

Visuomotor Representations

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Abstract

The contribution of ventral stream information to the variability of movement has been the focus of much attention, and has provided numerous researchers with conflicting results. These results have been obtained through the use of discrete pointing movements, and as such, do not offer any explanation regarding how ventral stream information contributes to movement variability over time. The present study examined the contribution of ventral stream information to movement variability in three tasks: Hand-only movement, eye-only movement, and an eye-hand coordinated task. Participants performed a continuous reciprocal tapping task to two point-of-light targets for 10 seconds. The targets were visible for the first five seconds, at which point vision of both the targets and the limb was occluded by liquid crystal goggles. Movement variability was similar in all conditions for the initial 5-second interval. The no-vision condition (final 5-seconds) can be summarized as follows: Ventral stream information contributed to an initial significant increase in variability across motor systems, though the different motor systems were able to preserve ventral information integrity differently. The results of these studies can be attributed to the behavioural and cognitive mechanisms that underlie the saccadic and manual motor systems.

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Dedication

I would like to dedicate this work to my best friend and love Stephanie Dotchin. Your never-ending supply of support, coupled with your smile allowed me to see through the tough times. Thank you from the bottom of my heart.

Table of Contents

PERMISSION TO USE	i
ABSTRACT	ii
ACKNOWLEDGEMENTS	iii
DEDICATION	iv
TABLE OF CONTENTS	v
LIST OF FIGURES	viii
1. LITERATURE REVIEW	1
1.1 Theories of motor control	3
1.2 Eye movements	8
1.3 Visuomotor systems theory	11
1.4 Visuomotor representations	15
2. GENERAL INTRODUCTION	20
3. EXPERIMENT 1	27
3.1 Methods	27
3.1.1 Participants	28
3.1.2 Apparatus	28
3.1.3 Task	29
3.1.4 Procedure	29
3.1.5 Data reduction and analysis	31
3.2 Results	33
3.3 Discussion	34
4. EXPERIMENT 2	36

4.1 Methods	38
4.1.1 Participants	38
4.1.2 Apparatus	38
4.1.3 Task	38
4.1.4 Procedure	38
4.1.5 Data reduction and analysis	39
4.2 Results	39
4.3 Discussion	40
5. EXPERIMENT 3	43
5.1 Methods	44
5.1.1 Participants	44
5.1.2 Apparatus	45
5.1.3 Task	45
5.1.4 Procedure	45
5.1.5 Data reduction and analysis	46
5.2 Results	46
5.3 Discussion	49
6. GENERAL DISCUSSION	51
6.1 Eye movement variability	52
6.2 Hand movement variability	53
6.3 Summary	54
7. CONCLUSION	56
7.1 Theories of motor control	56

7.2 Internally held representations	61
7.3 Concluding remarks	63
8. REFERENCES	64

List of Figures

Figure 1.1: Mueller-Lyer illusion	14
Figure 2.1: Exponential decay	26
Figure 2.2: Logarithmic decay	26
Figure 3.1: Apparatus	28
Figure 3.2: Data reduction illustration	32
Figure 3.3: Isolated hand function	33
Figure 4.1: Isolated eye function	40
Figure 5.1: Movement profiles	46
Figure 5.2: Coordinated eye movement function	47
Figure 5.3: Coordinated hand movement function	48

1. LITERATURE REVIEW

The neurological foundation of movement has been researched for over a century, generating a body of literature that has sought to explain the role of the central nervous system with respect to intentional movement. The true diversity of this body of literature is reflected in the broad scope of researchers contributing to this base of information. One prominent field within this line of inquiry has examined the idiosyncrasies associated with human movement production. Human movement production can be conceptualized as being governed by many nervous system processes that determine how one is able to interact with his/her environment. This set of processes has been documented throughout the course of the last one hundred years, and has allowed for the development of a template describing movement from intention to completion.

Movement intention can be defined as one's conscious decision to act, and, within the confines of this definition, implies that most actions are goal-centered. The formulation of goal-centered movements can be thought to reflect the activity of specific cortical areas. That is, movement plans and the subsequent action are formulated by the prefrontal lobes of the brain (e.g., dorsolateral prefrontal cortex). The division of the frontal lobes of the brain is commonly thought to reflect five different functions: 1) The Perceiver, 2) The Verbalizer, 3) The Motivator, 4) The Attender, and 5) The

Coordinator (Faw, 2000; for a comprehensive review see Faw, 2003). These areas interact with each other and other areas of the brain to produce the intention to move.

The Perceiver's role in movement intention is concerned with providing information about the environment to one's consciousness (Passingham, 1995). Operating in the right-hemisphere portion of the ventral-lateral prefrontal cortex, it allows the brain to define the relationship between objects with respect to size, color, shape, and function. The Perceiver operates primarily in conjunction with The Verbalizer (left-hemisphere portion of the ventral-lateral prefrontal cortex). The Verbalizer is a specialized language area, and is responsible for the integration of both auditory and visual interpretation of language. It is intuitive, therefore, that the interaction of these two systems is of paramount importance to the formulation of goal-directed movements. These two systems allow one to perceive the environment, and to integrate language cues—through either visual or auditory mediums—into the formulation of intent.

The roles of The Motivator and The Attender represent the executive functions with the highest limbic associations (Fuster, 1999). That is, these executive regions of the brain interact at a high level with both the amygdala and hippocampus. The Motivator can be thought of as the structure that represents one's intentions with respect to emotions (amygdala), and is located on the ventral/medial-orbital surface of the prefrontal cortex. The Attender is defined as the region responsible for representing one's self in space and time, and is a frontal-cortical extension of a hippocampal stream of information. This stream is thought to direct attention toward both internal and external objects and

events. These two executive functions allow for emotions and memory to be used during the formulation of movement intention.

Finally, The Coordinator is the prefrontal portion of the cortex that is responsible for providing information pertaining to one's spatial location within the environment. This executive function is located on the dorsal-lateral prefrontal cortex, and communicates extensively with the somatosensory and associational areas of the parietal cortex. The role of this area of the brain has been extensively documented as the primary location responsible for the formulation of movement plans (Ungerleider & Mishkin, 1982, Milner & Goodale, 1995). With the interaction of these 5 executive areas, one is able to program goal directed movements based on environmental (visual and auditory cues), and internal cues (memory, emotions, and somatosensory information). The resulting movements that reflect these structures' functions have been described in great detail, resulting in several theories of movement.

1.1 Theories of motor control

After the intent to move is established, the requisite action must be carried out by the neuromuscular system in some fashion. Predicting the nuances of the action, however, become increasingly difficult because of excess degrees of freedom (Bernstein, 1967). To render this concept more concrete, consider the simple action of turning on a radio. There are innumerable ways that this action can be performed (i.e., different joint positions, different hand positions, etc), yet the simplest of actions are performed in a largely predictable manner. Because of the relative predictability of human movement,

several motor control theories have been developed that attempt to provide an answer to two pertinent questions: *Why* human behaviour follows a certain movement pattern and *what* are the resulting physiological mechanisms?

The first solution can be thought of as an energy-minimization solution. Labeled the Minimum-Jerk Trajectory hypothesis (MJT), this motor control theory states that all conscious goal-directed movement is the result of an energy-minimization protocol (Hogan & Winters, 1990). That is, when the intent to move is established, the body will solve the excess degrees of freedom problem in a way that minimizes the energy cost associated with the movement. Again, considering the act of turning on a radio: one's actions would consist of 'smooth' spatial and temporal characteristics. A selected movement, therefore, would reflect a straight trajectory pattern while not accelerating or decelerating with great suddenness. This relationship can be described as having two variables, D (movement distance) and T (movement time). By minimizing D, and optimizing T (dependent on the purpose of the intended movement), one is able to predict the subtleties of the associated action. MJT, however, is less able to produce a clear answer for the second part of the question relating to the physiological mechanisms behind the movement. While this model would predict that muscles would be selected based on movement efficiency, this question remains largely unanswered. Using MJT, one is not able clearly describe which muscles would be used to accomplish the action.

One motor control theory that directly addresses the question of muscular involvement is the Equilibrium Point Hypothesis (EPH) (Feldman & Levin, 1995). This theory states that once a goal-directed movement is selected, the end-position of the system has to be calculated first. With this information, higher cortical centres make use of the inherent feedback properties of muscles to regulate the end-position of the movement. Within the confines of this theory, muscles about a joint can be thought of as existing in a natural state of length (and subsequent tension). Higher brain centres (e.g., premotor cortex) then specify that certain muscles should change length in a manner that would satisfy the required end position, and allow lower nervous system structures (i.e., spinal reflexes and muscle spindles) to manage the action. The main shortfall of this theory is that it cannot adequately satisfy the first question of *why* one goal position would be favored above another. That is, it cannot solve the excess degrees of freedom problem.

Other authors have proposed yet another theory concerning the planning of movement: The Motor Program Theory (MPT). The central tenet of MPT is that higher brain centers organize and execute command patterns that are carried out by the periphery in a top-down manner (Schmidt et al., 1979). The command patterns display a stereotyped sequence of activation, contraction, and movement. Contrary to EPH, proponents of MPT would argue that the muscles are passive contributors to the movements, rather than regulatory mechanisms. Returning once again to the example of turning on a radio, higher cortical centres (i.e., sensorimotor cortex) would specify the type and duration of muscle contraction that would result in an appropriate end-position. From a MPT

perspective, both questions of *what* and *why* can be addressed as the responsibility of higher cortical structures.

One final prominent theory of motor control is Dynamical Systems Theory (DST) (Carson & Kelso, 2004; Kugler, Kelso, & Turvey, 1982). DST relies on the concept that each movement can be thought of as being either stable or unstable by nature. The stability of a movement is determined by certain constraints, which are both cognitive and musculoskeletal in nature. The most self-evident example of a constraint is the physical range of motion limitation associated with any particular joint. For example, an elbow joint is bound by the physics of a hinge joint. A stable movement about the elbow, therefore, would be performed in a set range of motion. Muscular constraints that will influence the stability of a movement are the starting position, the contractility of a muscle, and the type of muscle (Flexor versus extensor). The cognitive constraints reflect several neurological mechanisms. First, there is much overlap in the sensorimotor cortex between muscle groups. The result of this phenomenon is that during widespread activation of the motor cortex, neurons within the CNS are either inhibited or disinhibited based on the initial activation. Thus, if the cortical area responsible for elbow flexion is active, all synergist muscles will have a high level of activation. Second, certain muscle groups are phylogenetically different than others. Flexor muscles, for example, can be identified as having more corticospinal motoneurons than extensors, leading to different activation characteristics. DST theorists would assert, based on this theory, that movements are selected based on their

stability. This one statement, hence, is able to provide an answer to both *why* and *what* questions.

