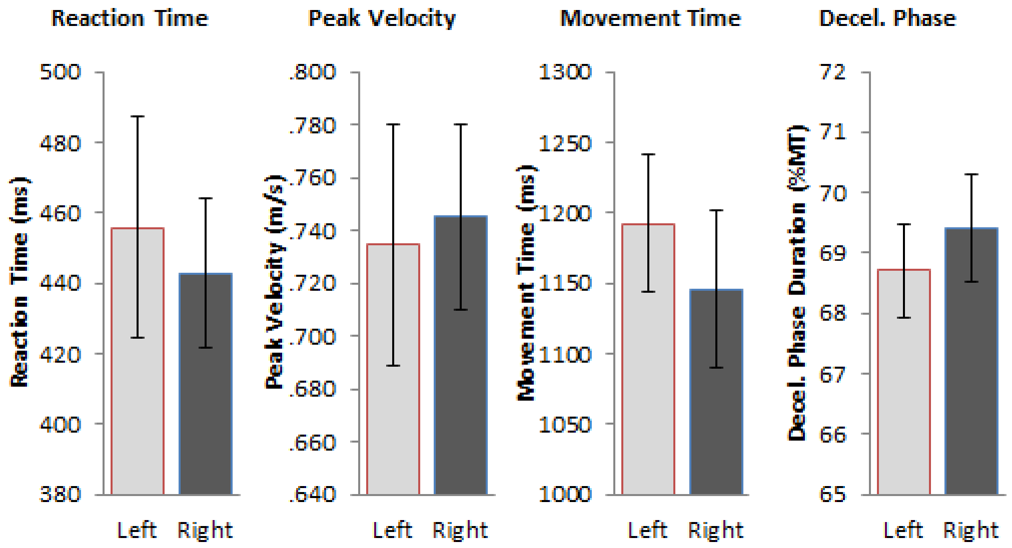


Figure 13 – Reach kinematics by Hand manipulation in the OPEN-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean.

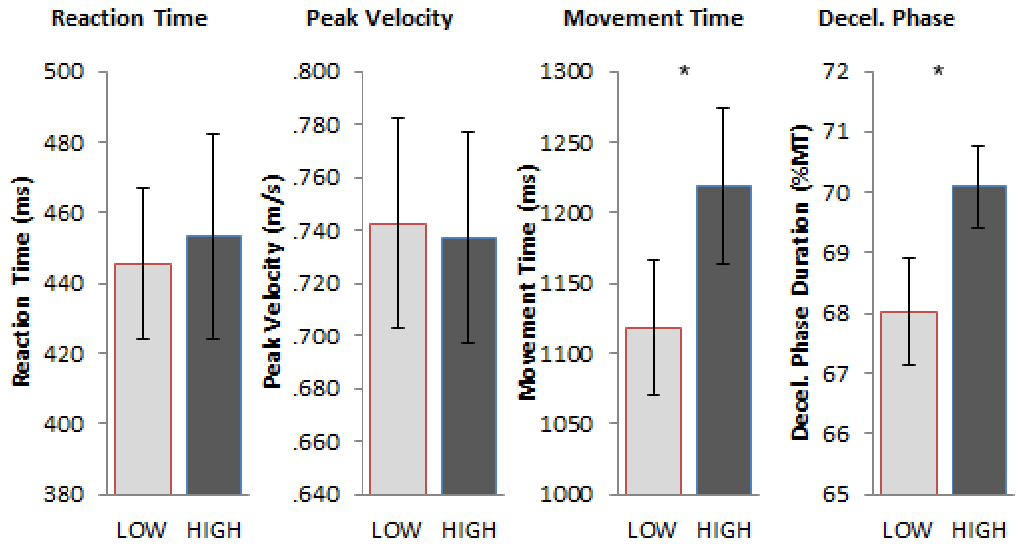


Figure 14 – Reach kinematics by Demand manipulation in the OPEN-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean.

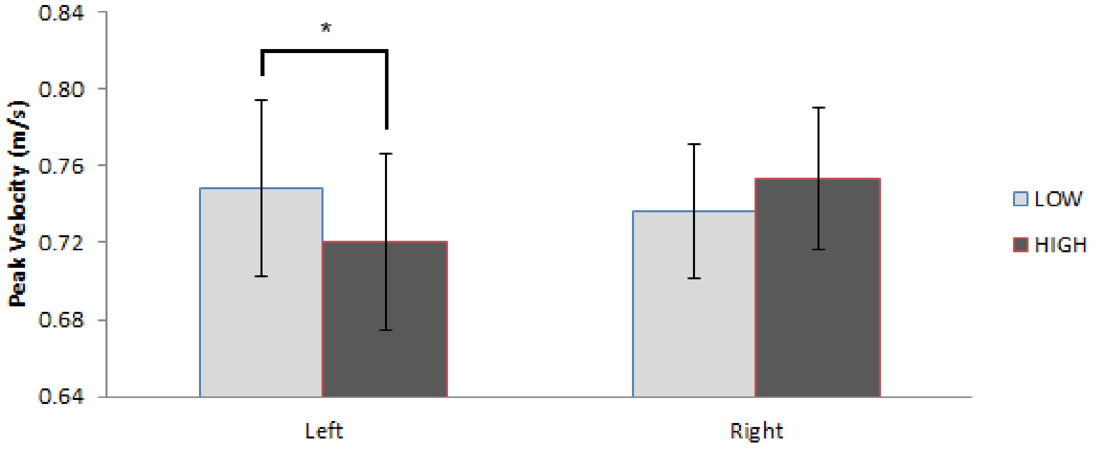


Figure 15 – Hand x Demand interaction on PV in the OPEN-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean. Left hand reach-to-grasp movements reach significantly higher peak velocities in the LOW demand condition than they do in the HIGH demand condition. The reverse is true for right handed reach-to-grasp movements, which reach higher PVs in the HIGH demand condition than they do in the LOW demand condition (though this difference is not significant).

Open-loop: Grasp Kinematics

Effects of hand (Fig. 16) and Demand (Fig. 17) are reported for the grasp kinematics in the OPEN-LOOP visual condition. No main effects of hand or demand or interaction were found in MGA. A borderline effect of demand was found in MGAt, (F(1,14)=3.998, *p*=.065) (Fig. 17) in which MGAt occurred earlier in the grasp in the HIGH demand condition (M=58.4, SE=0.7%) than in the LOW demand condition (M=59.8, SE=0.7%). A borderline effect of hand was also found in the vMGA (F(1,14)=3.956, *p*=.067) (Fig. 16) where MGA was more variable for the left hand (M=4.25, SE=.37 mm) than for the right hand (M=3.58, SE=.42 mm).

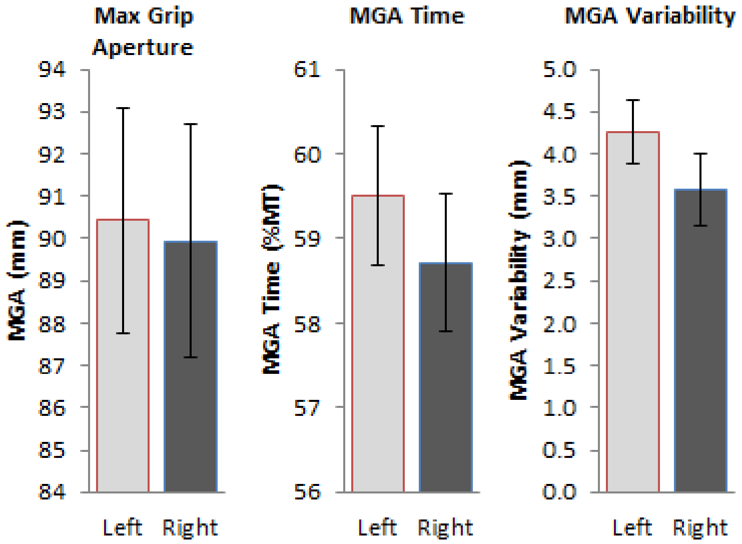


Figure 16 – Grasp kinematics by Hand manipulation in the OPEN-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean.

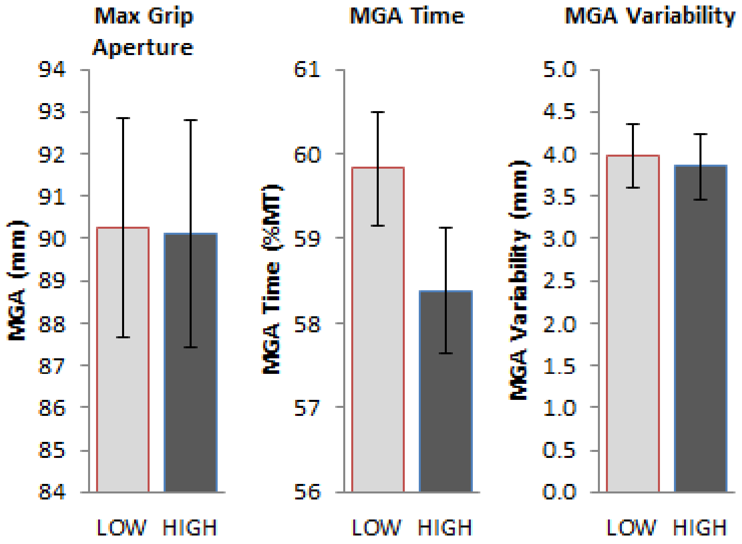


Figure 17 – Grasp kinematics by Demand manipulation in the OPEN-LOOP visual condition (Experiment 1). Columns represent means ± standard error mean.

Delay: Reach Kinematics

Effects of hand (Fig. 18) and demand (Fig. 19) are reported for the reach kinematics in the DELAY visual condition. No main effect of hand or demand or interaction was found in RT. A borderline effect of demand was found for PV (F(1, 14)=3.614, *p*=.078). Reach-to-grasp movements in the LOW demand condition (M=.662, SE=.03 m/s) reached higher PVs than movements in the HIGH demand condition (M=.642, SE=.03 m/s). For MT there was a main effect of hand (F(1,14)=4.589, *p*=.050) (Fig. 18) and a main effect of demand (F(1,14)=21.768, *p*<.001) (Fig. 19) but no significant interaction (*p*>0.1). Left handed reach-to-grasp movements took longer (M=1381, SE=45 ms) than their right handed equivalents (M=1339, SE=49 ms). Also, when reaching for a glass in the HIGH demand condition, reaches took longer to complete (M=1407, SE=47 ms) than they did in the LOW demand condition (M=1312, SE=47 ms). We also found a main effect of demand on DPt (F(1,14)=13.885, p=.002) (Fig. 19) as participants spent a significantly larger percentage of the reach decelerating in the HIGH demand condition (M=73.6, SE=0.7%) than in the LOW demand condition (M=72.0, SE=0.8%).

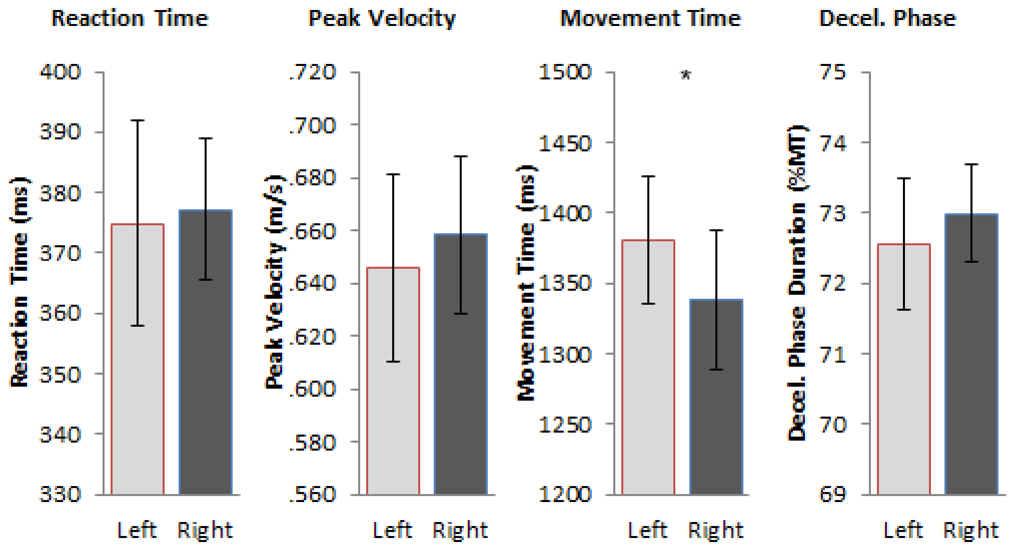


Figure 18 – Reach kinematics by Hand manipulation in the DELAY visual condition (Experiment 1). Columns represent means ± standard error mean.

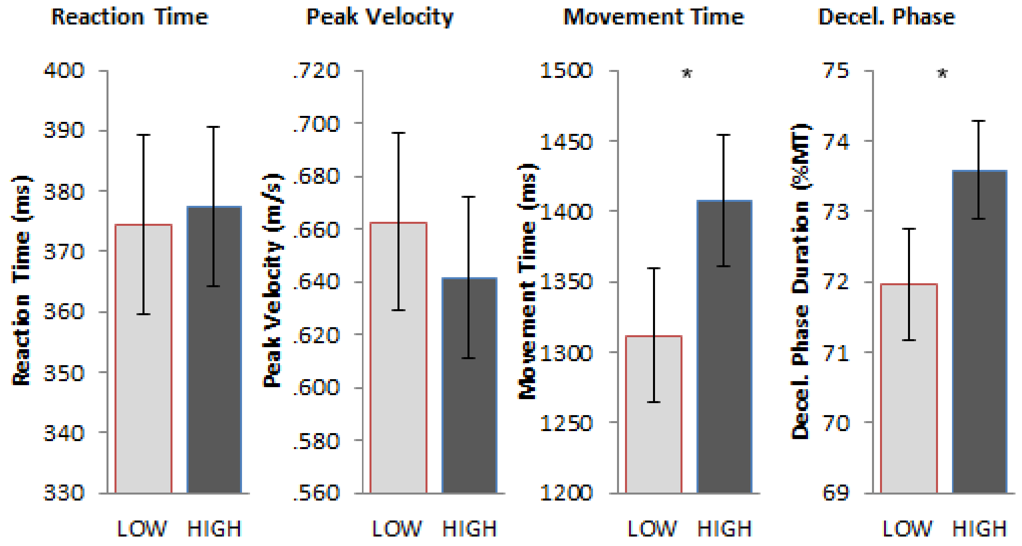


Figure 19 – Reach kinematics by Demand manipulation in the DELAY visual condition (Experiment 1). Columns represent means ± standard error mean.