After establishing the intention and mechanism to move, one must finally describe the movement itself. Through the analysis of kinematics and other parameters, one is able to quantify the patterns of the movement. Among the first examinations of human action was the seminal publication by Woodworth (1899). It was proposed that each movement was made up of an initial propulsion phase, followed immediately by a control phase. The first segment (propulsion) could be thought to reflect the programming of the movement, while the second segment represented a visually-guided 'homing in' phase. That is, during the first part of the movement, vision was used to program the trajectory of the movement, while vision during the second part of the movement was used to make adjustments in a feedback-oriented manner. In a slightly more controlled and eloquent manner, this two-phase manner of describing movement was recently expanded (for a comprehensive review, see Elliott, Helsen, & Chua, 2001); one of the more recent models of movement is the *Optimized Submovement Model* (Meyer et al., 1988). This model proposes that movements can be thought to reflect several ballistic movements/submovements. The first phase of motion reflects the largest ballistic movement, however, in the event that the first movement is somewhat erroneous (i.e., movement too far or too short), visual feedback signals are then used to program secondary corrective movements. The template used to describe movement intention to completion, while detailed for limb movement, is not able to fully describe

all human movement processes. Specifically, the oculomotor system (eye movement) is governed by a different set of structures and conditions (Glover, 2004).

1.2 Eye movements

In contrast to limb movements, eye movements operate under a different set of constraints. The behaviour of the oculomotor system is reflective of the anatomy of the retina; although the regular visual field spans an approximate 200 degrees, only the central degree yields high visual acuity (Goldberg, Eggers, & Gouras, 2000). The most common behaviour of the oculomotor system, hence, is to locate targets of interest in the environment and to bring them into foveal vision. This is accomplished in a semi-autonomous manner through a highly specialized system of neural and muscular structures.

The neural control of eye movements has been extensively researched, and has consequently produced a template with which one might categorize visual functions. The first type of eye movement, termed vestibule-ocular movement (VOM), is designed to keep objects of interest in the fovea during minor head movements (Goldberg et al., 2000). This particular function of the visual system operates on the following premise: When the head is rotated in one particular direction, vestibular input gives rise to motor commands that rotate the eye in the opposite direction using an identical velocity. The second type of eye movement is known as the optokinetic reflex (OR), and is simply an extension of VOM (Goldberg et al., 2000). OR movements are produced when a person's head is producing a sustained rotation, rather than a small movement.

The third type of eye movement is designed to maintain a visual fixation on a moving target, and as such, is known as smooth pursuit movement (SPM). SPMs are under voluntary control and rely on the calculation of the motion kinematics of the object of interest (Goldberg et al., 2000). A complementary type of eye movement is also able to keep moving targets of interest on the foveal region of the retina. Vergent movements (VM) are the only eye movements in which the eyes move in a disconjugate manner; that is, the eyes do not move in the same direction (Goldberg et al., 2000). VMs are able to keep objects in foveation as they approach and distance themselves from the observer. This is most easily seen by the phenomenon of ‘crossing one’s eyes’.

The final –and most salient to this undertaking—type of eye movement is known as the saccadic eye movement, and can occur as often as 173, 000 times per day (Abrams, Meyer, & Kornblum, 1989). Saccades are conducted in a unique manner that exploits the physical system in which it operates. Changing the location of the foveal region is executed through the control of three complementary muscle pairs, which move the eyes in a ballistic manner (Goldberg et al., 2000). The first muscle pair (medial and lateral rectus muscles) is responsible for the adduction and abduction of the eyes. Intuitively, the inferior and superior muscles elevate and depress the eye, while the superior and inferior oblique muscles assist in elevation/depression as well as produce some torsion of the globe. Of interest to note, eye movements do not operate in a biphasic manner. That is, during a saccade, antagonist muscles do not need to be activated to slow the speed of the globe. The viscous nature of the eye socket provides

enough force to decelerate the eye. These muscles behave in a predictable manner; all movements are produced without any source of feedback (Enderle, 2002). This results in the heavy use of corrective secondary movements when foveation of a target is erroneous (for a comprehensive review see Abrams et al., 1989). Finally, saccades are highly stereotyped in nature, with movements displaying a wave-like velocity profile (Goldberg et al., 2000). That is, depending on the speed and distance of the saccade, the corresponding kinematic wave will either be steeper or longer-lasting in nature.

In order to gain a comprehensive appreciation of eye movements, foundational neural structures must be examined in further detail. For the sake of brevity, however, the neural structures associated with the saccadic system will be the only ones covered. The saccadic system is constructed around one sub-cortical structure: The superior colliculus (SC). The SC receives information about the environment directly from the retina, as well as from higher cortical structures (Munoz & Fecteau, 2002). The resulting behaviour of the saccadic system, therefore, reflects both non-conscious and conscious processes. A non-conscious saccade might occur if one was observing a thunder storm. Lightning flashes occupy a very brief moment in time, yet they can still be foveated. This foveation occurs because a bright flash of light on the peripheral retina causes an automated saccade to the target area (Enderle, 2002). A conscious saccade occurs each time one reaches the end of a sentence on a page of script. Cortical centres specify that the eyes must return to the left-hand side of the page, and the superior colliculus brings the region of interest into foveal vision.

The mechanisms within the superior colliculus that control foveal position are quite simple. The SC is retinotopically mapped; every position on the SC corresponds to a certain position on the retina. The surface of the SC is also covered with two different types of burst cells: Fixation cells and saccadic cells. At the most basic level, fixation neurons and saccadic neurons behave exactly how one might expect: During a pause in eye movement the fixation neurons are active, and during motion the saccadic neurons are active. When one type of cell fires, cells representing the other function are inhibited from firing. The result of this interplay is that one type of cells is constantly active on the SC. In order to change between states (e.g., to move from fixation to saccade), fixation or burst cells overcome inhibition and direct the eye to the other behaviour (Munoz & Fecteau, 2002). The SC then sends motor commands to the three pairs of ocular muscles to execute the said behaviour.

1.3 Visuomotor systems theory

Among the first comprehensive examinations of the visual system was performed by Schneider (1969). This seminal work introduced a two-compartment model that represented a stark departure from the traditional monolithic description of the visual system. Much of this departure was supported by the idea that the superior colliculus was responsible for the visual coding of spatial information, resulting in a 'what versus where' distinction. That is, separate streams of vision were responsible for either perceiving objects, or placing objects within the environment. While the function of the superior colliculus has undergone substantial refinement, the 'what versus where' distinction has served as a catalyst for further research into the visual system.

The 'what versus where' concept was a prominent aspect of Ungerleider and Mishkin's 1982 anatomical model. Using lesions in a primate brain, certain areas were identified as essential to either cognitive function or movement production. The anatomical pathways for each stream of vision were presented as follows: The 'what' pathway moved from the primary visual cortex to the inferotemporal lobe, while the 'where' stream utilized a pathway from the visual cortex towards the posterior parietal cortex. Specifically, it was noted that primates with lesions surrounding the inferotemporal lobe had deficiencies in certain cognitive recognition tasks, while primates with lesions to the posterior parietal cortex displayed deficiencies in movement production. The work by Ungerleider and Mishkin (1982), hence, gave considerable credence to the 'what versus where' hypothesis, as definite neural structures could now be associated with different functions. This influential publication not only provided a more comprehensive understanding of past research, it also served as a starting point for an expansion of visually centered research.

The dichotomous visual system description has undergone further refinement, with one group of researchers establishing a new descriptive model. The 'Perception Action' model of vision has taken the anatomical mapping established by Ungerleider and Mishkin, and has elaborated upon both the neural structures involved in each stream of vision, as well as the respective functions that the structures serve (Dankert & Goodale, 2001; Milner & Goodale, 1995; Goodale & Haffenden, 1998). The line of information once known as the 'where' stream of vision has been labeled the Dorsal Stream,

whereas the line of information pertaining to the 'what' stream of vision is now known as the ventral stream of vision. These two new categories represent one's actions within the world, and the perception of one's environment, respectively.

The differences between streams of vision begin at the retinal level. Two projections arise from retinal cells and travel to the visual cortex: Magnocellular projections and parvocellular projections (Milner & Goodale, 1995). Magnocellular projections are thought to be the main source of information used by the dorsal stream of vision, because of the high sensitivity to contrast and high firing rate of these retinal cells. These attributes predispose the magnocellular system to movement detection (Milner & Goodale). Dorsal stream of information processing uses this environmental information in an egocentric manner. That is, environmental information is encoded so that objects are viewed in relation to a person's body. All movements, hence, are executed using dorsal stream information. The parvocellular stream of vision, conversely, can be thought of as the primary source of information used by the ventral stream of vision. Parvocellular structures encode environmental information in a manner that yields high spatial resolution and a sensitivity to color. These attributes predispose the parvocellular structures to cognitive processes (Milner & Goodale). Ventral stream of information processing uses this environmental information in an allocentric manner; information is encoded so that objects are viewed in relation to other objects in one's surroundings. Cognitive processing of information, such as object recognition, is the responsibility of ventral stream processing.

The broad acceptance of this model can be partially explained by the ability to predict visual behaviour within human participants. Two of the most frequently used experimental methods are the illusion paradigm and patient case study paradigm (Goodale & Humphry, 1998). Illusion studies require that participants interact on both a cognitive and movement-oriented basis with some illusory display. Using the Mueller-Lyer illusion (Figure 1.1) as an example, it is evident that although the two horizontal lines are the same length, they appear different. During an experiment, participants will state that the two middle segments are different lengths, but if asked to reach out and grasp the two objects in succession, they will perform the two reaches in an identical manner. The visual pathway responsible for interpreting the stimulus, therefore, must differ from the visual pathway responsible for interacting with the stimulus. There are cases, however, in which the dorsal stream of vision may become temporarily or permanently disrupted. During these instances, the ventral stream of vision is required to provide information necessary to plan and guide movements.

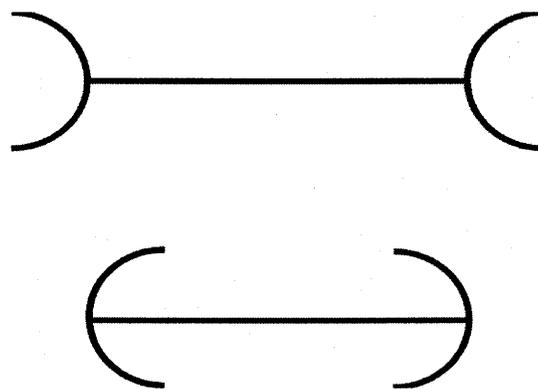


Figure 1.1: Mueller-Lyer Illusion

Although illusion studies provide support for the perception-action model, neuropsychological paradigms are also used. Through the use of single patient case studies, one is able to observe the behaviour of patients who have suffered damage to specific brain regions. The most cited of these is the case of D. F., a patient who displays symptoms consistent with visual form agnosia, as a result of damage to her ventrolateral occipital lobe (Milner et al., 1991). While she is still capable of interacting with her environment, she has lost the ability to recognize objects and shapes. If D. F. is presented with a glass of water, she is able to interact correctly with it without being able to identify it as a glass of water. The complementary example of this is patient R. V., who has suffered damage to her posterior parietal region (Goodale et al., 1994). While she is able to recognize objects and can speak to their respective function, she has extreme difficulty interacting with objects. Drawing from the glass of water example, she would be able to identify the object, but would have extreme difficulty interacting with it. While either stream of vision can be used for both dorsal and ventral tasks, albeit with limited success, the nuances of these occurrences have been well documented.

1.4 Visuomotor representations

From an historical perspective, the first major undertaking regarding the existence of iconic memory can be traced back to Sperling's 1960 publication. His assertion that one is able to "... see more than is remembered," implies that information regarding a stimulus can be stored for a short time after it is obscured (p. 1). During Sperling's experiment, participants were presented a series of letters for a brief period of time.

They were then required to report exactly which letters they remembered seeing in the array. When participants were instructed to recall these letters after a short delay (approximately 150 ms), they were able to recall more than can be attributed to their immediate memory capacity. Sperling attributed this phenomenon to the existence of a rapidly decaying visual representation. Applying these results to the perception-action model, iconic memory would be a process associated with the ventral stream of vision.

While Sperling's series of experiments focused on cognitive tasks, a new line of inquiry into motor representations has developed. That is, researchers are examining whether a visuomotor representation can be used to plan and control movements. The first such experiment used a locomotion task to elucidate the possible uses of a memorial representation (Thompson, 1983). Using this paradigm, participants were required to walk to a target that was positioned 3-15 meters away, in either a full vision condition, or in a no-vision delay condition. In the no-vision delay condition, participants would be instructed to wait several seconds with the room lights extinguished before walking to the target. Thompson concluded that if a participant could reach a target in less than 8 seconds (delay + movement time), the accuracy of movement would be equivalent to a full vision condition. Unfortunately, there was one large methodological limitation to this study: A natural confound existed between movement time and target distance. That is, it took participants longer to reach a further target. Because of this limitation, several researchers posed a similar question using a simple motor task.

In an influential study, Elliott and Madalena examined the existence of a memory-based visual representation using a discrete pointing task (1987). Using a series of three studies, participants were asked to make pointing movements to a target location in both full vision and no vision delay conditions. During the full vision condition, participants were given an auditory cue as a signal to make a pointing movement to a target located approximately 30 centimeters away in front of the participants' midline. During the no-vision delay conditions, the same auditory cue was given, but the lights were extinguished prior to movement initiation (0-, 2-, 5-, and 10-second delays). The main finding in this study was that participants were able to maintain accuracy during movement if the delay was under 2-seconds in length. While this represented a stark departure from Thompson's 8-seconds, the assertion that a memory-based representation can be used to accurately guide movements supported Sperling's initial hypothesis.

Recently, several authors have continued to question the extent to which ventral stream information can aid movement execution (Heath, Westwood, & Binsted, 2004; Westwood & Goodale, 2003; Westwood, Heath, & Roy, 2003). The studies by Westwood et al., as well as Heath et al., have arrived at a consensus regarding the use of ventral stream information for the planning of movement: Representations cannot be used to plan or control accurate reaching movements. These three studies have made use of a similar task as the Elliott and Madalena study (1989), by measuring the influence that time delays have on reaching movements. Using discrete reaching delays, results established that movement variability and accuracy degrade without the use of

dorsal stream information. This phenomenon has been labeled the Real Time Hypothesis (Westwood & Goodale, 2003).

To summarize the literature with respect to dorsal and ventral streams of information, consider the following situation (Figure 1.2). When the frontal executive regions form the intent to act, dorsal stream information must be processed by various neural structures. The dorsal stream travels from the primary visual cortex to several different cortical structures depending on which motor system is to be used. Information pertaining to limb and body movement must be passed from the parietal regions to the premotor cortex, which in turn sends information to the motor cortex in order to finalize

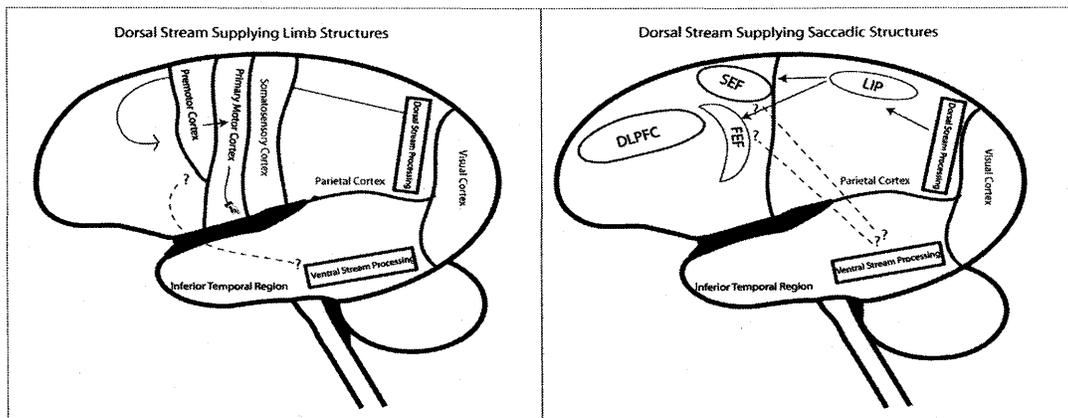


Figure 1.2: Dorsal and ventral information supply to frontal structures

movement planning (left side illustration, solid line). When the dorsal stream is disrupted, the ventral stream of information must provide environmental details to the premotor cortex (left side illustration, broken line). That is, different visual information is used to program movement. With respect to the saccadic system, dorsal stream

information must be sent from the lateral intraparietal region to the frontal and supplementary eye fields (right side illustration, solid line). These regions instruct the superior colliculus to consciously produce saccades. During normal functioning, this processes occurs seamlessly. When the dorsal stream is somehow disrupted, ventral stream projections must be sent to the frontal and supplementary eye fields (right side illustration, broken line). How ventral stream information is passed to dorsal structures, and how it is used remains speculative.

2. GENERAL INTRODUCTION

Within every human movement lie countless neural processes that govern the way in which we interact with our environment. Central to these processes is the visual system, which allows us to not only place ourselves within the environment, but to coordinate our actions with what we perceive about us. Early work in the area of vision and movement proposed a single-compartment model, in which one stream of vision was responsible for creating a single representation of the world (for a comprehensive review see Milner & Goodale, 1995). Other evidence, however, suggests a two-compartment model is more consistent with our knowledge of the visual system (Lacquaniti et al., 1997; Milner & Goodale, 1995; Schneider, 1969; Ungerleider & Mishkin, 1982). This dichotomous perspective has facilitated a more profound understanding of the mechanisms behind the perception of the world and our actions within it.

The theory of a divided visual system has been the topic of much recent attention (Dankert & Goodale, 2001; Glover, 2004; Goodale & Haffenden, 1998; McIntyre, Stratta, & Lacquaniti, 1998; Milner & Goodale, 1995). The two-part model proposed by Schneider in 1969 has been supplanted by what is known as the perception-action model (Milner & Goodale, 1995). This model suggests that there are two distinct streams of vision that follow separate anatomical pathways out of the visual cortex. The

first pathway, or dorsal stream of vision, originates in the visual cortex and travels to the posterior parietal cortex. The ventral stream, conversely, originates in the visual cortex but travels to the inferior portions of the temporal and parietal cortices. These divergent anatomical pathways give rise to a dichotomy of function.

The primary purpose associated with the dorsal stream of vision is to provide information used to program and control movements. To this end, the dorsal stream encodes information regarding the environment using an egocentric reference frame. That is, the dorsal system views the environment as it relates to someone acting within it. Using this frame of reference, objects surrounding a person are viewed in relation to his/her body. The nature of the dorsal stream of vision requires that it draws much of its environmental information from the magnocellular projections from the retina (Milner & Goodale, 1995). These projections have developed an affinity to detect edges of objects in order to facilitate movement execution. To illustrate this phenomenon, consider an example of someone turning on a radio. In order to execute this movement, information regarding the distance and the angle of the radio must be computed as it relates to someone's hand.

The ventral stream, conversely, is designed to capture information within the environment for cognitive use. The ventral stream, therefore, encodes information regarding the environment using an allocentric reference frame. An allocentric reference frame codes information using an external frame of reference, designed to interpret information requiring cognitive interpretation. The nature of the ventral stream,

therefore, relies primarily on information from the parvocellular projections originating in the retina (Milner & Goodale, 1995). The parvocellular structures are able to encode information with a high spatial resolution, and can also differentiate between colors. Returning to the example of a radio situated in the environment, the ventral stream of vision would determine that the radio is a dark shade of gray, and that the word 'power' is situated next to a button.

There are cases, however, in which either the dorsal stream or ventral stream of vision may become permanently disrupted. The loss of the dorsal stream of vision is termed visual ataxia, and results in the loss of one's ability to execute smooth, coordinated movements (Goodale et al., 1994; Milner et al., 2001; Perenin, & Vighetto 1988; Revol et al., 2003). Ventral stream lesions can cause a condition known as visual agnosia, resulting in the loss of cognitive visual processing of information, such as object recognition. (Goodale, Jakobson, & Keillor, 1994; Milner et al., 1991). In patients who have lost either processing pathway, the remaining stream of vision is required to serve both purposes. In one particular example, patient I. G. had a bilateral dorsal stream lesion, and could not perform fluid movements when instructed to grasp an object. However, when I. G. was instructed to perform a reaching movement to a remembered object, thus using the ventral stream of vision, the movement was performed with a greater degree of accuracy (Milner et al., 2001). This result indicates that ventral stream information can be successfully used during some movement tasks.

The differences in movement accuracy between dorsal and ventral streams of vision have also been examined in healthy populations. Perhaps the first analysis of movement execution based on ventral stream information, was an experiment by Thompson in 1983. This particular research paradigm required participants to walk to various targets within the environment. Specifically, participants were required to walk to a target that was positioned 3-15 meters away, in either a full vision condition, or in a no-vision delay condition. In the no-vision delay condition, participants would be instructed to wait several seconds with the room lights extinguished before walking to a given target. In this experiment, movement variability served as the dependent measure; that is, if participants could move with the same degree of accuracy with or without vision, they must be drawing on a highly accurate source of visual information. Thompson concluded that if a participant could reach a target in less than eight seconds (delay + movement time), the accuracy of movement would be equivalent to a full vision condition. The assertion was made, therefore, that visual representation (i.e., ventral stream information) integrity was held for approximately eight seconds.