Delay: Grasp Kinematics

Effects of hand (Fig. 20) and demand (Fig. 21) are reported for the grasp kinematics in the DELAY visual condition. There were no main effects of hand or interactions between Hand X Demand in any kinematic measures of the grasp. Main effects of demand, however, were found in all three measures: MGA (F(1,14)=5.805, *p*=.030), MGAt (F(1,14)=16.662, *p*=.001) and vMGA (F(1,14)=5.541, *p*=.034) (Fig. 21). Grasps directed toward glasses in the HIGH demand condition had smaller MGAs (M=93.6, SE=2.8 mm) than did grasps in the LOW demand condition (M=94.7, SE=2.9 mm). MGAt was earlier in the HIGH demand condition (M=51.5, SE=1.0%) than in the LOW demand condition (M=54.3, SE=1.0%). Finally, variability was lower in the HIGH demand condition (M=3.15, SE=.31 mm) when compared to the LOW demand condition (M=3.81, SE=.47 mm).

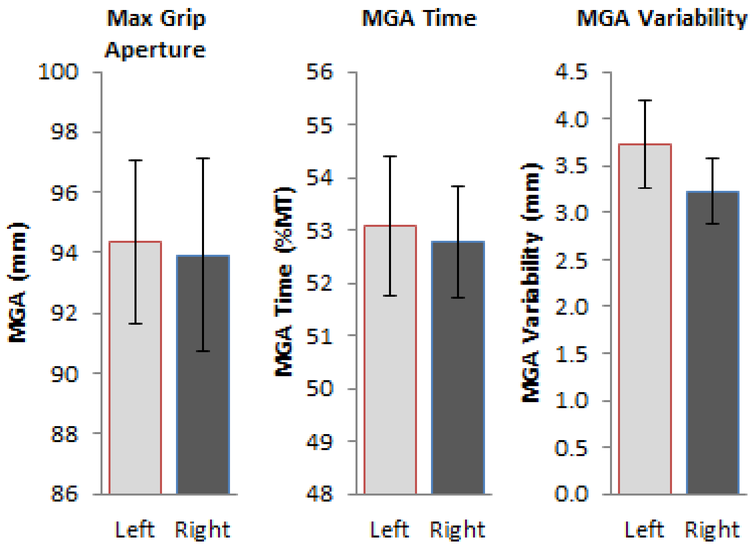


Figure 20 – Grasp kinematics by Hand manipulation in the DELAY visual condition (Experiment 1). Columns represent means ± standard error mean.

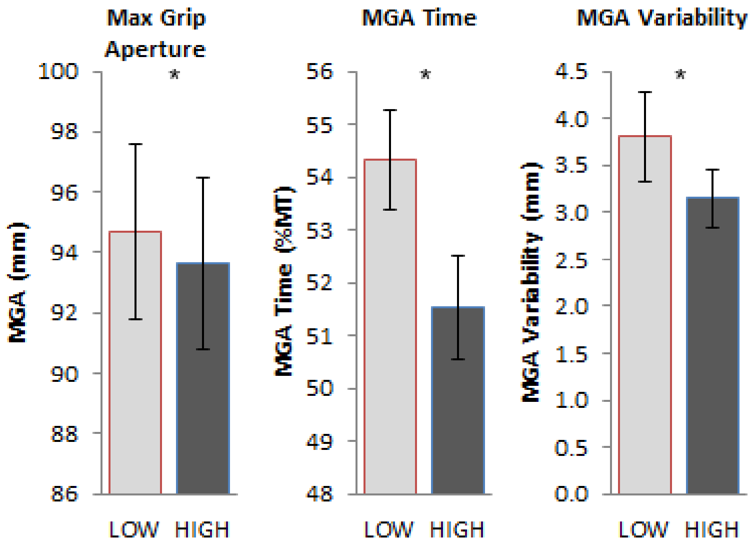


Figure 21 – Grasp kinematics by Demand manipulation in the DELAY visual condition (Experiment 1). Columns represent means ± standard error mean.

Experiment 1: Discussion

The purpose of this study was to investigate the presence (or lack thereof) of manual asymmetries in the reach-to-grasp movement. Based on aiming and reach-to-point literature we hypothesized that increasing task demands would accentuate differences between the hands. We tested participants under three visual conditions, reasoning that manual asymmetries would be due to visual-feedback from the dorsal vision-for-action system, and thus would be found only in the CLOSED-LOOP condition.

We identified some manual asymmetries in both reach and grasp kinematics. A borderline effect of hand used was found on MT in the CLOSED-LOOP condition, where right-handed movements were completed in less time than were left-handed movements. This effect was also observed in the DELAY condition, however, indicating it may not be entirely resultant from dorsal stream asymmetries. vMGA was significantly different between hands in the CLOSED-LOOP condition, wherein right-handed movements had more consistent MGAs than did left-handed movements. This effect is in accordance with the finding that right handed aiming movements exhibit greater accuracy than do left handed aiming movements (Elliott & Chua, 1996; Elliott, et al., 1993; Fisk & Goodale, 1985; Roy & Elliott, 1989; Woodworth, 1899). This effect was only significant in the CLOSED-LOOP condition, when visual feedback was available. When reach-to-grasp movements were executed without ongoing visual feedback (OPEN-LOOP) the effect was borderline (p=.067). The effect was not present in the DELAY condition.

We observed two Hand X Demand interactions. In the CLOSED-LOOP condition, left-handed vMGA was significantly higher than right-handed vMGA in the LOW demand condition only. In the OPEN-LOOP condition, PVs achieved in the LOW demand condition were significantly higher than those achieved in the HIGH demand condition, but only during left-handed movements. No other Hand X Demand interactions were observed.

In sum, the results from this experiment demonstrate significant manual asymmetries in visually-guided reach-to-grasp movements in vMGA and PV, and borderline asymmetries in MT. Because the demand manipulation did have a significant effect on both the reach and grasp kinematics, we postulated that borderline asymmetries may reach significance in a more challenging task. The goal of the second experiment was to accentuate manual asymmetries by increasing the task difficulty beyond that of Experiment 1. We attempted this by substituting the target glass for a taller, narrower 60 ml (2 fluid oz.) shot glass (104 mm tall, 38 mm diameter at the mouth and base). With this change, we hoped to capitalize on the fact that smaller targets produce larger relative maximal grip apertures relative to target size (Muelenbroek, Rosenbaum, & Vaughn, 2001) as well as larger inter-trial variability of MGA (Tretriluxana, Gordon, & Winstein, 2008). We also reasoned that the longer MTs and associated increases in DPt seen when grasping smaller targets (Kudoh et al., 1997) would prove to be additional sources of manual asymmetries.

Experiment 2: Methods

Participants

17 participants (15 female) participated using a shot glass (small glass group). Each participant gave informed consent, in accordance with the local ethics review board. Each participant was tested individually.

Materials, Procedure, and Analyses

Materials and procedure were identical to those of Experiment 1, save that participants completed the task using a smaller, 2 oz. shot glass (104 mm tall, 38 mm across at the mouth and base). An average of 9.2% of trials per subject (± 4.1%) were missing critical data or were considered failures, and as such were excluded from analysis. Any subject missing more than 20% of trial data for any reason was removed from analysis.

Experiment 2: Results

Significant (or approaching significant) main effects and interactions are reported below. Means and standard errors of all measurements are reported in Table 3. ANOVA results (F-statistics and significance) are reported in Table 4.

Table 3 – Results of Experiment 2. Means and standard errors are reported for all reach and grasp kinematic measures.

			RT (ms)	PV (m/s)	MT (ms)	DPt (% MT)	MGA (mm)	MGAt (% MT)	vMGA (mm)
CLOSED-LOOP	LEFT	LOW	476 (22)	0.667 (0.03)	908 (43)	61.2 (0.9)	57.3 (1.9)	65.5 (1.8)	3.71 (0.3)
		HIGH	468 (23)	0.661 (0.03)	959 (42)	62.8 (1.0)	57.8 (2.1)	61.7 (1.9)	3.69 (0.4)
	RIGHT	LOW	454 (32)	0.686 (0.03)	857 (38)	62.5 (0.9)	57.4 (1.6)	67.2 (2.0)	2.94 (0.2)
		HIGH	471 (27)	0.673 (0.03)	922 (41)	64.7 (0.8)	57.1 (1.7)	64.0 (2.0)	3.36 (0.3)
OPEN-LOOP	LEFT	LOW	464 (24)	0.599 (0.03)	1325 (62)	73.6 (1.0)	69.7 (2.2)	50.2 (1.8)	4.51 (0.4)
		HIGH	441 (23)	0.588 (0.03)	1425 (54)	75.3 (0.8)	69.6 (2.5)	49.5 (1.8)	4.15 (0.5)
	RIGHT	LOW	441 (23)	0.643 (0.03)	1240 (52)	73.9 (0.5)	68.1 (2.1)	51.5 (1.8)	4.22 (0.6)
		HIGH	468 (17)	0.603 (0.03)	1409 (64)	76.2 (0.8)	68.2 (2.2)	48.9 (2.0)	4.13 (0.3)
DELAY	LEFT	LOW	369 (18)	0.485 (0.02)	1648 (65)	77.0 (1.1)	73.1 (2.4)	45.2 (2.0)	5.00 (0.4)
		HIGH	362 (20)	0.462 (0.02)	1830 (82)	78.3 (1.3)	73.9 (2.7)	42.4 (1.9)	4.36 (0.6)
	RIGHT	LOW	358 (20)	0.480 (0.02)	1695 (58)	79.0 (0.8)	70.9 (2.6)	43.7 (2.0)	4.12 (0.4)
		HIGH	382 (21)	0.466 (0.02)	1829 (59)	80.1 (0.8)	71.2 (2.6)	43.0 (2.3)	4.58 (0.5)

Table 4 – ANOVA results of Experiment 2. Significant results (*p*<.05) are marked with an asterisk (*). Borderline effects (.05<*p*<.1) are marked with a cross (†).

		RT	PV	MT	DPt	MGA	MGAt	vMGA
CLOSED-LOOP	Hand	0.06	1.15	9.03*	2.79	0.06	1.26	3.75†
	Demand	0.10	2.36	13.24*	34.25*	0.13	17.80*	0.44
	Hand X Demand	0.74	0.39	0.51	0.46	1.29	0.09	1.97
OPEN-LOOP	Hand	0.01	2.99	2.53	0.78	0.58	0.11	0.10
	Demand	0.02	15.91*	50.46*	23.29*	0.00	6.59*	0.55
	Hand X Demand	3.32†	5.08*	3.10	1.08	0.02	3.25†	0.16
DELAY	Hand	0.10	0.01	0.31	6.60*	1.54	0.06	0.35
	Demand	0.95	11.65*	55.18*	10.50*	0.87	8.53*	0.11
	Hand X Demand	2.81	1.63	1.64	0.13	0.22	2.29	2.38

Closed-loop: Reach Kinematics

Effects of hand (Fig. 22) and demand (Fig. 23) are reported for the reach kinematics in the CLOSED-LOOP visual condition. No main effects of hand or demand or interaction was found in RT or PV. For MT there was a main effect of hand (F(1,16)=9.033, *p*=.008) (Fig. 22) and a main effect of demand (F(1,16)=13.237, *p*=.002) (Fig. 23) but no significant interaction (*p*>0.4). Left handed reach-to-grasp movements took significantly longer (M=933, SE=41 ms) than did right handed movements (M=890, SE=39 ms). Also, when reaching for a glass in the HIGH demand condition, reaches took longer to complete (M=940, SE=40 ms) than they did in the LOW demand condition (M=883, SE=40 ms). We also found a main effect of demand on DPt (F(1,16)=34.252, *p*<.001) (Fig. 23) as participants spent a significantly larger percentage of the reach decelerating in the HIGH demand condition (M=63.7, SE=0.7%) than in the LOW demand condition (M=61.8, SE=0.7%).

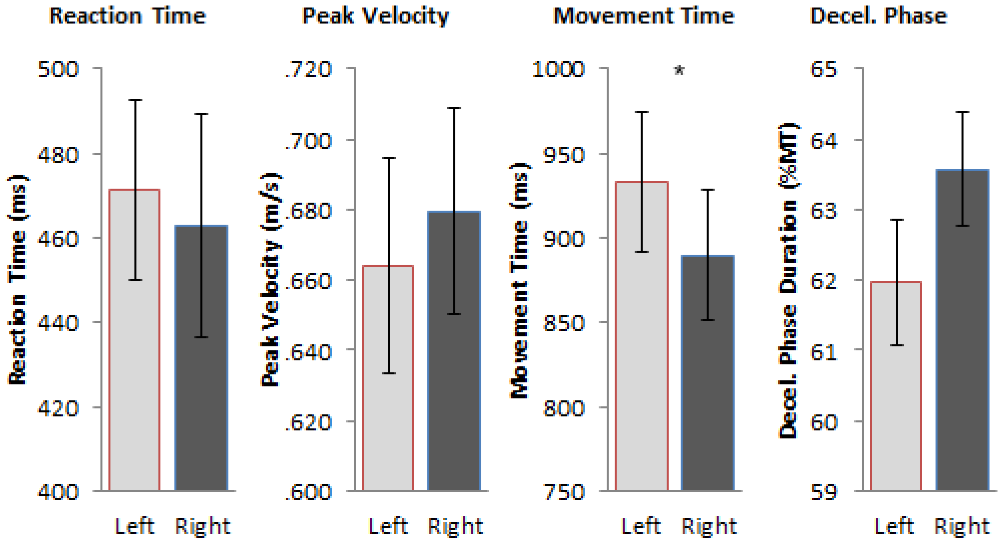


Figure 22 – Reach kinematics by Hand manipulation in the CLOSED-LOOP visual condition (Experiment 2). Columns represent means ± standard error mean.

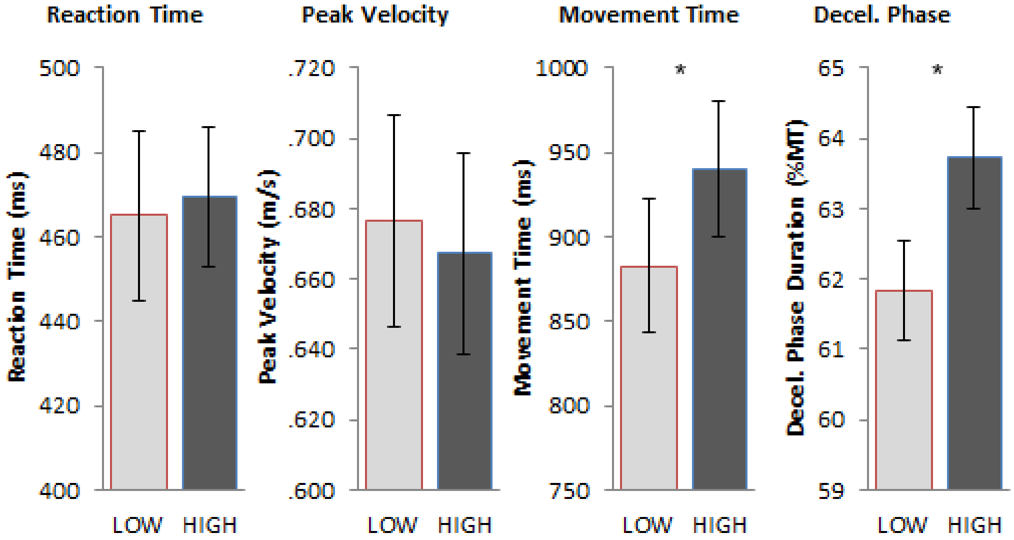


Figure 23 – Reach kinematics by Demand manipulation in the CLOSED-LOOP visual condition (Experiment 2). Columns represent means ± standard error mean.

Closed-loop: Grasp Kinematics

Effects of hand (Fig. 24) and demand (Fig. 25) are reported for the grasp kinematics in the CLOSED-LOOP visual condition. No main effects of hand or demand or interaction between hand and demand was found in MGA. A main effect of demand was found in MGAt (F(1,16)=17.797, *p*<.001) (Fig. 25). MGAt occurred earlier in the grasp in the HIGH demand condition (M=62.9, SE=1.8%) than in the LOW demand condition (M=66.3, SE=1.6%). A borderline effect of hand was also found in the vMGA (F(1,16)=3.751, *p*=.071) (Fig. 24) where MGA was more variable for the left hand (M=3.70, SE=.34 mm) than for the right hand (M=3.15, SE=.20 mm).

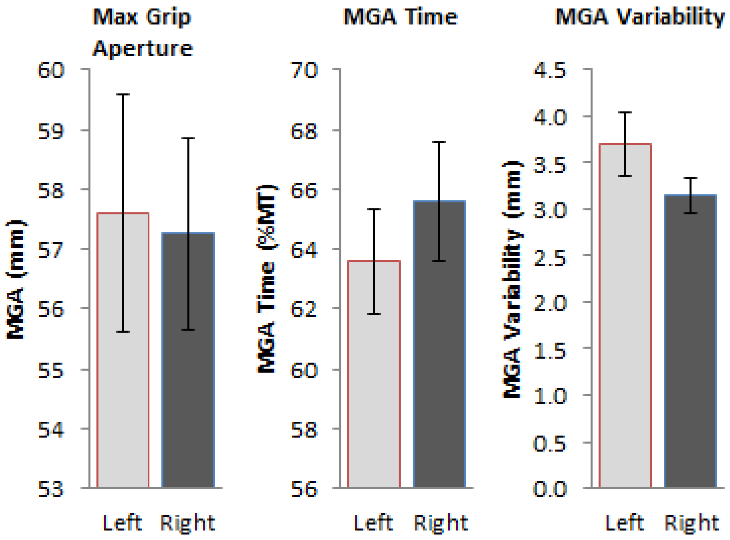


Figure 24 – Grasp kinematics by Hand manipulation in the CLOSED-LOOP visual condition (Experiment 2). Columns represent means ± standard error mean.

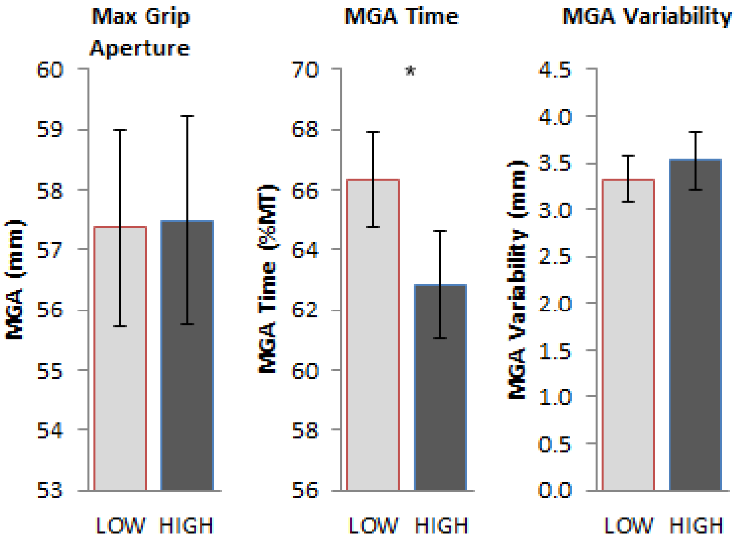


Figure 25 – Grasp kinematics by Demand manipulation in the CLOSED-LOOP visual condition (Experiment 2). Columns represent means ± standard error mean.

Open-loop: Reach Kinematics

Effects of hand (Fig. 26), demand (Fig. 27), and interactions (Fig. 28) are reported for the reach kinematics in the OPEN-LOOP visual condition. A borderline interaction between Hand and Demand was found on RT (F(1, 16)=3.315, *p*=.087). This effect may be due to the direction of difference between demand conditions for either hand; the left hand reacts more quickly in the HIGH demand condition, while the right hand reacts more quickly in the LOW demand condition (Table 3). The source of this effect is uncertain, however, as follow-up paired sample t-tests showed that no hand differences existed in either demand condition (*p*>.19), and demand conditions were not significantly different with either hand (*p*>.07).

A main effect of demand was observed on PV (F(1,16)=15.910, *p*=.001) (Fig. 27). Participants reached significantly higher PVs in the LOW demand condition (M=.621, SE=.03 m/s) than they did in the HIGH demand condition (M=.596, SE=.03 m/s). We also found a significant Hand X Demand interaction in PV (F(1,16)=5.082, *p*=.039) (Fig. 28). Reach-to-grasp movements completed with the right hand reached significantly higher PVs (t(16)=5.941. *p*<.001) in the LOW demand condition (M=0.64, SE=.03 m/s) than in the HIGH demand condition (M=0.60, SE=.03 m/s). This effect was not present in the left-handed movements (*p*>.3).

A main effect of demand was observed on MT (F(1,16)=50.463, *p*<.001), and DPt (F(1,16)=23.294, *p*<.001) (Fig. 27). When reaching for a glass in the HIGH demand condition, reaches took longer to complete (M=1417, SE=56 ms) than they did in the LOW demand condition (M=1283, SE=55 ms). With respect to DPt, participants spent a significantly larger percentage of the reach decelerating in the HIGH demand condition (M=75.7, SE=0.7%) than in the LOW demand condition (M=73.8, SE=0.7%).

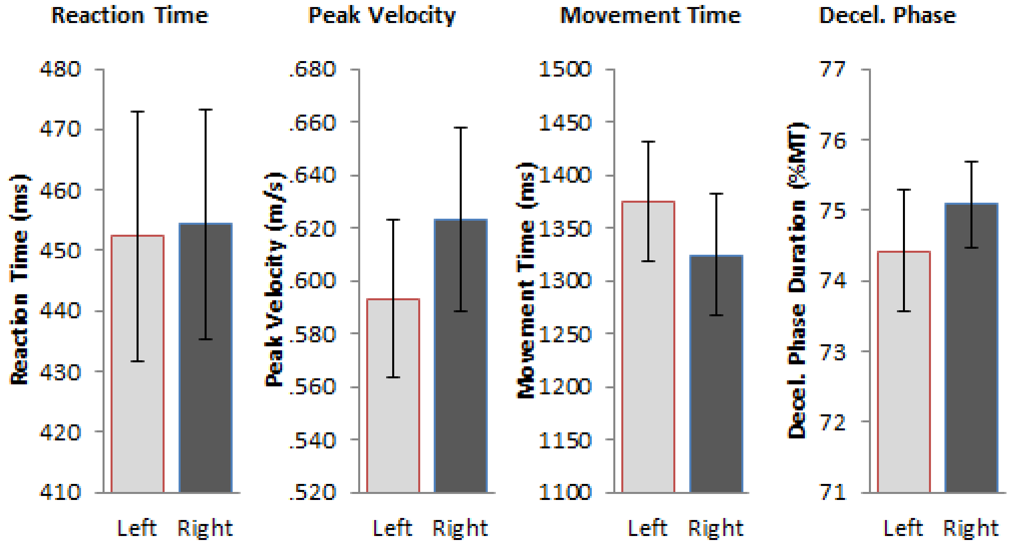


Figure 26 – Reach kinematics by Hand manipulation in the OPEN-LOOP visual condition (Experiment 2). Columns represent means ± standard error mean.

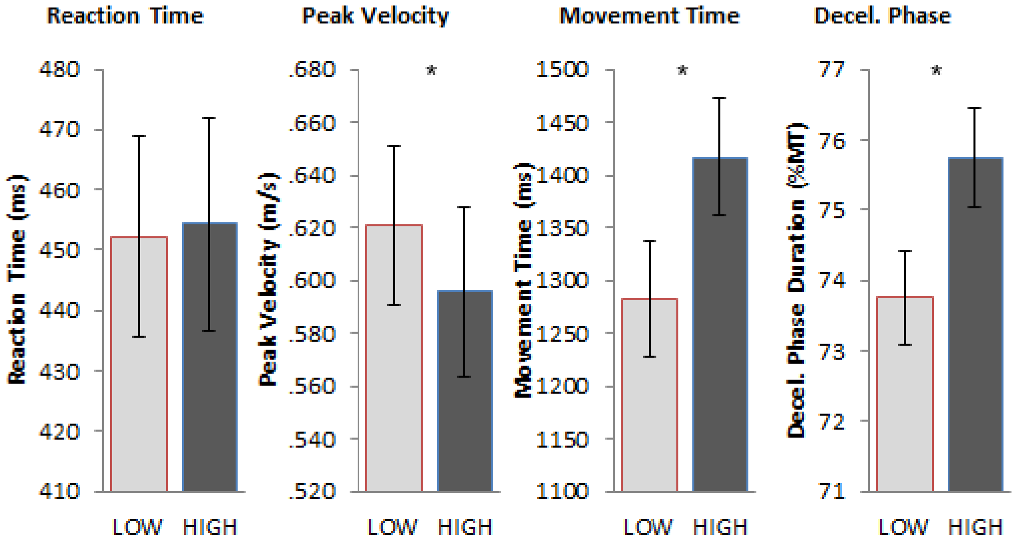


Figure 27 – Reach kinematics by Demand manipulation in the OPEN-LOOP visual condition (Experiment 2). Columns represent means ± standard error mean.

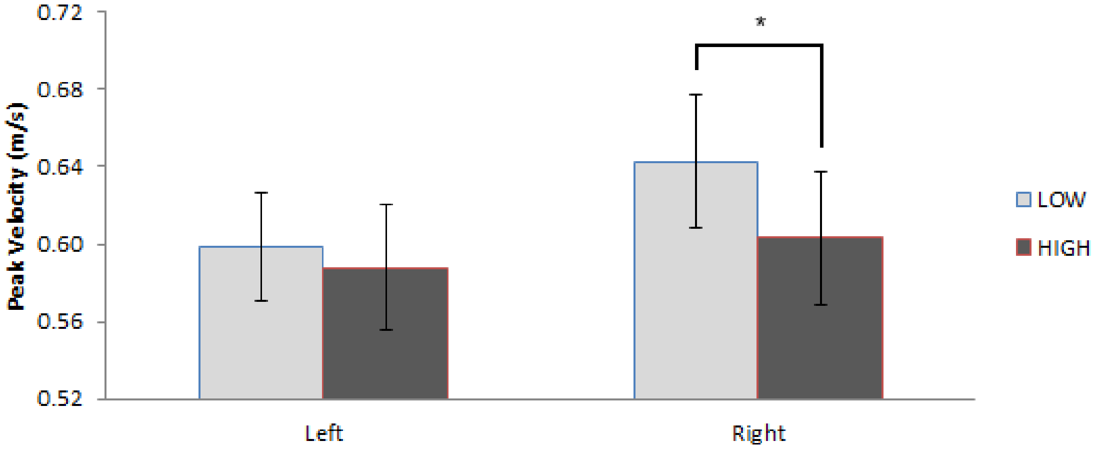


Figure 28 – Hand x Demand interaction on PV in the OPEN-LOOP visual condition (Experiment 2). Columns represent means ± standard error mean. Right hand reach-to-grasp movements achieve significantly higher peak velocities in the LOW demand condition than they do in the HIGH demand condition. There is no effect of demand during reach-to-grasp movements made with the left hand.

Open-loop: Grasp Kinematics

Effects of hand (Fig. 29) and demand (Fig. 30) are reported for the grasp kinematics in the OPEN-LOOP visual condition. No main effects of hand or demand or interactions between hand and demand were found in MGA or vMGA. A main effect of demand was found in MGAt, (F(1,16)=6.593, *p*=.021) (Fig. 30). MGAt occurred earlier in the grasp in the HIGH demand condition (M=49.2, SE=1.7%) than in the LOW demand condition (M=50.9, SE=1.6%). We also found a borderline interaction between hand and demand in MGAt (F(1, 16)=3.254, *p*=.09). Follow-up t-tests revealed that this effect was due to a significant effect of demand in reaches completed with the right hand (t(16)=.825, *p*=.005). In reaches completed with the right hand, MGAt occurred earlier in the grasp in the HIGH demand condition (M=48.9, SE=2.0) than the LOW demand condition (M=51.5, SE=1.8). This effect was not significant in reaches completed with the left hand (*p*>.4).