Elliott and Madalena continued to examine the efficacy of visual representations using a discrete pointing task (1987). In a series of three studies, participants were asked to make pointing movements to target locations in the following conditions: Full vision of the target, no vision with a 0-second delay, and no vision with 2-, 5- and 10- second delays. During the full vision condition, participants were given an auditory cue as a signal to make a pointing movement to a target located 25-35 cm away in the sagittal plane. During the no-vision delay conditions, the same auditory cue was given, but the

lights were extinguished prior to movement initiation. The most striking finding was that participants were able to maintain accuracy during movement if the delay was under 2-seconds in length. While this was substantially less than Thompson's 8-seconds, both studies claimed the existence of a highly-accurate visual representation that could be used to execute movements.

Recently, several studies have continued the examination surrounding the existence of visuomotor representations (Westwood & Goodale, 2003; Westwood, Heath, & Roy, 2003; Heath, Westwood, & Binsted, 2004). The studies by Westwood and colleagues, as well as Heath and colleagues have arrived at a consensus regarding the use of visual representations: Ventral stream information cannot be used to plan or control accurate reaching movements. These three studies have made use of a similar paradigm as the Elliott and Madalena study, by measuring the influence that time delays have on reaching movements. Participants would be required to make discrete reaching movements to targets positioned approximately 15-30 cm away in the sagittal plane. During some conditions, vision of the target or of the limb would be removed either prior to or in conjunction with movement initiation. Results of these studies have all demonstrated that when vision of the target is removed, movement variability increases immediately. This is in direct conflict with any theory of a visual representation abetting the execution of movement.

An alternative hypothesis has emerged from one group of authors: Real time programming (Westwood & Goodale, 2003). According to this theory, the dorsal stream

of vision is posited as the only stream that can produce an accurate movement. Further, this stream of vision must be able to provide information until the instant before one produces a movement. In the absence of information from the dorsal stream, ventral stream information must be used resulting in a decrease in accuracy and an increase in variability. While the Real Time hypothesis does not negate the existence of a highly-accurate ventral stream representation, it contends that one cannot be used in lieu of real-time vision for the planning or control of movements.

Although the Real Time hypothesis has gained considerable support as of late (Westwood, Heath, & Roy, 2003; Heath, Westwood, & Binsted, 2004), one might criticize it as being too simplistic in its interpretation of the data. Through the Real Time hypothesis, one can predict that variability will increase immediately upon removal of vision, but one cannot predict how that variability will change as a function of time. Several possibilities can coexist within the confines of the Real Time hypothesis: The decay in variability that occurs without vision could reflect an exponential or logarithmic decay to name just two (see Figures 1 and 2). By examining the function representing movement variability, therefore, a more sophisticated interpretation is possible. That is, the defining aspect of the analysis becomes one's criterion regarding a significant increase in variability.

Depending on the set criterion, therefore, it becomes possible to support either the Real Time hypothesis, or a hypothesis that would claim the use of a highly accurate representation from the same decay function. Consider Figures 2.1 and 2.2: Using

standard analysis (i.e., discrete pointing movements), one would only be able to consider statistical differences between any two points. This would lead to the conclusion that because variability increased when vision of the environment is removed, ventral representations do not abet movement execution. If the data is interpreted using a time-function, the nuances of the data can be interpreted. In the case of Figure 1, therefore, it might be argued that the plateau in variability seen before the large increase might be the result of a highly accurate representation. A similar argument can be made for Figure 2. While discrete-point analysis may rule out ventral stream contributions to movement accuracy, one might contend that variability does not reach its plateau until a second or two after vision is removed. This might be the exact representation that Elliott and Madalena reported in 1987.

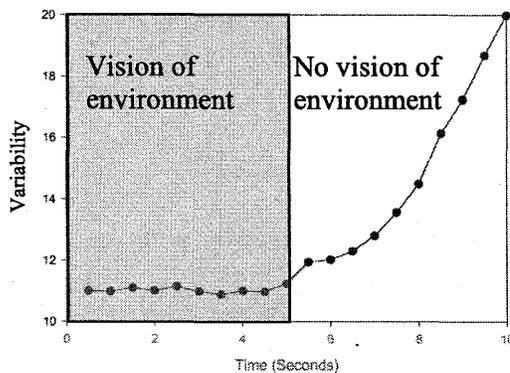


Figure 2.1: Exponential Decay

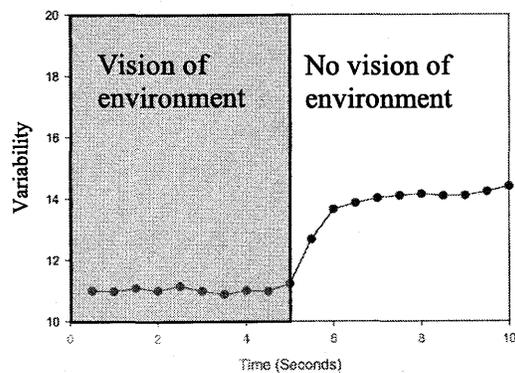


Figure 2.2: Logarithmic Decay

3. Experiment 1

This study follows the line of inquiry established by Elliott and Madalena (1987), albeit with several refinements. First, a continuous task was used in order to establish a psychometric function representing movement variability. Past research has made use of reciprocal tasks to examine variability, with results being consistent with discrete tasks (Binsted & Elliott, 1999b). The consistency between tasks indicates that the same behavioural mechanisms underlie both discrete and continuous tasks. During past research, participants were free to move their eyes during reaching movements. It has been well documented, however, that during sequenced hand and eye movements, the amplitude of the hand movement can be influenced by the amplitude of the eye movement (van Donkelaar, Lee, & Drew, 2002a). To ascertain the variability associated exclusively with limb movements, therefore, eye movements were strictly controlled. Through the use of this control, we were able to precisely document the role of ventral stream representations on pointing movements. It was hypothesized that while movement variability would increase upon removal of vision, the shape of the curve (i.e., a small plateau in variability after vision was removed) would be consistent with a highly accurate ventral representation (e.g., Elliott & Madalena 1987; c.f., Westwood & Goodale, 2003).

3.1 Methods

3.1.1 Participants

11 participants were recruited from the University of Saskatchewan community. Participants were strongly right-handed as determined by the Waterloo Handedness Questionnaire (Bryden, 1977), and were screened for movement disorders. Participants indicated their willingness to participate by signing a consent form. The study was carried out with the approval of the University of Saskatchewan's Behavioural Ethics Committee, in accordance with the declaration of Helsinki.

3.1.2 Apparatus

The task was performed on a rear-projection screen, mounted at waist level and angled at 45 degrees (Figure 3.1). Targets were projected upon the screen via a NEC VT465 LCD projector operating at 1800 ANSI lumens. Each participant was equipped with an infrared emitting diode (IRED) placed on the fingernail of his/her right index finger. The movement of the IRED was tracked using a 3-dimensional motion analysis system (Visualeyez VZ3000, Phoenix Technologies), recording at 200 Hz. Eye movements were recorded using a video oculographer sampling at 250 Hz (Eyelink II, SR Research). Participants also made use of a chin rest in an attempt to minimize head movement.

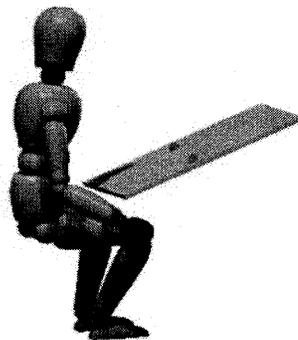


Figure 3.1: Apparatus

3.1.3 Task

Participants were instructed to make reciprocal pointing movements to two horizontally opposed targets for a total of 10 seconds. After the initial five seconds, the targets were extinguished, and participants were required to continue the pointing movements to where they remembered the targets being. During the back-and-forth pointing movements, participants maintained a central visual fixation. All participants were told to move as quickly and as accurately as possible.

3.1.4 Procedure

In order to examine the psychometric function associated with movement variability, a continuous task was required. To this end, participants performed a reciprocal tapping task between two point-of-light crosshair targets positioned 30 centimeters apart in the horizontal plane. The cross hairs were composed of two horizontally crossed 3 centimeter lines. A total of 72 trials were collected, with each data collection session lasting approximately 35 minutes. Participants performed the tapping task for a total of ten seconds. For the initial five seconds, the two targets were visible; after which the targets were extinguished for a total of five seconds. During this no-vision period, participants were instructed to continue their reaching movements to where they remember the targets being. Variability of movement endpoints was measured as representing one's use of a visual representation to execute movements. The increase in movement variability, hence, served as the dependent measure.

The 72 trials were divided into six conditions (A-F) composed of 12 trials each. Participants would begin each trial with their index fingers on either the right or left target. The start position of the finger was varied according to condition: Conditions A-C began on the right side, while Conditions D-F began on the left. These conditions appeared randomly without replacement throughout data collection to ensure that an even number of trials began on either side. During each trial, one of three possible target arrays was randomly illuminated. This randomization led to each participant completing a different number of trials for any given array. All target arrays required the same amplitude of movement, but were positioned in different locations within peripersonal space. Specifically, the first target array was aligned with the participant's midline, the second was shifted 5 centimeters to the right of midline, and the third was shifted 5 centimeters to the left of midline. Trials were carried out in dimmed lighting to reduce the influence of context on the pointing movements. Although the reduced lighting obscured most of the environment, light from the projector permitted vision of the limb at all times.

During data collection, participants were required to maintain a central visual fixation. The central fixation was monitored by having the participants wear an eye tracker (Eyelink II, SR Research) measuring pupil movement at 250 Hz. Trials in which the eye deviated from the central fixation were discarded from the analysis. Through this control, it was possible to remove all trials in which eye movements might influence hand movements.

3.1.5 Data reduction and analysis

Analysis of the psychometric function representing visuomotor representations was conducted in the following manner. Variability scores were organized along a time-continuum in 500 millisecond bins. To this end, movement end-point location of each pointing movement was calculated as the location at which the limb trajectory changed direction in the transverse plane. These end-point locations were then compared to the location of the target, resulting in a deviation score representing variability. The deviation scores were then examined by a regression analysis to ensure that no systematic drift –what occurs when movement amplitude remains the same, but the location of that amplitude is shifted either to the right of left— influenced the variability scores. If no systematic drift was detected, deviation scores surrounding the right target would be transformed (i.e., multiplied by -1) so that a positive deviation score would represent an overshoot of the target while a negative deviation score would represent an undershoot of the target.

Overshoot and undershoot scores for each trial were placed along a time continuum based on when they occurred during the ten second interval. Each trial generated approximately 2-3 deviation scores per second. One subject across all trials would have approximately 150 and 200 scores per second. This time continuum was then divided into 500msec bins (i.e., 1.0 seconds, 1.5 seconds, etc), each holding between 75 and 100 values. The standard deviation of each bin was calculated, resulting in one variability score for each 500 millisecond epoch (Figure 3.2). An overall group function was then calculated simply by taking the arithmetic mean of time points across subjects.

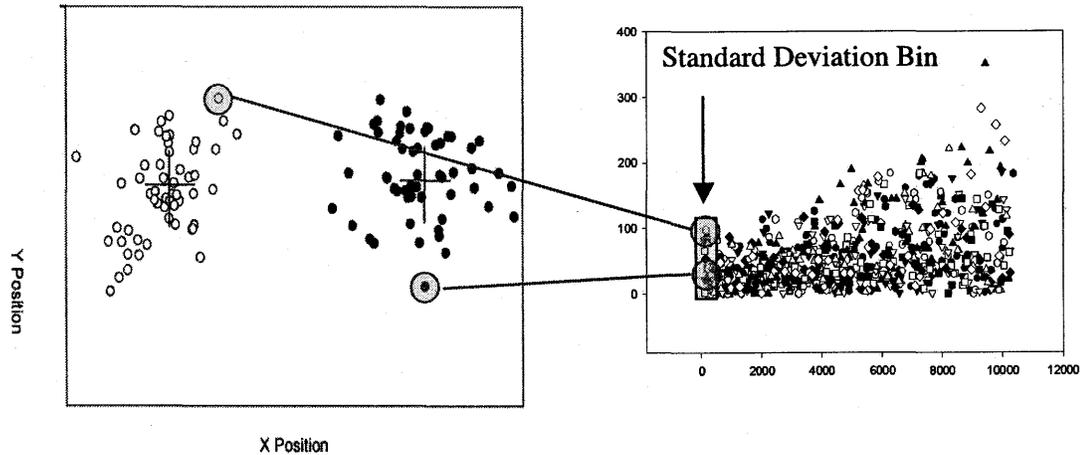


Figure 3.2: Data reduction illustration

the data. That is, linear contrasting would provide initial information regarding the decay pattern representing movement variability. Further, t-tests were conducted to determine the time point at which variability increased once the targets were occluded. The t-tests compared 500 millisecond bins against each other from removal of vision onwards until a significant result was found. A Bonferonni correction was used in the cases where more than one test was required. Finally, Akaike's Information Criterion (AIC) was used as a post-hoc analysis in order to determine what type of function best suited the data during the no vision condition. AIC is based on a likelihood ratio test designed to compare different models of best fit. Specifically, it determines a goodness-of-fit ratio while assigning a cost to adding parameters. While AIC does not utilize a P value, it does compute the likelihood of correctness of any given model based on standard non-linear regression assumptions. The first and final time points had to be

removed because of an insufficient number of data points used to calculate a standard deviation score (fewer than 50 points in some participants).

3.2 Results

Overall there was a significant main effect of time $F(4.936, 49.356) = 29.230, p < 0.001$ (Figure 3.3). The slope of the line representing the initial five second interval (full vision of targets) did not differ significantly from zero, $F(1, 8) = 0.061, p = 0.811$. There was a significant increase in movement variability between 5.5 and 6.0 seconds $t(10) = -2.871, p = 0.017$. The final five second interval (no vision of targets) displayed a significant linear trend $F(1, 10) = 40.35, p < 0.001$. The probability that the linear trend best represented the data was 0.6385, with an $r^2 = 0.9325$.

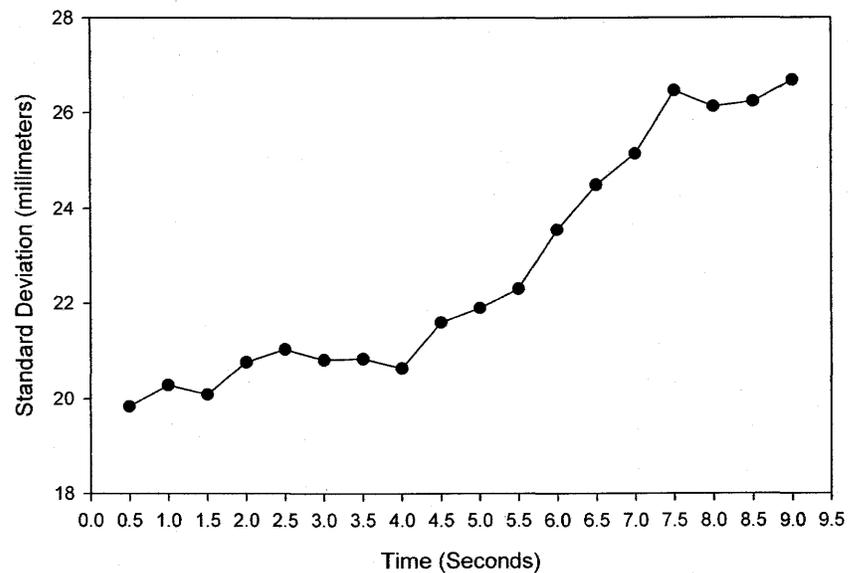


Figure 3.3: Isolated hand movement function

3.3 Discussion

Overall, participants completed the reciprocal taping task with an average movement time of 328 milliseconds. During the first half of the trial, participants performed the task in a relatively consistent manner. Variability increased significantly 500 milliseconds after the removal of vision. The decay representing movement variability reflected a significant linear trend.

When examining the increase in variability, it should be noted that no significant increase occurred immediately upon removal of vision (interval between 5.0sec and 5.5sec). This result is not intuitively consistent with the Real Time hypothesis. Proponents of this hypothesis would suggest that variability should make an immediate increase upon removal of vision. There are two possible explanations for this phenomenon. The first would be consistent with the results found by Elliott and Madalena, in which movement variability would not degrade immediately upon removal of vision (1987). Their results suggested that movement variability remained consistent until a time point just under two seconds post removal of vision. The 0.5 second plateau that immediately follows removal of vision, therefore, might be indicative of a highly-accurate visuomotor representation. An alternate explanation is, however, available. Because of the continuous nature of this task, participants would often be in the middle of a movement when the targets were occluded. This would result in a pointing movement being planned and largely carried out with the use of vision. These pointing movements should be expected to be less variable than those planned and carried out without vision of the targets. The stability of this time point, hence,

could simply reflect the idiosyncrasies of the task. To further support this viewpoint, the stability in variability lasted approximately the same duration as the average time to complete one movement. This explanation seems far more likely when one considers the influence of vision on the planning and online control of movement.

If the idiosyncrasies of the task caused the plateau in variability, the results become consistent with the Real Time Hypothesis. In the absence of dorsal stream processing, movement variability increased immediately, and degraded along a specific trajectory. The linear decay seen in the psychometric function, therefore, may arise from a progressive loss of integrity of the ventral stream information. Returning for a moment to our original hypotheses, we were only able to support the first statement: Movement variability increased immediately upon removal of vision. The function did not, however, display any significant plateau characteristics that could be attributed to highly accurate ventral stream information.

Reductionist methods employed in this experiment only permitted limited generalizations. That is, when people perform actions with or without vision, eye movements are rarely, if ever, constrained. How the eye behaves in such situations can have a profound influence on the movements of the hand (Binsted, Chua, Helsen, & Elliott, 2001). Although the nuances of eye movements are well documented, it is unclear how saccadic movements might respond within the confines of this task. In a second experiment, eye movement variability was examined in an effort to understand how its behaviour might influence similar hand movements.

4. EXPERIMENT 2

The saccadic system is composed of a unique set of neurological structures, designed to bring objects of interest into foveal vision (Goldberg, Eggers, & Gouras, 2000). Central to these structures is the superior colliculus, the controlling centre for all eye movements (Munoz & Fecteau, 2002). In order to accomplish foveation of the targets, the superior colliculus makes use of two different phases of motion. The first phase is simply a ballistic movement designed to rotate the eye towards a target. If the ballistic phase is perfectly carried out, the saccade is successful and does not require secondary corrective movements. In the case that the ballistic movement does not result in foveation, secondary corrective movements must adjust the saccade. During normal functioning, dorsal stream information provides coordinate information to the superior colliculus for the ballistic phase of movement. In the absence of dorsal stream information, however, this environmental detail must be drawn from a secondary source. That is, the ventral stream of vision must provide environmental information to the superior colliculus (SC) to guide the eye movement.

The higher cortical structures responsible for the ballistic phase of movement are quite numerous. The ballistic phase of movement is governed by such structures as the frontal and supplementary eye fields, visual cortex, dorsolateral prefrontal cortex (DLPFC), and lateral intraparietal sulcus to name a few (for a comprehensive review, see Munoz

& Fecteau, 2002). All of these structures lie along a dorsal pathway from the visual cortex to the frontal lobes, and might act in a manner similar to the dorsal structures responsible for limb movement. What is not known about these structures, however, is their capacity to integrate ventral stream information for the execution of eye movements. Are these structures able to maintain movement integrity in the absence of dorsal information? One study cites significant differences in dorsal/ventral function with respect to eye movements; Binsted and Elliott (1999b) have shown that when interacting with illusory stimuli, the eye is far more susceptible to the effects of the illusion than the hand. The differences between the saccadic and manual motor systems, therefore must be examined in greater detail.

One must question whether the saccadic system might respond in a similar way as the motor system in the absence of dorsal information. Some authors have speculated that saccadic system behaviour cannot be predicted by visuomotor system behaviour (Glover, 2004). In the context of this experiment, therefore, it is not known if eye movements will behave in a manner consistent with the Real Time hypothesis, or if they will reflect some tendencies consistent with a highly accurate representation. Will movement variability increase immediately upon removal of vision, or will saccades remain highly accurate while using ventral stream information? We hypothesized that, similar to Experiment 1, saccadic variability (much like pointing variability) would immediately increase upon occlusion of the targets. Further, it was hypothesized that the differences in neural structures between limb and eye movements would give rise to a different mathematical decay curve (i.e., second-order trend as opposed to linear trend).

4.1 Methods

4.1.1 Participants

10 different participants were recruited from the University of Saskatchewan community. Participants all had normal or corrected to normal vision, and were screened for movement disorders. Participants indicated their willingness to participate by signing a consent form. The study was carried out with the approval of the University of Saskatchewan's Behavioural Ethics Committee, in accordance with the declaration of Helsinki.

4.1.2 Apparatus

The task was performed on a rear-projection screen, mounted at waist level and angled at 45 degrees, such that a participant's head was approximately 50 centimeters from the cross-hair targets. Targets were projected upon the screen via a NEC VT465 LCD projector operating at 1800 ANSI lumens. Eye movements were recorded using a video oculographer sampling at 250 Hz (Eyelink II, SR Research). In an effort to control head movement, participants were required to use a height-adjustable chin-rest while wearing the eye tracker.