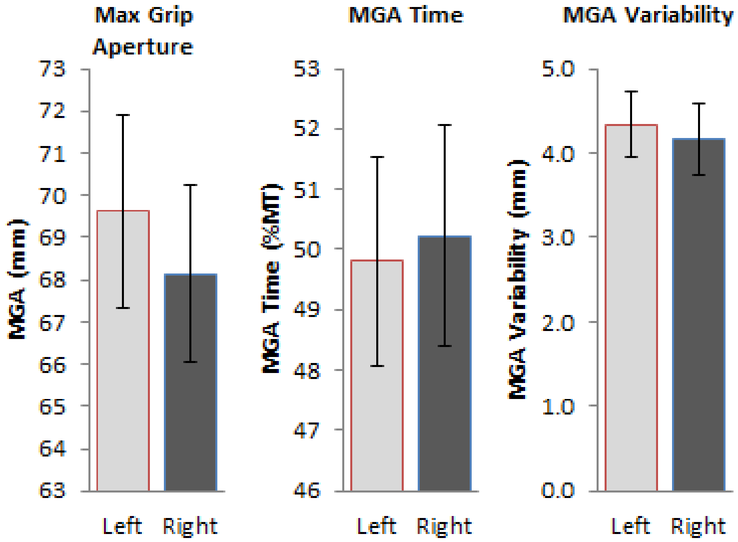


Figure 29 – Grasp kinematics by Hand manipulation in the OPEN-LOOP visual condition (Experiment 2). Columns represent means ± standard error mean.

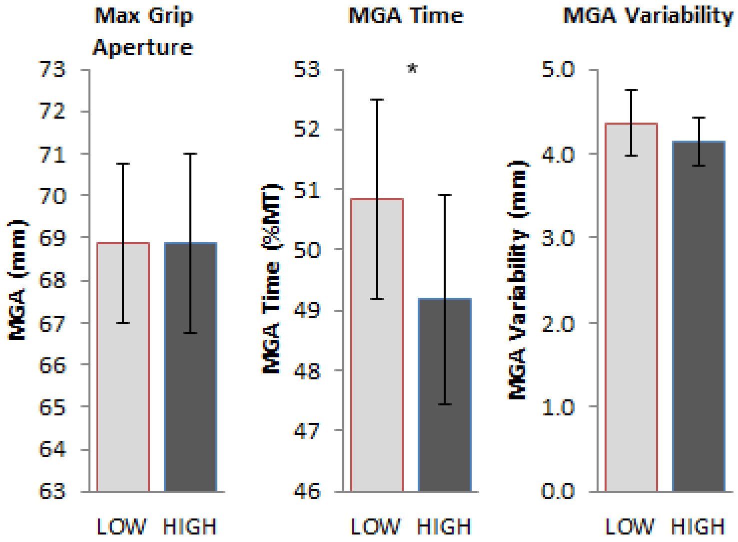


Figure 30 – Grasp kinematics by Demand manipulation in the OPEN-LOOP visual condition (Experiment 2). Columns represent means ± standard error mean.

Delay: Reach Kinematics

Effects of hand (Fig. 31) and demand (Fig. 32) are reported for the reach kinematics in the DELAY visual condition. No main effects of hand or demand or interaction was found in RT. A main effect of demand was found on PV (F(1,16)=11.650, *p*=.004) and MT (F(1,16)=55.177, *p*<.001) (Fig. 32). Participants reached significantly higher PVs in the LOW demand condition (M=.483, SE=.02 m/s) than they did in the HIGH demand condition (M=.464, SE=.02 m/s). When reaching for a glass in the HIGH demand condition, reaches took longer to complete (M=1830, SE=68 ms) than they did in the LOW demand condition (M=1671, SE=57 ms).

For DPt there was a main effect of hand (F(1,16)=6.602, *p*=.021) (Fig. 31) and a main effect of demand (F(1,16)=10.497, *p*=.005) (Fig. 32) but no significant interaction (*p*>0.3). Participants spent less of the movement decelerating during left-handed movements (M=77.7, SE=1.2%) than during right-handed movements (M=79.5, SE=0.7%). Participants also spent a significantly larger percentage of the reach decelerating in the HIGH demand condition (M=79.2, SE=1.0%) than in the LOW demand condition (M=78.0, SE=0.9%).

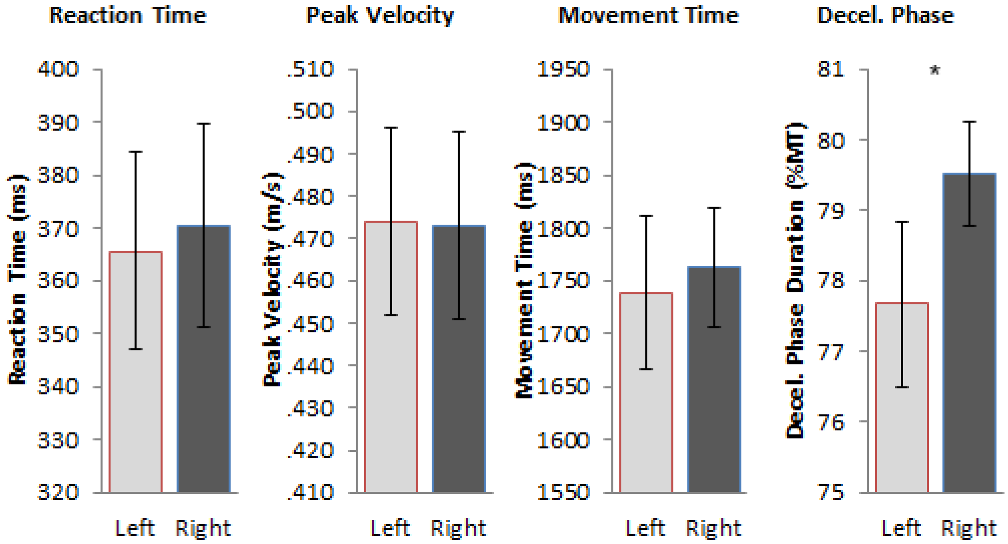


Figure 31 – Reach kinematics by Hand manipulation in the DELAY visual condition (Experiment 2). Columns represent means ± standard error mean.

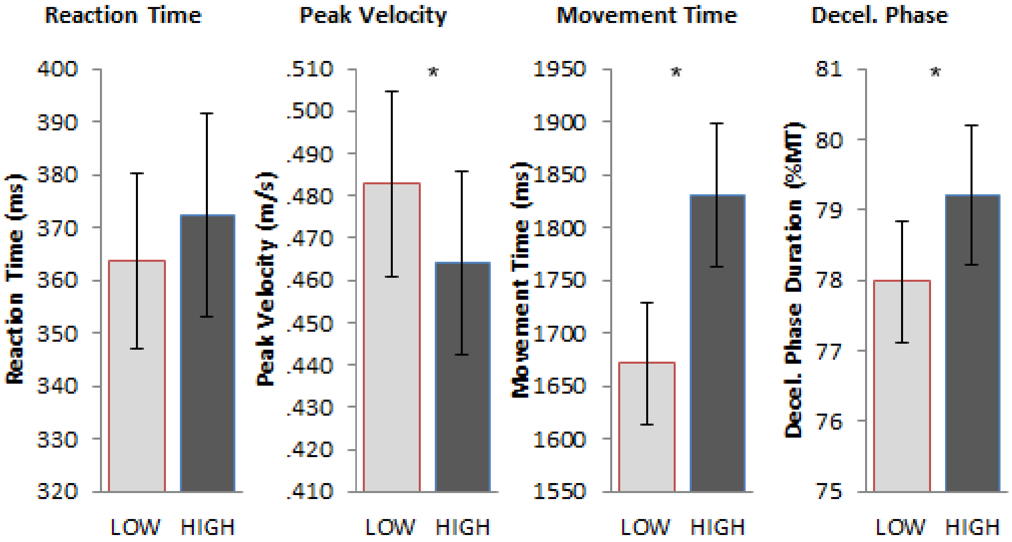


Figure 32 – Reach kinematics by Demand manipulation in the DELAY visual condition (Experiment 2). Columns represent means ± standard error mean.

Delay: Grasp Kinematics

Effects of hand (Fig. 33) and demand (Fig. 34) are reported for the grasp kinematics in the DELAY visual condition. No main effects of hand or demand or interactions between hand and demand were found in MGA or vMGA. A main effect of demand was found in MGAt (F(1, 16)=8.534, *p*=.010) (Fig. 34). MGAt occurred earlier in the grasp in the HIGH demand condition (M=42.7, SE=1.8%) than in the LOW demand condition (M=44.5, SE=1.8%).

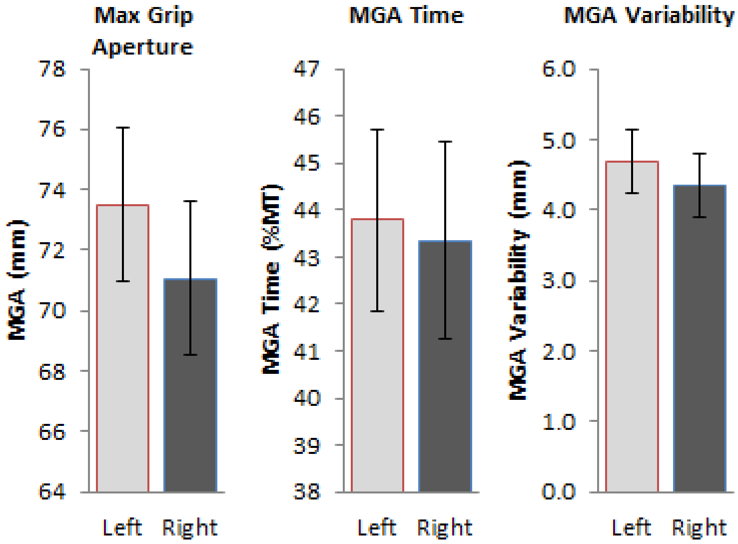


Figure 33 – Grasp kinematics by Hand manipulation in the DELAY visual condition (Experiment 2). Columns represent means ± standard error mean.

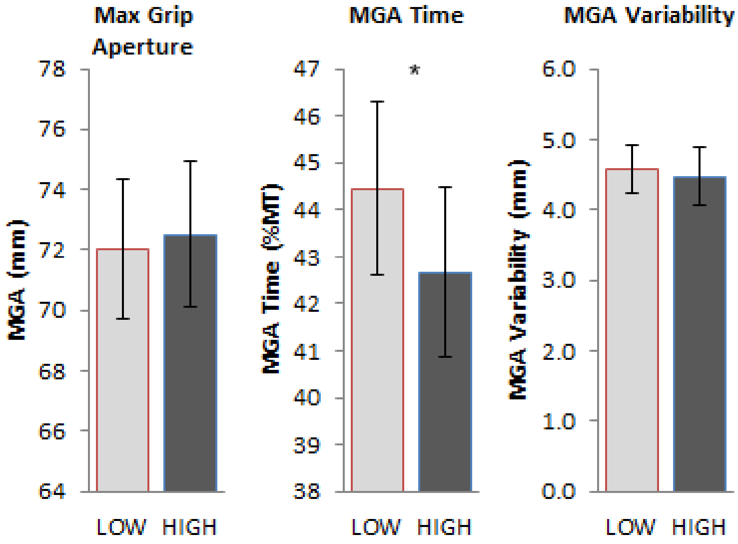


Figure 34 – Grasp kinematics by Demand manipulation in the DELAY visual condition (Experiment 2). Columns represent means ± standard error mean.

Chapter 3: General Discussion and Caveats

Discussion

Research has shown that when using the right hand, right-handed people complete reaching movements (i.e., aiming and pointing) with greater end-point accuracy and speed than when using the left hand (Elliott & Chua, 1996; Elliott, et al., 1993; Fisk & Goodale, 1985; Roy & Elliott, 1989; Woodworth, 1899). These results led to the suggestion that the left hemisphere may be more specialized for visuomotor control, a speculation that dates to the early 20th century, with work done by Woodworth and Liepmann (Liepmann, 1925; Woodworth, 1899). The purpose of this thesis was to investigate if manual asymmetries in the reach-to-grasp action exist based on two hypotheses: 1) manual asymmetries are resultant from asymmetries in the dorsal vision-for-action system; and 2) manual asymmetries are significant only in a demanding task.

To test these hypotheses, we devised an experiment wherein we asked subjects to reach for, grasp, and sip from a glass of water under various visual-feedback and demand conditions. By manipulating visual-feedback availability, we produced dorsal stream- and ventral stream-guided reach-to-grasp movements. Visually-guided reach-to-grasp actions (our CLOSED-LOOP condition) are controlled by the dorsal stream, while memory-guided reach-to-grasp actions (our DELAY visual condition) are controlled by the ventral stream. We hypothesized that manual asymmetries would appear in the CLOSED-LOOP visual condition, but not the DELAY visual condition. The OPEN-LOOP condition may receive input from both visual streams: early portions of the reach-to-grasp movement may benefit from residual input from the dorsal stream (i.e., input which has not yet decayed) while the latter, control-phase portion of the movement would rely on memory-based information (Hu, Eagleson, & Goodale, 1999). We manipulated task difficulty by changing the level of water in the target glass. The HIGH demand condition used a full glass of water, while the LOW demand condition used a nearly empty glass of water. Woodworth showed that the accuracy and smoothness advantages enjoyed in right-handed reaching movements were only apparent when participants completed pointing movements at normal or quickened speeds; if participants were allowed to slow down their movements, thereby reducing the demands of the task, manual asymmetries disappeared (Woodworth, 1899). Based on these results, we hypothesized that the HIGH demand condition would produce stronger manual asymmetries than would the LOW demand condition. In Experiment 1, we used a standard size drinking glass as the target. In Experiment 2, we decreased the width and increased the height of the target, thereby increasing the demands of the task.

In the following sections I will review and discuss the effects of our manipulations on the kinematic measures of the reach-to-grasp movement on a variable by variable basis. In the final section, we will discuss these effects as they relate to the thesis hypotheses.

Reaction Time

No Hand differences were found in RT in any of the visual conditions. Neither did we find an effect of Demand, which is consistent with previous reports (Castiello, Bennett, & Stelmach 1993b; Prabhu, Lemon, & Haggard, 2007).

Many reaching studies have been performed which demonstrate a left hand reaction time advantage for reaching/pointing movements in right handed participants (Boulinguez, Nougier, & Velay, 2001a; Carson, Chua, Elliott, & Goodman, 1990; Carson, Goodman, Chua, & Elliott, 1993; Elliott, et al., 1993; Velay, Daffaure, Raphael, & Benoit-Dubrocard, 2001; for review, see Grouios, 2006). However, as we have shown here (and has been reported elsewhere), no such reaction time advantage is evident in the reach-to-grasp movement. We suspect this effect disappears because reach-to-grasp movements, despite having a reach component and a grasp component (Jeannerod, 1986a), are not simply the sum of reach and grasp components. In order to produce an accurate reaching/pointing movement, the visuomotor system must account for egocentric location, relative movement, and target size in 2 dimensions (i.e., area of a point to be touched). By contrast, to produce an accurate grasp, the visuomotor system must account for shape and size in 3 dimensions (i.e., volume, or area of two opposing points to be grasped), target fragility, frictional coefficients (if the target is to be picked up or moved), and a host of other factors in addition to those intrinsic to the reach. Because of the increased complexity in the reach-to-grasp movement, the parameters assessed when producing accurate grasps are more complex than those assessed in producing accurate reaches. We conclude that, for this reason, the reach-to-grasp movement is more than simply the sum of a reaching movement and a grasping movement. This speculation is supported by a study from Castiello, Bennett, and Stelmach (1993b), who found that perturbations to a target location post-movement initiation are reflected in changes in the grasp kinematics before they are reflected in reach kinematics. Thus, despite the physical requirement that the reach be completed before the grasp can occur, the grasping component is not necessarily activated after the reaching component of the same movement. This would imply that reaction time, traditionally measured from the initiation of the reaching component of a movement, is subject to influence from the neurological and physiological requirements of preparing the grasping component of that movement (Castiello, Bennett, & Stelmach, 1993b). If the right-hemisphere/left-hand system has an advantage in processing spatial information (as evidenced by shorter reaction times in reaching movements), this advantage is attenuated by the additional informational processing necessary to produce an accurate grasping movement.

Peak Velocity

There were no main effects of Hand on PV in either experiment, regardless of visual-feedback condition (Tables 2 and 4). We also did not observe a main effect of Demand or interaction of Hand X Demand on PV in the visually-guided (CLOSED-LOOP) condition. However, in the memory-guided (DELAY) condition we found a main effect of Demand in both experiments. In Experiment 1 this was a borderline effect, in Experiment 2 the effect was statistically significant. In both experiments PVs achieved in the LOW demand condition were higher than those in the HIGH demand condition. Because this effect was observed in the memory-guided (DELAY) condition, we interpret it as evidence that the ventral stream's influence produces a slowing of the reach-to-grasp movement in the HIGH demand condition, especially as task difficulty increases. It is possible to speculate that in the DELAY condition the PV achieved in reach-to-grasp movements is more strongly affected by changes in perceived demand precisely because this condition is guided by memory. Memory, as discussed previously, is subjective, vulnerable to illusory influence (e.g., Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Hu & Goodale, 2000) and is exclusively based on perception. In our HIGH demand condition, we perceive a glass that may spill if we reach for it too quickly; we can easily picture ourselves bumping or spilling the glass in a situation where we have misperceived the distance to the target, or over-estimated our ability to stop quickly. By contrast, in the visually-guided (CLOSED-LOOP) condition the perceptual influence of the ventral stream is overridden by the continuing feedback from the dorsal stream. The result being that, in the CLOSED-LOOP condition, PVs remain high regardless of the changing demands of the task.

Interestingly, in the OPEN-LOOP condition and in both experiments, we observed a Hand X Demand interaction. In Experiment 1, during left-handed reach-to-grasp movements, participants achieved lower peak velocities in the HIGH demand (i.e., full glass) condition; this was not the case for right-handed movements, which achieved similarly high PVs in both demand conditions. This result supports the hypothesis that manual asymmetries are contingent on task difficulty. Experiment 2 showed that the right hand attains higher PVs in the LOW demand conditions whereas the left hand is equally slow in both HIGH and LOW demand conditions. In fact, the right hand in the HIGH demand condition achieves similar PVs as the left hand in both demand conditions; it is only the right hand in the LOW demand condition that demonstrates higher PVs. These results support my thesis Hypothesis III, that asymmetries in the reach-to-grasp movement are contingent upon task difficulty, and that these asymmetries favour the left-hemisphere/right-hand system.

Movement Time

We observed main effects of Demand on MT across all visual-feedback conditions in both experiments. Our demand manipulation achieved its intended effect, as reach-to-grasp movements toward targets in the LOW demand condition were completed in significantly less time than those same movements in the HIGH demand condition.

Contrary to results reported in previous studies which reported no kinematic differences between hands (Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana, Gordon, & Winstein, 2008), we observed a main effect of Hand on MT in the CLOSED-LOOP condition in both experiments. In Experiment 1 this was a borderline effect, however in Experiment 2 the effect achieved significance. In both experiments, the right hand completed the reach-to-grasp movement in less time than did the left hand, supporting the idea of left-hemisphere/right-hand advantages in the vision-for-action system and previous findings in the reaching (i.e., aiming and/or pointing) domain. One possible reason why I was able to identify manual asymmetries is our choice of target and task. In the studies cited above, the target used was a solid wooden peg

(Grosskopf & Kuhtz-Buschbeck, 2006) or a tape-wrapped cylinder (Tretriluxana, Gordon, & Winstein, 2008), neither of which carry any negative consequence from being knocked over. In contrast, the drinking glasses used in our experiments would spill if knocked over. This may constitute an increased level of risk associated with the grasp, which may in turn tease out asymmetries (Woodworth, 1899). Additionally, by using an ecologically valid task (i.e., take a sip from the water glass following the grasp), we may have been able to expose manual asymmetries which were previously hidden (Seegelke, Hughes, & Schack, 2011). Intriguingly, movement times were also shorter for the right hand in the DELAY condition in Experiment 1 (but not in Experiment 2). It is possible that the right hand movement time advantage is a property of handedness (i.e., a consequence of practice) but this possibility would fail to explain why it had not been shown in previous studies or in Experiment 2.

Deceleration Phase Duration

We observed main effects of Demand on DPt across all visual-feedback conditions in both experiments. Consistent with the results of previous studies, this effect was independent of hand used (Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana, Gordon, & Winstein, 2008).

In Experiment 2 we observed a main effect of Hand in the DELAY condition, wherein participants spent more time proportionally in the deceleration phase of right-handed reach-to-grasp movements. This effect in the DELAY condition is consistent with reports from a number of reaching studies (Elliott et al., 1993; Heath & Binsted, 2007; Roy & Elliott, 1989) that show longer deceleration phase durations in memory-guided conditions. The fact that this effect was present in Experiment 2 and absent in Experiment 1 may be related to previous findings showing that reach-to-grasp movements towards smaller objects exhibited longer proportional deceleration periods than did those towards larger objects (Kudoh et al., 1997). This is consistent with our findings, as the target width in Experiment 2 was less than that in Experiment 1.

Maximum Grip Aperture

We found no main effect of Hand or interaction of Hand X Demand on MGA. In Experiment 1, we observed a main effect of Demand on MGA in the DELAY condition only, where the LOW demand condition produced reach-to-grasp movements with wider MGAs than did the HIGH demand condition. This effect is consistent with the results reported by Hu, Eagleson, and Goodale (1999), who found that memory-guided reach-to-grasp movements were susceptible to perceptual manipulations. Hu, Eagleson and Goodale (1999) showed that grasps produced from memory are influenced by our visual perception of size, rather than an object's actual size. The level of water in the HIGH demand condition (i.e., full glass) may have made the glass appear smaller in the ventral stream's view by way of the Delboeuf illusion (Delboeuf, 1865). In this illusion, the outer circle in a double-concentric circle set appears smaller than an identically-sized empty circle. If the surface of the water in the HIGH demand condition was perceived as a second circle within the rim of the glass, then this may have made the outer edge of the glass (i.e., the outer circle) appear smaller (Gentaz & Hatwell, 2004; Suzuki & Arashida, 1992). This illusion would not transfer to CLOSED-LOOP visual condition as it has been shown that perceptual illusions do not affect visually-guided grasping (Aglioti, DeSouza, & Goodale, 1995).

Time of Maximum Grip Aperture

As discussed in the Introduction, Jeannerod described prehension as a combination of reach-to-grasp movements (Jeannerod, 1984). The grasping component of prehension (i.e., grip formation) must be synchronized with the reaching component such that the closing aperture of the grip is spatially coincident with the target (Jeannerod, 1986b). The time of maximum grip aperture is therefore a measure of the coordination of the two facets of prehension. As normal MGAt occurs at approximately 70% of MT, deviation from this time may indicate a decoupling of the “normal” reaching and grasping components; alternatively, earlier MGAt may be a compensatory strategy for dealing with target uncertainty. Tables 1 and 3 demonstrate earlier relative MGAt values in the DELAY condition than in the CLOSED-LOOP condition in both experiments. These results are consistent with those of others (Jackson, Jackson, Harrison, Henderson, & Kennard, 1995; Schettino, Adamovich, & Poizner, 2003).

We did not find differences between the hands on MGAt in any of our visual conditions. We did observe a main effect of Demand on MGAt in all our vision manipulations, in both experiments. In the HIGH demand condition, MGAt always occurred significantly earlier in the reach-to-grasp movement than it did in the LOW demand condition. While an earlier MGAt may indicate uncertainty, we must address the possibility that this effect may be a corollary of the Demand effect on MT discussed above. Specifically, If the absolute duration of the movement was longer in the HIGH demand condition, but the absolute timing of the MGA was unchanged between conditions, then the relative timing of MGA would change. MGAs occurring at the same absolute time in both demand conditions would appear relatively earlier in the HIGH demand condition. If you convert the relative values of MGAt (reported in Tables 1 and 3) to absolute values and investigate the demand effect anew, the effect of demand disappears in the CLOSED-LOOP condition in both experiments ($p>.05$). However, the effect is still present in the OPEN-LOOP (both experiments) and DELAY conditions (Experiment 2 only), indicating that the ventral stream may be responsible for the effect of demand on MGAt. This is consistent with the manner in which we manipulated demand; because the dimensions of the target did not change between LOW and HIGH conditions, the manipulation did not affect MGAt in movements guided by the dorsal stream. The *perceived* demand of the task changed with our manipulation, making MGAt vulnerable to a demand effect in the OPEN-LOOP and memory-guided (DELAY) conditions.

Variability of Maximum Grip Aperture

Studies have shown us that reach-to-point actions performed with the right hand have greater endpoint accuracy than do actions performed with the left hand (for review, see Grouios, 2006). End-point accuracy in reach-to-grasp movements is difficult to measure, as a manipulable object may have an infinite number of points from which it can be successfully grasped (Klatzky, Pellegrino, McCloskey, & Doherty, 1989). Instead, accuracy of the grasp may be evaluated from the maximum grip aperture (MGA) measurement; accurate and efficient reach-to-grasp movements will demonstrate consistent MGAs that closely scale to the size of the target to be grasped. Previous researchers have shown that reducing visual feedback (Wing, Turton, & Fraser, 1986) and increasing task difficulty (Mon-Williams & Bingham, 2011) will both increase the variability of MGA (vMGA). A high vMGA shows that the reach-to-grasp movement (and presumably, the motor plan from which it is produced) may be inconsistent (i.e., less accurate) between trials.

During visually-guided movements in Experiment 1, we found a significant difference in vMGA between the left and right-handed reach-to-grasp movements. Specifically, maximum grip apertures produced by the right hand were less variable than those produced by the left hand. The absence of this effect in the memory-guided movement supports my hypothesis that the dorsal stream is responsible for manual asymmetries in the reach-to-grasp movement, and that these asymmetries favour the right hand.

In Experiment 2 we increased the demands of the task, hypothesizing that this manipulation would increase the significance of borderline effects observed in Experiment 1, and in so doing highlight additional manual asymmetries. The visual-feedback and demand manipulations were identical to those in Experiment 1. The results of this experiment showed that the vMGA effect observed in the CLOSED-LOOP condition was not as strong as in Experiment 1. This borderline effect of Hand seen in Experiment 2 could be due to a ceiling effect. One could speculate that variability of MGA had reached a maximum level. By comparing vMGA values from both experiments (Tables 1 and 3), one can see that the vMGAs achieved by either hand in Experiment 2 were as high as, and not different from, those achieved by the left hand in Experiment 1.

We also found a significant interaction of Hand x Demand in Experiment 1. This interaction, however, was in the opposite direction from what was predicted. Right-handed maximum grip apertures were less variable than left-handed MGAs in the LOW demand condition, but not in the HIGH demand condition. It is possible to speculate that the full glass may be acting as a more constant stimulus. While the target glass in the LOW demand condition, being nearly empty, may be viewed as a possible spill-risk in *some* movements, the full glass may be viewed as a possible spill-risk in *all* or *nearly all* movements. This distinction may reduce variability in the HIGH demand condition, thereby masking observable hand differences. We will return to this point later in the discussion.

Hypotheses

In the following section we will review the effects of Hand and Demand as they relate to my thesis hypotheses and predictions.

Hypothesis I

My first hypothesis was that manual asymmetries in the vision-for-action system can be documented by studying manual asymmetries in the kinematics of the reach-to-grasp movement. We tested this by documenting the kinematics of the reach-to-grasp movement of left- and right-handed reach-to-grasp movements while maintaining the functional symmetry of the required actions. Thus, any kinematic asymmetries identified may be attributed to asymmetries within the neural origins of the movement.