4.1.3 Task

The eyes performed the identical reciprocal task described in Experiment 1.

4.1.4 Procedure

The overarching goal of this experiment was to establish the psychometric function associated with eye movement variability in the presence of ventral stream information. The total number of trials, time of data collection, length of trial, and dependent measure were all identical to Experiment 1. Further, the number of conditions, starting position procedure, and randomization of three target arrays was conducted in the same manner as Experiment 1. Movement end-point was calculated as the point at which gaze shifted direction in the x-plane. Movement amplitude, expressed in degrees for each target array, was 34°. The first time point had to be removed from the analysis due to an insufficient number of data points (fewer than 50 data points in some subjects).

4.1.5 Data reduction and analysis

Data reduction and analysis was conducted in an identical manner to Experiment 1.

4.2 Results

There was an overall main effect of time $F(2.671, 24.041) = 25.144, p < 0.001$ (see Figure 4.1). The slope of the line representing the initial five second interval (full vision of targets) did not differ significantly from zero, $F(1, 8) = 0.2015, p = 0.193$. There was a significant increase in movement variability between 0 and 500 milliseconds after vision of the targets was removed $t(9) = -5.582, p < 0.001$. Without vision of the targets, the curve displayed a significant linear trend $F(1, 9) = 11.176, p = 0.009$. The probability that the linear trend best represented the data was 0.8984 with an $r^2 = 0.4825$.

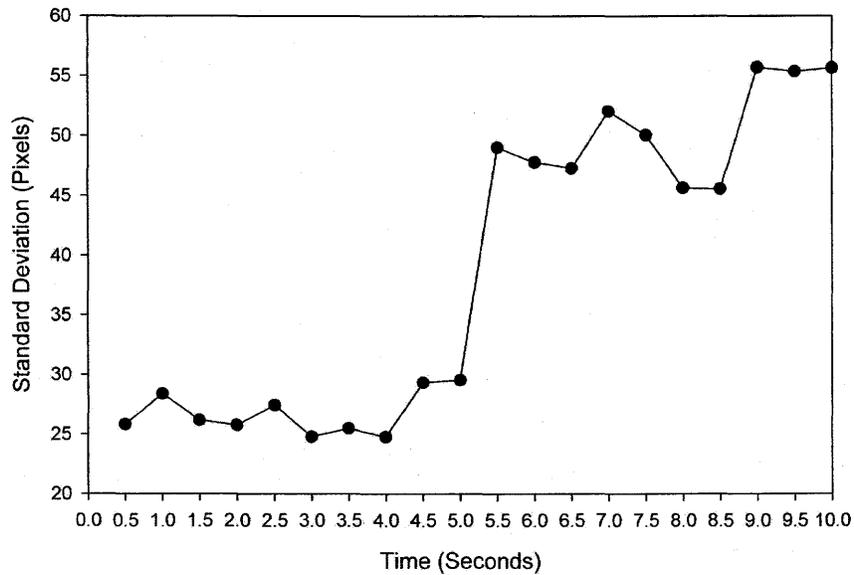


Figure 4.1: Isolated eye movement function

4.3 Discussion

The saccadic movement time can be partitioned into saccadic duration and fixation duration. The saccadic duration was observed to have a mean value of 48 milliseconds with a mean fixation time of 287 milliseconds. During the first half of the trial, participants performed the task in a relatively consistent manner, with the slope of the line representing variability not differing significantly from zero. The second half of the trial revealed a far more stochastic performance, yet still yielded a significant linear trend. It should be noted, however, that this linear trend did not predict the data well. The opening segment of this function, where participants had full vision of the targets, was performed in a highly stereotyped manner. This indicates that in full vision of the

targets, participants were able to perform the task accurately based on available visual information. The final five seconds, or no-vision condition, was performed in a highly variable manner that yielded a linear decay in variability. The implication here is that immediately upon removal of vision, the change in visual condition precluded participants from performing accurate movements. Finally, the emergent function is characterized by one largely obvious and highly significant step increase in variability. Specifically, variability significantly increased despite the nature of the task in which vision of the targets could have been removed mid-saccade. The explanation of this large step in variability can be found, however, by considering the two-component control process of the saccadic system.

Each saccade can be broken down into two phases: An initial ballistic movement, and a series of secondary corrective movements. The ballistic movement is designed to propel the eye toward a target region, and the secondary corrective movements ensure that the target lands in the foveal region. In the case of our experiment, the ballistic phase might not have access to detailed environmental information. In the absence of dorsal vision, movement information is drawn from a different cortical zone. Specifically, environmental details must be drawn from the medial temporal lobe, which may not provide the same amount of environmental detail (Nyffeller et al, 2004). The result of this is a ballistic movement executed with an inherently higher amount of variability.

The use of secondary corrective movements will also be negatively affected by the occlusion of the targets. Without vision of the targets, the act of correcting errors in the

ballistic phase of movement is not possible (Enderle, 2002; Gaveau et al., 2003). Specifically, the ballistic phase of movement relies on a series of three muscle pairs that fire without any source of proprioceptive feedback (Enderle, 2002). The result of this action is that any errors in the ballistic phase of movement cannot be corrected using muscle length as a control parameter. Online retinal signals regarding target position serve to correct erroneous ballistic movements non-consciously (Gaveau et al., 2003). When there is an absence of corrective retinal signals, any ballistic movement errors cannot be corrected using this form of feedback. The observed decay in movement variability, therefore, may be attributed to the combination of ballistic movements that are programmed using a more variable source of information, and an inability to use non-conscious corrective processes.

Without vision of the targets, movement variability increases immediately in a manner consistent with the Real Time hypothesis. This is not consistent with our stated hypothesis, but is consistent with the results of research on limb movements (Westwood & Goodale, 2003). This consistency implies that all motor systems might behave in a similar manner in the absence of dorsal stream information. The psychometric function representing eye movement variability adds valuable insight into the use of ventral stream representations. Although the saccade data lends considerable support to the real-time hypothesis, it is not known how saccadic behaviour might influence the behaviour of the hand if both saccadic and limb movements were performed in a coordinated task. The question of interacting motor systems and representations led to a final study in which participants performed a hand-eye coordinated task.

5. EXPERIMENT 3

Research examining the interaction between the eye and hand during movement is quite extensive (Binsted, Chua, Helsen, & Elliott, 2001; Binsted & Elliott, 1999a; Marconi et al, 2001; van Donkelaar, Siu, & Walterschied, 2004). When one is planning a reaching movement, information from the dorsal processing stream is passed along to the posterior parietal cortex, to an area known as the posterior reach region. This location is responsible for the translation of visual information into coordinates that the premotor cortex can utilize to program limb movements (Batista, Buneo, Snyder, & Anderson, 1999). Traveling a similar pathway, from the visual cortex via the lateral intraparietal region to the frontal and supplementary eye fields is a stream of information that is responsible for regulating activity in the superior colliculus (Munoz & Fecteau, 2002). The degree to which these pathways influence one another is unclear, but it has been established that reaching and saccadic movements can have an impact on one another (van Donkelaar, 2002a). The third experiment addresses the question of how the saccadic and motor streams interact, and how the variability functions will change as a result of this interplay.

Although the literature on eye-hand coordination leads one to expect some form of interaction between eye and hand variability, it is difficult to predict how it will be manifest in the behavior. Although extreme, one possibility might be a complete

convolution of the independent functions. That is, the hand function might change from a linear decay, and adopt the step function seen in the eye data. Conversely, the eye and the hand may behave independently indicating that ventral stream processes do not interact in the same fashion as dorsal processes (Binsted, Chua, Helsen, Elliott, 2001). Given the myriad of possibilities, we hypothesize that the function representing eye movement variability will reflect some linear decay pattern. The decay associated with saccadic variability might be shifted or augmented in some way, but should still reflect the same function. Without target location information, secondary corrective movements will still be largely inefficient (Gaveau et al., 2003). Additionally, the function representing the hand movement variability in the presence of eye movements will not reflect a linear decay pattern. The literature suggests that the saccadic and manual motor systems interact in some way, and should cause a differently shaped decay pattern. Simply put, the differences that one might expect from eye-hand coordination effects will have a greater influence on the movement of the limb than the eye.

5.1 Methods

5.1.1 Participants

9 participants (who did not participate in either of the first two experiments) were recruited from the University of Saskatchewan community. Participants were all strongly right-handed as determined by the Waterloo handedness questionnaire, had normal or corrected to normal vision, and were free of movement disorders. Participants indicated their willingness to participate by signing a consent form. The study was

carried out with the approval of the University of Saskatchewan's Behavioural Ethics Committee, in accordance with the declaration of Helsinki.

5.1.2 Apparatus

The task was performed on a rear-projection screen, mounted at waist level and angled at 45 degrees. Targets were projected upon the screen via a NEC VT465 LCD projector operating at 1800 ANSI lumens. In an effort to control head movement, participants were required to use a height-adjustable chin-rest while wearing the eye tracker. Eye movements were recorded using a video oculographer sampling at 250 Hz (Eyelink II, SR Research). Each participant was equipped with an infrared emitting diode (IRED) placed on his/her right index finger. The movement of the IRED was tracked using a 3-dimensional motion analysis system (Visualeyez VZ3000, Phoenix Technologies), recording at 200 Hz.

5.1.3 Task

The final experiment's task was modeled after the first two. Participants were instructed to move both their index fingers and their eyes back and forth between two targets in a temporally sequenced manner.

5.1.4 Procedure

The task was similar to both Experiments 1 and 2, as the same reciprocal tapping task was employed. In Experiment 3, however, participants were required to perform a hand-eye coordinated tapping task. That is, participants were instructed to move both their

eyes and index finger between two point-of-light targets as quickly and accurately as possible. Participants were equipped with both the video oculographer, and the IRED on their index fingers. Sampling rate and equipment set-up were identical to the above studies. The first two time points had to be removed from the analysis due to an insufficient number of data points (fewer than 50 data points in some subjects).

5.1.5 Data reduction and analysis

Data reduction and analysis was conducted in an identical manner to the first two experiments.

5.2 Results

Individual trials were composed of coordinated hand and eye movements (Figure 5.1).

Prior to removal of vision, movements were temporally sequenced, although end-point locations were not highly correlated with respect to spatial location ($r=0.025$). This is consistent with past research indicating that coordinated hand and eye movements do not

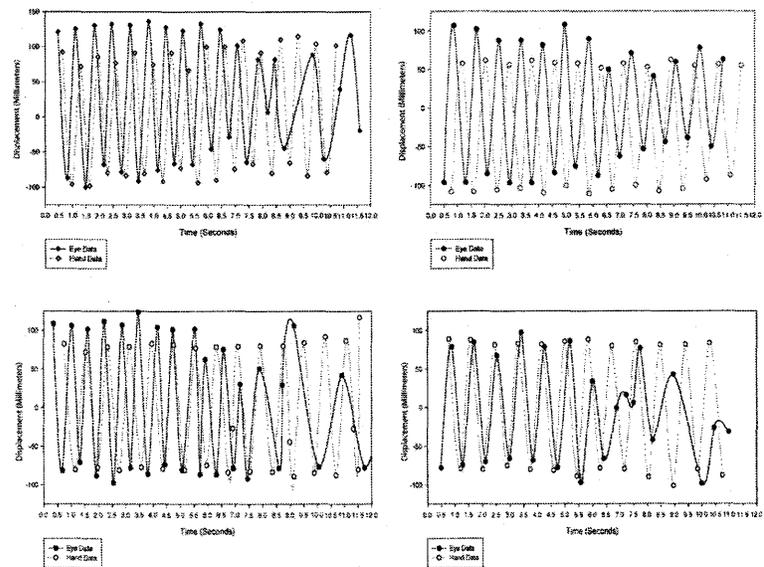


Figure 5.1: Individual movement profiles

tend to be spatially correlated (Binsted & Elliott, 1999). In the absence of vision, hand movements continued the rhythmic pointing while eye data did not consistently continue the temporal sequencing. Average movement time for the pointing task was 351 ms, while average movement (saccade and fixation) time for saccades was 362 ms.

There was an overall main effect of time in the eye movement function $F(2.213, 17.703) = 27.686, p < 0.001$ (see Figure 9). The slope of the line representing eye movements in full vision of the targets did not differ significantly from zero, $F(1, 7) = 0.003, p = 0.961$. There was also a significant increase in movement variability between 5.0 and 5.5 seconds $t(8) = -3.143, p = 0.014$. The eye data without full vision of targets revealed a significant linear trend, $F(1, 8) = 30.565, p = 0.001$, as well as a significant second-order trend, $F(1, 8) = 14.609, p = 0.005$. The decay associated with eye movement variability would be 0.9641 more likely to reflect a second-order trend with an $r^2 = 0.8461$.

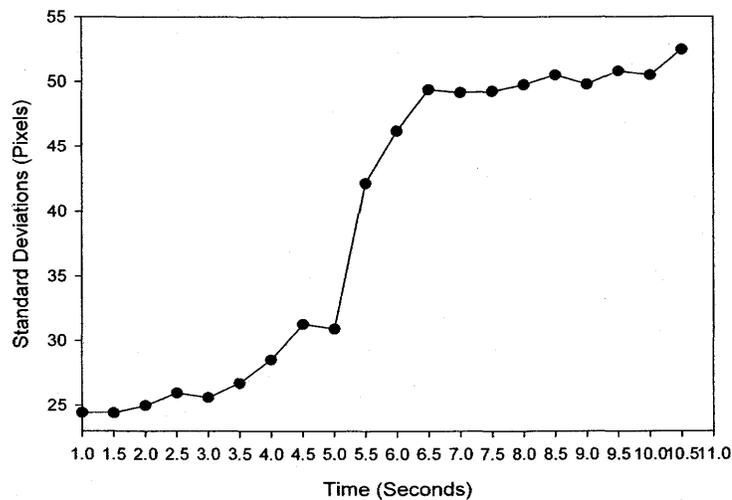


Figure 5.2: Coordinated eye movement function

There was a main effect of time in the overall hand function $F(2.036, 16.289) = 8.146$, $p=0.003$ (see Figure 8). The slope of the line representing hand movements in full vision of the targets did not differ significantly from zero, $F(1, 7)=0.078$, $p=0.788$. There was also a significant increase in movement variability between 5.5 and 6.0 seconds $t(8)=-3.429$, $p=0.009$. The hand data without vision of targets displayed a significant linear trend $F(1, 8)=12.878$, $p=0.007$. The decay associated with hand movement variability would be 0.8638 more likely to reflect a linear trend with an $r^2=0.9362$.

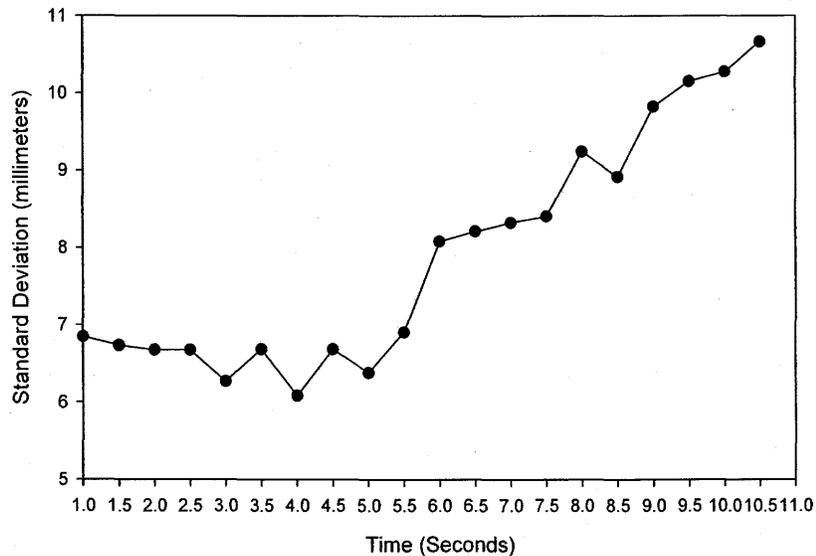


Figure 5.3 Coordinated hand movement function

5.3 Discussion

The hand data displayed an average movement time of 351 milliseconds, while the eye data displayed an average movement time of 362 milliseconds. The saccadic response time can be partitioned into saccadic duration and fixation duration. The saccadic duration was observed to have a mean value of 52 milliseconds with a mean fixation time of 310 milliseconds. With vision of the targets, both eye and hand behaved in a relatively stable manner; the eye and hand were temporally sequenced, without displaying a high spatial correlation. Without vision of the targets, the decay in hand variability was more likely to reflect a linear trend than a second-order trend while the decay in eye movement variability was more likely to reflect a second-order trend. Further, without vision of the target the temporal sequencing became largely disrupted. The no vision condition did not display any large increases in variability, indicating that participants were able to utilize visual information of the targets to modulate their movements. Interestingly, both curves display a significant increase in variability after vision of the targets was removed, although the increase was 500 milliseconds later in the hand data.

These results allow speculation regarding the differences between the ventral stream information utilized by the eye and hand. Specifically, the question of how many ventral stream projections exist must be addressed. The eye and the hand data represented different psychometric functions: The hand reflected a linear function whereas the eye reflected a second-order trend. Two possible explanations of this phenomenon are possible. The first is that both manual and saccadic motor systems

receive two separate streams of ventral information from the visual cortex. This common source hypothesis seems unlikely, because it implies that the ventral information traveling to the saccadic system is inherently more variable than information sent to the manual motor system. The second, and far more plausible possibility is that one stream of information serves both the saccadic system and the manual motor systems. If this is the case, the differences in the curves must be the result of different integration of information into motor commands. This explanation seems more likely because of the cortical differences in planning mechanisms. Whereas the saccadic system relies on the frontal and supplementary eye fields, DLPFC, and SC (Munoz & Fecteau, 2002) to carry out saccades, the manual motor system makes use of the posterior parietal cortex, premotor cortex, and motor cortex (Saron, Schroeder, Foxe, & Vaughan, 2001). The differences in the number of control structures, coupled with different behavioural properties of the system conceivably influence how environmental information is stored and utilized.

6. GENERAL DISCUSSION

This series of studies has examined the use of ventral stream representations by different movement systems. To that end, the first study examined how pointing movements utilize this representation in isolation from any eye movement. The second study documented how the eye used the same ventral representation as the hand to guide saccades. The final experiment illustrated the differences that occur in both limb and eye movement variability when the task was performed by both systems in a coordinated manner. Overall, participant utilization of this stored information changed as one moved from a single motor system task to a coordinated motor system task.

In summary, the present results provide behavioural evidence suggesting that ventral stream information is a highly variable source of information for the execution of movement. All three studies support past claims that ventral stream information is inherently variable and cannot be used to program accurate movements. Unlike past research, however, we were able to document the precise decay patterns associated with movements that are executed using ventral representations. Finally, the movement variability seen in the hand-eye coordinated task indicates that ventral stream representations are utilized in a different manner depending on the number of motor systems using the data synchronously.

6.1 Eye movement variability

The function representing eye movement variability changed from a linear function seen in Experiment 2, to a second-order function in the presence of hand movements. Two possible explanations might account for this. Information within reach-related neurons in the premotor cortex might provide some stability to nearby saccade related neurons in the same cortical region. Saccade related neurons within the premotor cortex have been linked to various other areas known to influence saccadic direction, such as the frontal eye fields (Saron, Schroeder, Foxe, & Vaughan, 2001). The interplay between saccadic and reach-related neurons, hence, could explain the differences in behaviour between experiments 2 and 3. A behavioural explanation might provide a more likely explanation given this set of circumstances. In the third experiment, participants did not have vision of the targets, but did have vision of their limb during the no vision condition. The possibility exists that the eye was able to draw some information regarding target position by the location of one's finger. This strategy would manifest itself in an improved ballistic phase of the saccade because the hand's decay in variability is far more gradual than the eyes. The end-location of one's index finger, hence, may serve as a temporary target for the eye. This information, however, was only able to abet the ballistic movement of the eye. The location of the finger could not be used for the secondary corrective movements, because it was perpetually in motion. The information provided to the saccadic system from pointing end-locations allowed for some improvements in variability, but as the hand became increasingly variable, so did the eye.

6.2 Hand movement variability

Although both hand-movement profiles displayed significant linear qualities in the full and no vision portions of their respective functions, a subtle difference should be noted. Between the epochs of 0.5 -1.0 second after occlusion of targets, there are significant increases in variability observed in both functions. In the third experiment, however, the amount of increase seen is far greater than that observed in the first experiment (i.e., when eye movement was not present). This rise can potentially be attributed to the neural interactions between hand and eye movements within the posterior parietal and premotor cortices. When initiating limb movements, spatial information is drawn from the posterior parietal cortex from a region known as the parietal reach region. The information is encoded in retinotopic coordinates, and needs to be translated into limb coordinates in order to plan a successful movement; this translation occurs within the premotor cortex. The premotor cortex translates this information in specific reach-related cells, which are modulated, however, by eye position (Marconi et al, 2001; van Donkelaar, Lee, & Drew, 2002b). That is, current eye position tends to have some influence on the direction and amplitude of hand movements.