Examples of kinematic manual asymmetries were found in both experiments. Because neither the requirements nor the mechanical constraints of the task (in either experiment) varied between hands, we presume that these kinematic asymmetries are due to hemispheric differences in either the motor-planning or motor-control aspects of the reach-to-grasp system. However, because we did not include a left-handed group in either of these experiments, we cannot say for certain that these manual differences favouring the right hand are a result of universal hemispheric asymmetries, or whether they are simply an effect of practice resulting from preferred use of the right hand.

Hypothesis II

My second hypothesis was that hemispheric asymmetries in the reach-to-grasp system are contingent on visual feedback availability. This hypothesis is based on Goodale and Milner's 1992 paper, which summarised 20 years of double-dissociation studies showing that the dorsal stream is essential for controlling visually-guided prehension (Goodale & Milner, 1992). We tested Hypothesis II by investigating the kinematics of the reach-to-grasp movement with either hand in various visual feedback conditions. In the CLOSED-LOOP condition, visual feedback of the moving hand and limb (as well as the target) was available throughout the reach-to-grasp movement. This condition allowed the dorsal stream to provide input towards both the planning and the online-control of the movement. In the OPEN-LOOP condition, visual feedback was available for planning immediately prior to the go-signal, but was removed from the control portion of the movement. The DELAY condition removed vision 2000 ms before movement was to be initiated, removing the dorsal stream's potential for input on both the planning phase and ongoing control phase of the movement (Hu, Eagleson, & Goodale, 1999). We predicted that manual asymmetries would only be significant in the visually-guided (CLOSED-LOOP) condition.

We found support for this hypothesis in MT and vMGA. In Experiment 2 we observed a main effect of Hand in the CLOSED-LOOP condition where right-handed movements were completed in less time than were left-handed movements (Table 4; Fig. 22). Because it was not present in the DELAY condition, this effect supports the hypothesis that hemispheric asymmetries in the reach-to-grasp system are contingent on visual feedback availability.

With respect to vMGA, we found that the right hand produced more consistent maximum grip apertures than did the left hand. The right hand vMGA was smaller than that of the left hand, but only in the CLOSED-LOOP visual condition. In the DELAY and OPEN-LOOP conditions, the vMGA difference between hands was not significant. We can assume that this asymmetry is due to differential input of the dorsal stream in the planning and production of grasps.

These results on reach-to-grasp actions are in line with those of reach-to-point movements that show shorter and less variable movements of the right hand when visual feedback is available (Elliott & Chua, 1996; Elliott, et al., 1993; Fisk & Goodale, 1985; Roy &

Elliott, 1989). Together these studies suggest that the left hemisphere is more specialized in producing faster and more accurate visually-guided actions.

Hypothesis III

Based on results from reaching studies which found manual asymmetries only in sufficiently difficult or speeded tasks (Elliott et al., 1993; Roy & Elliott, 1989; Woodworth, 1899), my third hypothesis was that hemispheric asymmetries in the vision for action system would be contingent upon task difficulty. We predicted that reach-to-grasp asymmetries should be more prominent in grasps requiring a higher degree of precision. These asymmetries should therefore have been manifest in the form of Hand x Demand interaction effects.

We found a Hand x Demand interaction in vMGA (Experiment 1) and in PV (both experiments). A puzzling finding in Experiment 1 is that MGA in right-handed movements was less variable than in left-handed movements, but only in the LOW demand condition. As argued previously, it is possible that full glasses are perceived as a more constant threat, reducing the MGA variability and thus masking hand differences. A similar effect has been reported by Krüger and colleagues, who found that participants responded with reduced joint-angle variability when the demands of a reaching task increased (Krüger, Eggert, & Straube, 2011). Additionally, our result is consistent with balance research, which shows that participants react to threatening situations by reducing joint movement variability (Brown & Frank, 1997; Laufer, Barak, & Chemel, 2006; Moseley & Hodges, 2006).

In Experiment 1, right-handed peak velocities were equally high in both demand conditions. The left hand was affected by demand, as demonstrated by reduced PVs in the HIGH demand condition. In Experiment 2 the left hand achieved equally low peak velocities in both demand conditions; it was only the right hand in the LOW demand condition that reached significantly higher PVs. In both experiments, the results suggest that the right hand is more adept at dealing with demand manipulations.

Although we observed Hand X Demand interactions in only two kinematic measures, the Demand manipulation was responsible for significant effects on most kinematic measurements. In Experiment 1, our HIGH demand condition elicited longer MTs, proportionally longer DPts, and proportionally earlier MGAts. These effects occurred across all visual feedback conditions. In addition to these effects, Experiment 2 revealed that our HIGH demand condition elicited significantly higher PVs in the OPEN-LOOP and DELAY conditions. Our Demand manipulation is therefore an effective way to bring kinematic variability into the reach-to-grasp movement.

Other Considerations

Because other studies have found visual feedback to be a significant source of kinematic variability (Jakobson & Goodale, 1991; Jeannerod, 1984; Wing, Turton, and Fraser, 1986), we ran post-hoc paired-sample t-tests on all kinematic measures to confirm that our vision manipulations produced significant differences within subjects. These tests reaffirmed our contention that the vision manipulation did indeed result in significant differences between the collapsed Hand and Demand conditions. The results of these tests showed that vision had a significant influence on nearly all the variables measured in the experiment (Tables 1 and 4), producing significant effects on MT, PV, DPt, MGA, and MGAt. Reach-to-grasp movements in both experiments showed that kinematic variables favoured reaches conducted with full visual feedback. In both Experiment 1 (Fig. 35) and Experiment 2 (Fig. 36), we can see that when comparing visually-guided (CLOSED-LOOP) and memory-guided (DELAY) reach-to-grasp movements (collapsed across Hand and Demand manipulations), visually-guided movements have higher PVs, shorter MTs, proportionally shorter DPts, smaller MGAs, and earlier relative MGAts. This effect of vision was consistent across both experiments.

The trend of our results is mostly consistent with the literature. However the differences between CLOSED- and OPEN-LOOP conditions in our study differ from those found previously. Results of past studies regarding the behaviour differences between -loop conditions have been inconsistent. Some researchers have found that OPEN-LOOP reaching (Elliott, 1988) and reach-to-grasp behaviour (Hu, Eagleson, & Goodale, 1999) closely resembles that of CLOSED-LOOP, while others (Westwood, Heath, and Roy 2001; Bradshaw and Watt 2002; Franz, Hesse, and Kolath 2007) find that OPEN-LOOP behaviour more closely resembles DELAY behaviour. Our results are mixed: kinematic behaviour in the OPEN-LOOP condition is closer to CLOSED-LOOP behaviour in PV. Conversely, the OPEN-LOOP condition is closer to DELAY behaviour in MT, DPt, MGA, and vMGA. Within our experiment, this distinction becomes even more pronounced when the demand of the reaching condition increases (i.e., in Experiment 2, or our HIGH demand condition). These results are consistent with those predicted by Glover's planning and control theory (Glover, 2004), which posits that early kinematic measurements (i.e., PV, RT) will be more strongly influenced by planning, and late kinematic measurements (MGA, deceleration phase) will be more influenced by online control. The OPEN-LOOP condition allows for control-influenced behaviour early in the reach (mimicking CLOSED-LOOP movements), but falls back onto pre-planned behaviour for the later kinematic aspects (thus appearing similar to movements in our DELAY condition). The current study highlights the importance of visual feedback in the control of reach-to-grasp movements. With respect to most kinematic measures our results demonstrate that the OPEN-LOOP condition was significantly different from the other two visual conditions and, as such, should not be used as a stand-in for either the CLOSED-LOOP (visually-guided) condition or the DELAY (memory-guided) condition.

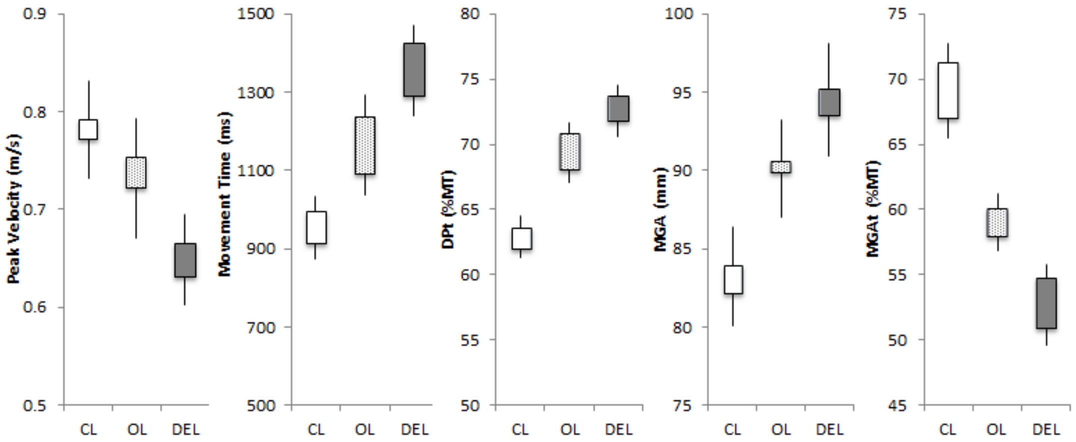


Figure 35 – Experiment 1 kinematic measurements in each visual feedback condition, collapsed across hand and demand manipulations. Box edges denote the highest/lowest average for respective kinematic measurement within respective visual condition. Bars are standard errors of highest/lowest averages. Results of paired-sample t-test show that visual conditions are significantly different from each other in all kinematic measurements (*p*<.001). [Note that these values are averages of all hand and demand conditions previously reported in Table 1.]

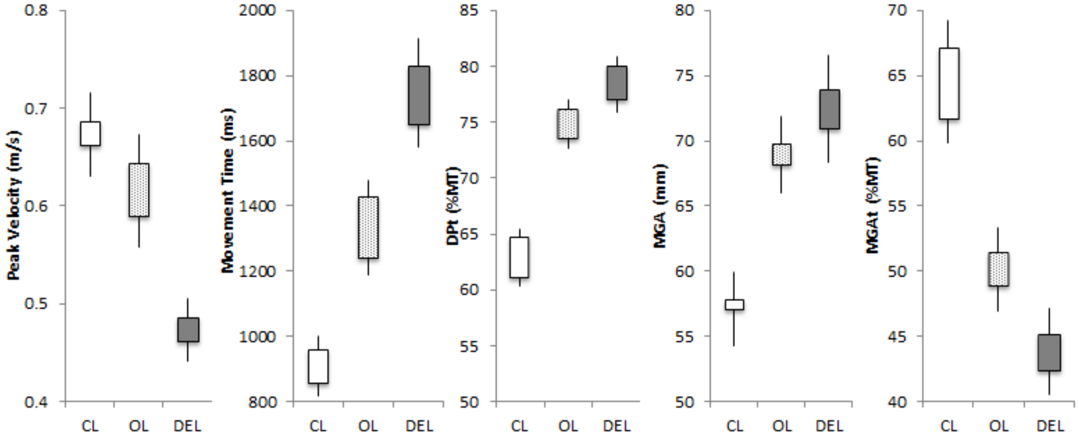


Figure 36 – Experiment 2 kinematic measurements in each visual feedback condition, collapsed across hand and demand manipulations. Box edges denote the highest/lowest average for respective kinematic measurement within respective visual condition. Bars are standard errors of highest/lowest averages. Results of paired-sample t-test show that visual conditions are significantly different from each other in all kinematic measurements (*p*<.001). [Note that these values are averages of all hand and demand conditions previously reported in Table 3.]

Caveats

Through the course of performing these experiments, analyzing the results, and writing this thesis, I have come across several problems which, had I been able to predict two years ago, I could have avoided by taking some precautions. This section will focus on changes I would make to the experimental design and methods.

Experimental Design

Task

Rather than have participants drink from a glass of water, I would replace the reach-to-grasp task with one where they simply moved the glass from a rest position (whose location would be tailored to account for changes in the length of each participant's reach) to a nearby platform, ideally above and behind the initial rest position. This placement would avoid the possibility of interactions arising from ipsilateral and contralateral movements, which may be kinematically different due to a practice effect arising from movement preferences (Stone, Bryant, & Gonzalez, In Press). Removing the command to drink would have two key benefits: first, the HIGH and LOW demand condition glasses would not require refilling after each trial, which would allow us to conduct more trials in the same amount of time. Second, it would allow us to replace the liquid in the glass with something other than water. By using fluids that are more or less dense than water, we could potentially eliminate (or, at least ameliorate) the difference in weight between demand conditions. I believe the increased control from maintaining a perfectly stable fluid level and constant weight between trials would outweigh the negative effects stemming from loss of ecological validity associated with a drinking task.

I would add several practice trials to the beginning of data collection, wherein participants could familiarize themselves with the experimental protocol, weight of targets, etc.

This would hopefully eliminate many behavioural errors (e.g., spilling, slow reaction to go signal, etc.) we observed in the current experiments.

Finally, I would eliminate the OPEN-LOOP visual condition from the experimental design. The benefits of the CLOSED-LOOP and DELAY visual conditions is that they are clearly delineated in the literature; the CLOSED-LOOP condition is visually-guided, and the DELAY condition is memory-guided. It is unclear which system has a dominant effect on kinematic behaviour in the OPEN-LOOP condition, as behaviour in the OPEN-LOOP condition may more closely resemble CLOSED-LOOP (Hu, Eagleson, & Goodale, 1999), or DELAY (Bradshaw and Watt 2002; Franz, Hesse, and Kolath 2007; Westwood, Heath, and Roy 2001), depending on which study you review. Eliminating this condition would serve to simplify the investigation considerably, as it would allow direct comparisons between ventral- and dorsal-stream guided reach-to-grasp movements without a hybrid condition clouding the analysis.

Measurements

To increase the accuracy of my measurements, I would implement the following changes to the experimental design. First, I would mark the end of the grasping movement by the initial movement of the target glass. I would accomplish this by using a trigger, placed beneath the target, which would send a signal to the Optotrak data collection software when the glass was moved. This would increase the precision of the MT endpoint marker. Second, regarding the placement of the IREDs on the participants' fingertips, I would seek to measure their placement as accurately as possible to minimize measurement differences between hands. In the current experiment, resting grip aperture varied between trials considerably, as participants did not necessarily return to the same type of resting position between trials; the anatomy of the hand caused the distance between IREDs in the rest position to vary by as much as 50% between trials. In the current experiments, we were able to compare grip aperture values between hands by using a correction factor (based on averaging the 10 smallest resting distances between IREDs), applied to each hand individually. In future experiments, I would like to measure the exact distance between IREDs on a 0 mm grip aperture by having participants pick up a small object by a very narrow wire handle, pinched between their index finger and thumb. This measurement would be taken at the beginning of each data collection session. This added control would allow for more accurate comparisons between hands.