When movements are being carried out in an open loop manner, as in our experiments, the translation of data between the posterior parietal cortex and premotor cortex is often incomplete (van Donkelaar, 1998), resulting in hand movement error being unduly influenced by eye movement error. That is, if the eye movement variability increases substantially, the hand movement variability should increase as well. In Experiment 1, participants did not make eye movements, and the result was a small increase in hand

movement variability. In the third experiment, however, eye movement variability increased substantially when vision of the targets was removed. This increase in variability, hence, could account for the larger jump in variability seen in Experiment 3. Further, the interaction between the visual and motor system could account for the increased slope of the decay seen in the final experiment (a difference of 0.148). The differences between the hand functions in Experiments 1 and 3, therefore, can be explained by the incomplete frame of reference transformation.

6.3 Summary

After examining the functions representing the decay in ventral stream information of hand-only movement, eye movement, and hand-eye synchronous movement, it can be said that the Real Time hypothesis predicted the behaviour in each case. In no instance did our data reflect tendencies toward a highly accurate source of information as previous authors have mentioned (Thompson, 1983; Elliott & Madalena, 1987). Further, our findings regarding ventral stream information allows for two generalizations to be made: 1) both the manual and saccadic motor systems initially respond in the same way to ventral stream information. This was demonstrated in the significant increases in movement variability immediately upon occlusion of the targets. Increases were seen in all sets of data, and speak to the similarities between motor systems. Paradoxically, we are also able to provide commentary regarding the differences between the motor systems using the same source of data: 2) the subsequent decay associated with ventral stream information differed across motor systems after the initial increase in variability.

This was seen in the differently shaped functions between eye and hand, and can be attributed to the different physical and neural constraints of each motor system.

7. CONCLUSION

7.1 Theories of motor control

Two statements can comprehensively summarize the results of the three experiments. The first relates to the overall differences in the usage of representations by the manual and saccadic systems: The manual motor system's representation is far more stable than the saccadic system. This was shown by the large step function that characterized both eye plots, suggesting that the structures responsible for limb movement are better able to preserve movement accuracy. The second statement is that some neural interaction changes the way in which different motor systems utilize representation information. Returning for a brief moment to the review of literature, one might question how the theories of motor control might address these summary statements.

Minimum Jerk Hypothesis (MJH) states that all movements are carried out in a manner consistent with an energy minimization protocol. To this end, movements reflect a smooth trajectory without sudden accelerations and decelerations. How might this account for the better performance displayed by the limb movement? One account for the limb advantage might be found in the controls used during the eye movement task. During both saccadic experiments, head movements were constrained in a way not found in regular life (i.e., participants were required to use a chin-rest). Perhaps if head movements were not restricted, participants would have used a combination of both

head rotation and saccadic movements to foveate the targets. This would certainly have required a saccade of decreased amplitude, resulting in oculomotor muscle contractions that were slower and shorter. A shorter, slower contraction may have been more accurate for this task. Using the MJH, therefore, one might predict that the artificial constraints imposed on the eye movements resulted in a behaviour that was not normal for the saccadic system. The limb movements were allowed to behave normally, thus were able to conform to the MJH.

The second statement regarding the differences between functions when eye and hand performed movements in synchrony is not one easily answered using MJH. The nature of the movements was the same in both individual and coordinated tasks, therefore, proponents of MJH would predict that there would be no changes whatsoever. The psychometric functions did, however, change as a result of a coordinated task. The possibility exists, however, that participants in the coordinated task were not able to perform the movements as fluently as possible due to limited attentional capacities in the frontal lobes. If one were to adopt this position, it could be said that the competition for attentional resources between the eye and the hand resulted in a different performance. Alternately, one might simply suggest that the MJH could not predict the results of this phenomenon.

Another theory of motor control discussed earlier is able to provide an eloquent explanation of the differences between limb and saccadic use of representations. Proponents of the Equilibrium Point Hypothesis (EPH) would assert that eye

movements would not be able to utilize the mechanisms behind EPH to the fullest extent, or indeed at all, because of the differences between muscle spindles in ocular and skeletal muscle. Recall that the EPH would claim that higher brain centres specify end position of muscles, and allow for spinal pathways and afferent feedback to carry out the action. The ocular muscles, lacking the amount of muscle spindles that skeletal muscles have, could not possibly reproduce accurate movement based on this premise. If the EPH is indeed the most accurate portrayal of the human motor system, eye movement variability should be intrinsically more variable than limb movements.

The changes between isolated and coordinated functions could also be predicted using the Equilibrium Point Hypothesis. One might posit that since two sets of muscle length commands are being sent simultaneously, they might somehow 'contaminate' each other with respect to movement amplitude and kinetic profile (van Donkelaar, Siu, & Walterschied, 2004). If this is the case, both movement profiles of eye and limb should change in the coordinated task to reflect the behaviour of the other. Our data confirmed this possibility through the resulting eye-hand coordination functions. During coordinated tasks, the saccadic use of representations reflects certain characteristics normally reserved for limb movement, while the limb's use of representations reflects saccadic idiosyncrasies. The EPH, therefore, can answer the two summary statements.

Motor Program Theory states that every voluntary action is carried out in a top-down manner. That is, higher cortical centres send efferent commands to muscles to carry out a desired action. From the perspective of MPT, the differences seen between the eye

and hand plots could be explained in two primary ways. First, it might be said that the commands being sent to the limbs reflected a system with less inherent noise and a more detailed set of muscle commands. This would predict that the eye's decay pattern should display a sharper increase in variability; a hypothesis consistent with the data. The second and more likely possibility would be an explanation that takes into account the nuances of the saccadic system. The highest visual acuity can be found in the foveal region of the retina. As such, objects of interest in the environment must be directed towards that area. The nature of the visual system, however, is that the fovea encompasses an area of approximately one degree per eye (Goldberg, Eggers, & Gouras, 2001). This results in a system that can inherently tolerate some error. That is, a saccade can land anywhere within approximately one degree of the target and still be considered successful. Commands sent to the saccadic system, therefore might simply be inherently more variable in an attempt to take advantage of this mechanism.

The observed differences between the isolated and coordinated functions are slightly more difficult to explain. One shortcoming of MPT is that there is no information known about the sharing of attentional resources during memory-based eye-hand coordinated movements. That is, is one system given preferential treatment with respect to attention? Based on the differences between individual and coordinated movements, it appears as though the eye receives more attentional resources during the coordinated task, because its psychometric decay function shows an improvement in decay, whereas the limb function shows a slight degradation in decay. Alternately, one might wish to explain it in a way consistent with EPH. Suppose for a moment that the commands for

eye and hand movement were prepared simultaneously. There might be some 'contamination' of information in this situation. The ambiguous nature of MPT, however, precludes any definitive statements as to why the psychometric functions might change.

Dynamical Systems Theory (DST) states that movements emerge based on their inherent stability. The differences between the decay observed in the eye plot and that in the limb plot, hence, is attributed to differences in stability. The question is, however, why the hand appears to be more stable than the eye. Both eye and limb movements occur because of motor unit contractions, both are goal-directed movements, and both were executed in a similar time frame. The differences in stability, hence, are not reflected in the execution of the task, but in the non-conscious physical properties of each system. Specifically, the use of afferent feedback from limb proprioceptors can account for the discrepancies in stability profiles. The feedback inherent to the skeletal muscles represents a system with a high amount of inherent stability. The extraocular muscles contract without any sources of feedback (Enderle, 2002), and might be considered to represent a less stable system. The extra afferent information available to the manual motor system, hence, accounts for the increased stability in the limb's psychometric function.

The differences between coordinated and uncoordinated movements are explained in an intuitive manner using DST. When several movements occur in a synchronous fashion, they are described as one system, rather than several smaller independent units. That is,

one system will inherently have a different profile than several smaller independent systems based on attentional resources, physical inertial differences from varying body postures, and many other factors. The results from this experiment can be interpreted in light of this information. Consider the results in the following manner: An isolated hand function and an isolated eye function each have some value assigned to them representing stability, with the hand's value being far greater (i.e., more stable). A coordinated task between the hand and the eye will also be assigned some value, representing a coordinated system. Because all systems are selected based on stability, stronger (i.e., more stable) parts of the system will 'assist' the weaker parts in an attempt to bolster systemic stability. In the case of a coordinated task, the hand movement's stability serves to stabilize the eye movement. This can be seen in the more gradual decay in movement variability during an eye-hand coordinated task. The hand, correspondingly, displays a step increase in variability that normally would characterize eye movements. That is, the hand became slightly less stable than it otherwise would have been. The hand's reduction in stability, however, was less than the gain in stability displayed by the saccadic system. The result was an overall increase in stability, thereby explaining the differences in psychometric functions.

7.2 Internally held representations

The differences between individual systems and coordinated systems can now be considered on a larger scale. Specifically, the interpretation of these results relied on several major assumptions. It was assumed that the decay seen in movement variability represented the degradation of held environmental information. Due to the continuous

nature of the task, however, it is possible that fatigue may have inflated error to some degree. The obvious control to this problem is to run an identical series of studies in which vision of the targets is not removed at all. During this control condition, any increase in movement variability due to fatigue could be used to covary out some of the variance seen in these experiments.

These three experiments also assumed that the nature of this internal store of information was singular. That is, the discussion to this point has focused on the neural structures that interact with a sole source of environmental information; while this is distinctly possible there are other ways that the data might be interpreted. Most notably, it is possible that the different decays in movement variability could be the result of disparate stores of environmental information; the saccadic system could be relying on one store of information while the limb is relying on a secondary source. If this is the case, it might be said that the source of saccadic information is more variable in nature than the source of limb information. This possibility could be discounted through the use of neural imaging techniques such as fMRI and PET scanning.

Another question that must be posed speaks to the diversity of sensory inputs: Do other senses contribute to environmental mapping? That is, visual information is assumed to be the sole source of information for internally held representations. One must assess the contributions of the other senses to the assembly of a spatial representation of the environment. The sense of touch, coupled with proprioceptive information might be particularly useful if one was to attempt to interact with some remembered object.

Somatic location information, therefore, might contribute to the integrity of stored environmental information. While olfaction and gustation may not be able to provide spatial information, auditory information might play a pivotal role in object location in space. These contributions should be examined in order to establish the possible interaction of different sensory modalities on movement variability.

7.3 Concluding remarks

Researchers have been developing templates with which to describe movement for the past 100 years, and with each attempt, more can be understood. All of this research relies on assumption and inference, but as technology and methods of measurement improve these assumptions become either supported or disproven. The end result of this process might be one comprehensive model that can encapsulate what human movement is and how it is accomplished. The research of today will play a foundational role in the forming of that template. Though our understanding of it is incomplete, today's process of viewing volitional acts will inevitably lead to an encyclopedic description human motion.

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