Participants

Were I to complete the above experiments again, I would conduct both experiments simultaneously, and have each participant complete both studies. This would allow me to compare the results of each experiment directly, and (hopefully) confirm that changing the size of the glass had the intended effect on the kinematics measured. Additionally, the current experiments both use a group of right-handed participants. For reasons reviewed in the Discussion section, including a left-handed group of participants would benefit our understanding in that it would help us to argue whether or not any observed manual asymmetries are a result of handedness, or a result of more basic hemispheric asymmetries in the visuomotor system.

Food for Thought

A puzzle remaining to be solved is the relationship between hand preference and kinematic differences between the hands during reach-to-grasp actions. One thing that becomes clear from this investigation (and those of others) is that there are kinematic differences between the hands during the reach-to-grasp movement, but that these differences are subtle. Many studies of hand preference for grasping have shown that approximately two thirds of grasping actions are carried out with the dominant right hand. If there are no prominent kinematic advantages to using the dominant hand for the reach-to-grasp movement, why then do we prefer it to such a large degree? Is the preference a remnant of asymmetries in the reach? Is there a metabolic cost to reaching/grasping integration (or left-hand use in general) of which we are unaware? Or is prehension coupled with the development of other motor functions such as praxis or speech, processes predominantly contained within the left hemisphere? These questions should guide future research into hemispheric asymmetries in visuomotor integration.

Bibliography

Aglioti, S., DeSouza, J., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology, 5*(6), 679-685.

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61*, 303-321.

Annett, M., & Annett, J. (1979). Individual differences in right and left reaction time. *British Journal of Psychology, 70*, 393-404.

Bauer, J. H., & Cooper, R. M. (1964). Effects of posterior cortical lesions on performance of a brightness-discrimination task. *Journal of Comparitive and Physiological Psychology, 58*, 84-92.

Benton, A. L., Varney, N. R., & Hamsher, K. S. (1978). Lateral differences in tactile direction perception. *Neuropsychologia, 16*, 109-114.

Benton, A., Hannay, H. J., & Varney, N. R. (1975). Visual perception of line direction in patients with unilateral brain disease. *Neurology, 25*(10), 907-910.

Berthier, N. E., Clifton, R. K., Gullapalli, V., McCall, D. D., & Robin, D. (1996). Visual information and object size in the control of reaching. *Journal of Motor Behaviour, 28*, 187-197.

Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., & Freund, H. J. (1998). Human anterior intraparietal area subserves prehension: A combined lesion and functional MRI activation study. *Neurology, 50*(5), 1253-1259.

Bootsma, R. J., Marteniuk, R. G., MacKenzie, C. L., & Zaal, F. (1994). The speed-accuracy trade-off in manual prehension: Effects of movement amplitude, object size, and object width on kinematic characteristics. *Experimental Brain Research, 98*, 535-541.

Boulinguez, P., Nougier, V., & Velay, J.-L. (2001a). Manual asymmetries in reaching movement control. I: Study of right-handers. *Cortex, 37*, 101-122.

Boulinguez, P., Velay, J.-L., & Nougier, V. (2001b). Manual asymmetries in reaching movement control. II: Study of left-handers. *Cortex, 37*, 123-138.

Boussaoud, D., Ungerleider, L. G., & Desimone, R. (1990). Pathways for motion analysis: Cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque. *The Journal of Comparative Neurology, 296*, 462-495.

Bradshaw, J. L. (1978). Human cerebral asymmetry. *Trends in Neuroscience, 1*(2), 113-116.

Bradshaw, M. F., & Watt, S. J. (2002). A dissociation of perception and action in normal human observers: The effect of temporal-delay. *Neurospcyhologia, 40*, 1766-1778.

Brinkman, J., & Kuypers, H. (1973). Cerebral control of contralateral and ipsilateral arm, hand and finger movements in the split-brain rhesus monkey. *Brain, 96*, 653-674.

Brown, L. A., & Frank, J. S. (1997). Postural compensations to the potential consequences of instability: Kinematics. *Gait and Posture, 6*, 89-97.

Brown, L. E., Halpert, B. A., & Goodale, M. A. (2005). Peripheral vision for perception and action. *Experimental Brain Research, 165*, 97-106.

Bryden, P. J., & Roy, E. A. (1999). Spatial task demands affect the extent of manual asymmetries. *Laterality, 4*(1), 27-37.

Bryden, P. J., Roy, E. A., & Mamolo, C. M. (2003). The effects of skill demands and object characteristics on the distribution of preferred hand reaches in working space. *Brain and Cognition, 53*, 111-112.

Carey, D. P., Hargreaves, E. L., & Goodale, M. A. (1996). Reaching to ipsilateral or contralateral targets: Within-hemisphere visuomotor processing cannot explain hemispatial differences in motor control. *Experimental Brain Research, 112*, 496-504.

Carlton, L. G. (1981). Visual information: The control of aiming movements. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology, 33*(1), 87-93.

Carnahan, H., & Elliott, D. (1987). Pedal asymmetry in the reproduction of spatial locations. *Cortex, 23*, 157-159.

Carson, R. G. (1989). Manual asymmetries: Feedback processing, output variability and spatial complexity - Resolving some inconsistencies. *Journal of Motor Behavior, 21*, 38-47.

Carson, R. G., Chua, R., Elliott, D., & Goodman, D. (1990). The contribution of vision to asymmetries in manual aiming. *Neuropsychologia, 28*, 1215-1220.

Carson, R. G., Chua, R., Goodman, D., Byblow, W., & Elliott, D. (1995). The preparation of aiming movements. *Brain and Cognition, 28*, 133-154.

Carson, R. G., Goodman, D., Chua, R., & Elliott, D. (1993). Asymmetries in the regulation of visuallly guided aiming. *Journal of Motor Behavior, 25*, 21-32.

Castiello, U. (1996). Grasping a fruit: Selection for action. *Journal of Experimental Psychology: Human Perception and Performance, 22*(3), 582-603.

Castiello, U., Bennett, K., & Stelmach, G. (1993a). The bilateral reach to grasp movement. *Behavioural Brain Research, 56*, 43-57.

Castiello, U., Bennett, K., & Stelmach, G. (1993b). Reach to grasp: The natural response to perturbation of object size. *Experimental Brain Research, 94*, 163-178.

Chieffi, S., & Gentilucci, M. (1993). Coordination between the transport and the grasp component during prehension movements. *Experimental Brain Research, 94*, 471-477.

Chow, K. L. (1951). Effects of partial extirpations of posterior association cortex on visually mediated behavior in monkeys. *Comparitive Psychology Monograph, 20*, 187-217.

Chua, R., Carson, R. G., Goodman, D., & Elliott, D. (1992). Asymmetries in the spatial localization of transformed targets. *Brain and Cognition, 20*, 227-235.

Cohen, G. (1973). Hemispheric differences in serial versus parallel processing. *Journal of Experimental Psychology, 97*, 349-356.

Connolly, J. D., & Goodale, M. A. (1999). The role of visual feedback of hand position in the control of manual prehension. *Experimental Brain Research, 125*, 281-286.

Crossman, E., & Goodeve, P. J. (1983). Feedback control of hand-movement and Fitts' Law. *Quarterly Journal of Experimental Psychology, 35A*, 251-278.

Damasio, A. R. (1984). The neural basis of language. *Annual Review of Neuroscience, 7*, 127-147.

Delboeuf, F. J. (1865). Note on certain optical illusions: Essay on a psychophysical theory concerning the way in which the eye evaluates distances and angles. *Bulletins de l'Académie Royale des Sciences, Lettres et Beaux-arts de Belgique, 19*, 195-216.

Doan, J., Whishaw, I. Q., Pellis, S. M., Suchowersky, O., & Brown, L. (2006). Motor deficits in Parkinsonian reaching: Dopa-sensitivity influenced by real-word task constraint. *Journal of Motor Behavior, 38*(1), 45-59.

Dodge, R. (1900). Visual perception during eye movement. *Psychological Review, 7*(5), 454.

Edwards, J. M., & Elliott, D. (1987). Effect of unimanual training on contrlateral motor overflow in children and adults. *Developmental Neuropsychology, 3*, 299-309.

Elliott, D. (1988). The influence of visual target and limb information on manual aiming. *Canadian Journal of Psychology, 42*, 57-68.

Elliott, D., & Allard, F. (1985). The utilization of visual feedback information during rapid pointing movements. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology, 37*(3), 407-425.

Elliott, D., & Chua, R. (1996). *Manual Asymmetries in Motor Performance.* (D. Elliott, & R. Chua, Eds.) CRC Press.

Elliott, D., & Madalena, J. (1987). The influence of premovement visual information on manual aiming. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology, 39*(3), 541-559.

Elliott, D., Binsted, G., & Heath, M. (1999). The control of goal-directed limb movements: Correcting errors in the trajectory. *Human Movement Science, 18*, 121-136.

Elliott, D., Lyons, J., Chua, R., Goodman, D., & Carson, R. G. (1995). The influence of target perturbation on manual aiming asymmetries in right handed individuals. *Cortex, 31*(4), 685-697.

Elliott, D., Roy, E. A., Goodman, D., Carson, R. G., Chua, R., & Maraj, B. K. (1993). Asymmetries in the preparation and control of manual aiming movements. *Canadian Journal of Experimental Psychology, 47*(3), 570-589.

Ettlinger, G., & Wegener, J. (1958). Somaesthetic alternation, discrimination and orientation after frontal and parietal lesions in monkeys. *The Quarterly Journal of Experimental Psychology, 10*(4), 177-186.

Fisk, J. D., & Goodale, M. A. (1985). The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral space. *Experimental Brain Research, 60*, 159-178.

Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology, 67*, 381-391.

Flindall, J. W., Rutschmann, T., Doan, J. B., & Gonzalez, C. L. (2012). Grasping without reaching: A kinematic analysis of vision, demand, and hand-use manipulations (poster). *Society for Neuroscience*, (p. 888.20). New Orleans.

Flourens, P. (1847). *Récherches experimentales sur les propriétés et les fonctions du systeme nerveux dans les animaux vertébrés.* Paris.

Flowers, K. (1975). Handedness and controlled movement. *British Journal of Psycholgy, 66*, 39-52.

Foley, H. J., & Matlin, M. W. (2010). *The Visual System*. Retrieved September 4, 2012, from Sensation & Perception: http://www.skidmore.edu/~hfoley/Perc3.htm

Franz, V. H., Hesse, C., & Kollath, S. (2007). Grasping after a delay: More ventral than dorsal? *Journal of Vision, 7*(9), article #157.

Frey, S. H., Vinton, D., Norlund, R., & Grafton, S. T. (2005). Cortical topography of human anterior intraparietal cortex active during visually guided grasping. *Cognitive Brain Research, 23*, 397-405.

Gallivan, J. P., Cavina-Pratesi, C., & Culham, J. C. (2009). Is that within reach? fMRI reveals the the human superior parieto-occipital cortex encodes objects reachable by the hand. *The Journal of Neuroscience, 29*(14), 4381-4391.

Gentaz, E., & Hatwell, Y. (2004). Geometrical haptic illusions: The role of exploration in the Müller-Lyer, vertical-horizontal, and Delboeuf illusions. *Psychonomic Bulletin & Review, 11*(1), 31-40.

Gentilucci, M., Chieffi, S., Daprati, E., Saetti, M. C., & Toni, I. (1996). Visual illusion and action. *Neuropsychologia, 34*, 369-376.

Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioural Brain Research, 27*, 3-78.

Gonzalez, C., & Goodale, M. A. (2009). Hand preference for precision grasping predicts language lateralization. *Neuropsychologia, 47*, 3182-3189.

Gonzalez, c., Ganel, T., & Goodale, M. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of Neurophysiology, 95*, 3496-3501.

Gonzalez, C., Whitwell, R. L., Morrissey, B., Ganel, T., & Goodale, M. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research, 182*, 275-279.

Goodale, M. A. (1988). Hemispheric asymmetries in motor control. *Behavioural Brain Research, 30*, 203-214.

Goodale, M. A. (1990). *Vision and Action: The Control of Grasping.* Norwood, New Jersey, USA: ABLEX Publishing Corporation.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience, 15*.

Goodale, M. A., Kroliczak, G., & Westwood, D. A. (2005). Dual routes to action: Contributions of the dorsal and ventral streams to adaptive behavior. *Progress in Brain Research, 149*, 269-283.

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

Goodale, M. A., Pelisson, D., & Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature, 320*, 748-750.

Gorniak, S. L., Zatsiorsky, V. M., & Latash, M. L. (2010). Manipulation of a fragile object. *Experimental Brain Research, 202*, 413-430.

Grosskopf, A., & Kuhtz-Buschbeck, J. P. (2006). Grasping with the left and right hand: A kinematic study. *Experimental Brain Research, 168*, 230-240.

Grouios, G. (2006). Right hand advantage in visually guided reaching and aiming movements: brief review and comments. *Ergonomica, 49*(10), 1013-1017.

Halverson, H. M. (1931). An experimental study of prehension in infants by means of systematic cinema records. *Genetic Psychology Monographs, 10*, 110-286.

Heath, M., & Binsted, G. (2007). Visuomotor memory for target location in near and far reaching spaces. *Journal of Motor Behaviour, 39*(3), 169-177.

Heath, M., Hodges, N. J., Chua, R., & Elliott, D. (1998). On-line control of rapid aiming movements: Unexpected target perturbations and movement kinematics. *Canadian Journal of Experimental Psycholgy, 52*, 163-173.

Holmes, S., Mulla, A., Binsted, G., & Heath, M. (2011). 2011. *Vision Research, 51*, 1941-1948.

Honda, H. (1982). Rightward superiority of eye movements in a bimanual aiming task. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology, 34*(4), 499-513.

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

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

Iwai, E., & Mishkin, M. (1969). Further evidence on the locus of the visual area in the temporal lobe of the monkey. *Experimental Neurology, 25*, 585-594.

Jackson, S. R., Jackson, G. M., Harrison, J., Henderson, L., & Kennard, C. (1995). The internal contol of action and Parkinson's disease: A kinematic analysis of visually-guided and memory-guided prehension movements. *Experimental Brain Research, 105*, 147-162.

Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research, 86*, 199-208.

Jakobson, L. S., Archibald, Y. M., Carey, D. P., & Goodale, M. A. (1991). A kinematic anaysis of reaching and grasping movements in a patient recovering from optic ataxia. *Neuropsychologia, 29*(8), 803-805.

Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior, 16*(3), 235-254.

Jeannerod, M. (1986a). Mechanisms of visuomotor coordination: A study in normal and brain-damaged subjects. *Neuropsychologia, 24*(1), 41-78.

Jeannerod, M. (1986b). The formation of finger grip during prehension. A cortically mediated visuomotor pattern. *Behavioural Brain Research, 19*, 99-116.

Judge, J., & Stirling, J. (2003). Fine motor skill performance in left- and right-handers: Evidence of an advantage for left-handers. *Laterality, 8*(4), 297-306.

Karl, J., Sacrey, L., Doan, J. B., & Whishaw, I. Q. (2012). Oral hapsis guides accurate hand preshaping for grasping targets in the mouth. *Experimental Brain Research, 221*(2), 223-240.

Keele, S. W. (1968). Movement control in skilled motor performance. *Psychological Bulletin, 70*, 387-403.

Kim, S.-G., Richter, W., & Ugurbil, K. (1997). Limitations of temporal resolution in functional MRI. *Magnetic Resonance in Medicine, 37*, 631-636.

Klatzky, R. L., Pellegrino, J. W., McCloskey, B. P., & Doherty, S. (1989). Can you squeeze a tomato? The role of motor representations in semantic sensibility judgments. *Journal of Memory and Language, 28*, 56-77.

Kluver, H. (1942). Functional significance of the geniculo-striate system. *Biological Symposia*, *7*, p. 253.

Kolb, B., & Whishaw, I. Q. (2006). *An Introduction to Brain and Behavior* (2nd ed.). New York, NY, USA: Worth Publishers.

Krüger, M., Eggert, T., & Straube, A. (2011). Joint angle variability in the time course of reaching movements. *Clinical Neurophysiology, 122*(4), 756-766.

Kudoh, N., Hattori, M., Numata, N., & Maruyama, K. (1997). An analysis of spatiotemporal variability during prehension movements: Effects of object size and distance. *Experimental Brain Research, 117*, 457-464.

Langolf, G. D., Chaffin, D. B., & Foulke, J. A. (1976). An investigation of Fitts' law using a wide range of movement amplitudes. *Journal of Motor Behavior, 8*, 113-128.

Laufer, Y., Barak, Y., & Chemel, I. (2006). Age-related differences in the effect of a perceived threat to stability on postural control. *Journal of Gerontology, 61A*(5), 500-504.

Layman, J. D. (1936). Functions of the superior colliculi in vision. *Journal of Genetic Psychology, 49*, 33-47.

Lenhard, A., & Hoffmann, J. (2007). Constant error in aiming movements without visual feedback is higher in the preferred hand. *Laterality, 12*(3), 227-238.

Liepmann, H. (1925). *Lehrbuch der Nervenkrankheiten.* (H. Curschmann, & F. Kramer, Eds.) Berlin, Germany: Springer.

Mackenzie, C. L., Marteniuk, R. G., Dugas, C., Liske, D., & Eickmeier, B. (1987). Three dimensional movement trajectory in a Fitts' task: Implications for control. *Quarterly Journal of Experimental Psychology, 39A*, 629-647.

Macknik, S. L., & Martinez-Conde, S. (2012, July 21). Size Illusions Trick the Brain. *Scientific American*. Retrieved September 13, 2012, from http://www.scientificamerican.com/article.cfm?id=size-illusions-trick-brain

Mamolo, C. M., Roy, E. A., Bryden, P. J., & Rohr, L. E. (2005). The performance of left-handed participants on a preferential reaching test. *Brain and Cognition, 57*(2), 143-145.

Marteniuk, R. G., & MacKenzie, C. L. (1990). Invariance and variability in human prehension: Implication for theory development. In M. A. Goodale, *Vision and action: the control of grasping* (pp. 49-64). Norwood, NJ: Ablex.

Marteniuk, R. G., MacKenzie, C. L., Jeannerod, M., Athenes, S., & Dugas, C. (1987). Constraints on human arm trajectories. *Canadian Journal of Psychology, 41*(3), 365-378.

Meissirel, C., Wikler, K. C., Chalupa, L. M., & Rakic, P. (1997). Early divergence of magnocellular and parvocellular functional subsystems in the embryonic primate visual system. *PNAS, 94*(11), 5900-5905.

Mieschke, P. E., Elliott, D., Helsen, W. F., Carson, R. G., & Coull, J. A. (2001). Manual asymmetries in the preparation and control of goal-directed movements. *Brain and Cognition, 45*, 129-140.

Milner, A. D., & Goodale, M. A. (2007). Two visual systems re-viewed. *Neuropsychologia, 46*, 774-785.

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

Mishkin, M. (1966). *Frontiers in Psysiological Psychology.* (R. W. Russel, Ed.) New York: Academic Press.

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

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

Mon-Williams, M., & Bingham, G. P. (2011). Discovering affordances that determine the spatial structure of reach-to-grasp movements. *Experimental Brain Research, 211*, 145-160.

Moseley, G. L., & Hodges, P. W. (2006). Reduced variability of postural strategy prevents normalization of motor changes induced by back pain: A risk factor for chronic trouble? *Behavioural Neuroscience, 120*(2), 474-476.

Muelenbroek, R. G., Rosenbaum, D. A., & Vaughn, J. (2001). Planning reaching and grasping movements: Simulating reduced movement capabilities in spastic hemiparesis. *Motor Control, 5*, 136-150.

Newcombe, F., Ratcliff, G., & Damasio, H. (1987). Dissociable visual and spatial impairments following right posterior cerebral lesions: Clinical, neuropsychological and anatomical evidence. *Neuropsychologia, 25*(18), 149-161.

Ocklenburg, S., & Gunturkun, O. (2012). Hemispheric asymmetries: The comparative view. *Frontiers In Psychology, 3*(5), 1-9.

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

Passingham, R., Perry, H., & Wilkinson, F. (1978). Failure to develop a precision grip in monkeys with unilateral neocortical lesions made in infancy. *Brain Research, 145*, 410-414.

Paulignan, Y., Frak, V. G., Toni, I., & Jeannerod, M. (1997). Influence of object position and size on human prehension movements. *Experimental Brain Research, 114*, 226-234.

Peters, M. (1980). Why the preferred hand taps more quickly than the non-preferred hand: Three experiments on handedness. *Canadian Journal of Psychology, 34*, 62-71.

Polman, R., Whiting, H., & Savelsbergh, G. (1996). The spatiotemporal structure of control variables during catching. *Experimental Brain Research, 109*, 483-494.

Prabhu, G., Lemon, R., & Haggard, P. (2007). On-line control of grasping actions: Object-specific motor facilitation requires sustained visual input. *Journal of Neuroscience, 27*(46), 12651-12654.

Purves, D., Augustine, G. J., Fitzpatric, D., Hall, W. C., LaMantia, A. S., & White, L. E. (Eds.). (2012). *Neuroscience* (5th ed.). Sunderland, Massachusetts, USA: Sinauer Associates, Inc.

Riek, S., Tresilian, J. R., Mon-Williams, M., Coppard, V. L., & Carson, R. G. (2003). Bimanual aiming and over attention: One law for two hands. *Experimental Brain Research, 153*, 59-75.

Roy, E. A., & Elliott, D. (1986). Manual asymmetries in visually directed aiming. *Canadian Journal of Psychology, 40*, 109-121.

Roy, E. A., & Elliott, D. (1989). Manual asymmetries in aimed movements. *Quarterly Journal of Experimental Psychology, 41a*, 501-516.

Roy, E. A., & Mackenzie, C. L. (1978). Handedness effects in kinesthetic spatial location judgements. *Cortex, 14*, 250-258.

Roy, E. A., Kalbfleisch, L., & Elliott, D. (1994). Kinematic analyses of manual asymmetries in visual aiming movements. *Brain and cognition, 24*, 289-295.

Rushworth, M. F., Krams, M., & Passingham, R. R. (2011). The attentional role of the left parietal cortex: The distinct lateralization and localization of motor attention in the human brain. *Journal of Cognitive Neuroscience, 13*, 698-710.

Sacrey, L. R. (2012). *Development and Degeneration of the Sensory Control of Reach-to-Eat Behvaiour (Doctoral Thesis).* Lethbridge: Department of Neuroscience.

Santello, M., & Soechting, J. F. (1998). Gradual modeling of the hand to object contours. *Journal of Neurophysiology, 79*(3), 1307-1320.

Santello, M., Flanders, M., & Soechting, F. (2002). Patterns of hand motion during grasping and the influence of sensory guidance. *Journal of Neuroscience, 22*(4), 1426-1435.

Savelsbergh, G., Steenbergen, B., & van der Kamp, J. (1996). The role of fragility information in the guidance of the precision grip. *Human Movement Science, 15*, 115-127.

Schettino, L., Adamovich, S., & Poizner, H. (2003). Effects of object shape and visual feedback on hand configuration during grasping. *Experimental Brain Research, 151*, 158-166.

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

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

Seegelke, C., Hughes, C., & Schack, T. (2011). An investigation into manual asymmetries in grasp behaviour and kinematics during an object manipulation task. *Experimental Brain Research, 215*, 65-75.

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

Smeets, J., & Brenner, E. (2001). Independent movements of the digits in grasping. *Experimental Brain Research, 139*, 92-100.

Soechting, J. F. (1984). Effect of target size on spatial and temporal characteristics of a pointing movement. *Experimental Brain Research, 83*, 618-632.

Steenhuis, R. E. (1996). Hand preference and performance in skilled and unskilled activities. In D. Elliott, & R. E. A, *Manual asymmetries in motor performance* (pp. 123-142). Boca Raton, Florida: CRC Press.

Stins, J. F., Kadar, E. E., & Costall, A. (2001). A kinematic analysis of hand selection in a reaching task. *Laterality: Asymmetries of Body, Brain and Cognition, 6*(4), 347-367.

Stone, K., Bryant, D., & Gonzalez, C. (In Press). Hand use for grasping in a bimanual task: Evidence for different roles? *Experimental Brain Research*.

Striemer, C., Chapman, C. S., & Goodale, M. A. (2009). Implicit processing of obstacles for immediate but not delayed reaching in a case of hemianopic blindsight. *Journal of Vision, 9*(8), 1163.

Suzuki, K., & Arashida, R. (1992). Geometrical haptic illusions revisited: Haptic illusions compared with visual illusions. *Perception & Pyshcophysics, 52*(3), 329-335.

Todor, J. I., & Smiley, A. (1985). Manual asymmetries in motor control. In E. A. Roy, *Advances in psychology, Volume 23. Neuropsychological studies of apraxia and related disorders* (pp. 309-344). Amsterdam: North-Holland.

Todor, J. I., Kyprie, P. M., & Price, H. L. (1982). Lateral asymmetries in arm, wrist, and finger movements. *Cortex, 18*, 515-523.

Tretriluxana, J., Gordon, J., & Winstein, C. J. (2008). Manual asymmetries in grasp pre-shaping and transport-grasp coordination. *Experimental Brain Research, 188*, 305-315.

Trevarthen, C. B. (1968). Two mechanisms of vision in primates. *Psychologische Forschung, 31*, 299-337.

van der Kamp, J., Savelsbergh, G., & Smeets, J. (1997). Multiple information sources in interceptive timing. *Human Movement Science, 16*, 787-821.

Vaughan, J., Barany, D. A., & Rios, T. (2012). The cost of moving with the left hand. *Experimental Brain Research, 220*, 11-22.

Velay, J. L., Daffaure, V., Raphael, N., & Benoit-Dubrocard, S. (2001). Hemispheric asymmmetries and interhemispheric transfer depend on the spatial components of the movment. *Cortex, 37*, 75-90.

von Hofsten, C. (1982). Eye-hand coordination in the newborn. *Developmental Psychology, 18*, 450-461.

Wallace, S. A., & Weeks, D. L. (1988). Temporal constraints in the control of prehensile movements. *Journal of Motor Behavior, 20*, 245-260.

Waller, D. (1999). Factors affecting the perception of interobject distances in virtual environments. *Presence, 8*(6), 657-670.

Warr, M. (1987). Fear of victimization and sensitivity to risk. *Journal of Quantitative Criminology, 3*(1), 29-46.

Westwood, D. A., Heath, M., & Roy, E. A. (2001). The accuracy of reaching movements in brief delay conditions. *Canadian Journal of Experimental Psychology, 55*(4), 304-310.

Wikimedia Foundation, Inc. (2012, August 27). *Two-streams hypothesis*. Retrieved September 15, 2012, from Wikipedia: http://en.wikipedia.org/wiki/Two-streams_hypothesis

Wing, A. M., & Fraser, C. (1983). The contribution of the thumb to reaching movements. *Quarterly Journal of Experimental Psychology, 35A*, 297-309.

Wing, A. M., Turton, A., & Fraser, C. (1986). Grasp size and accuracy of approach in reaching. *Journal of Motor Behavior, 18*(3), 245-260.

Winstein, C. J., Grafton, S. T., & Pohl, P. S. (1997). Motor task difficulty and brain activity: Investigation of goal-directed reciprocal aiming using positron emission tomography. *Journal of Neurophysiology, 77*, 1581-1594.

Woodworth, R. S. (1899). The accuracy of voluntary movement. *Psychological Review*, (Supplement 2).

Zeki, S. M. (1978). Functional specialisation in the visual cortex of the rhesus monkey. *Nature, 274*, 423-428.

Zihl, J., & von Cramon, D. (1979). The contribution of the 'second' visual system to directed visual attention in man. *Brain, 102*(4), 835-856.