GREATER DISTRACTOR INTERFERENCE DURING VERTICAL SACCADES: THE TIME COURSE OF HORIZONTAL, VERTICAL AND OBLIQUE SACCADIC CURVATURE

by

Kaitlin Elizabeth Wiggins Laidlaw
Hons. B.Sc., The University of Toronto, 2007

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF ARTS
in
The Faculty of Graduate Studies
(Psychology)
THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)
August 2010

© Kaitlin Elizabeth Wiggins Laidlaw, 2010
Abstract

In three studies, we characterize the effect of a nearby distractor on vertical, horizontal and oblique saccadic curvature under normal saccade preparation times. In Experiments 1 and 2, participants made saccades to targets in the presence or absence of a nearby distractor. Consistent with previous findings, longer-latency vertical saccades showed greater curvature away from a distractor than did oblique or horizontal saccades. At short latencies, vertical saccades showed greater curvature towards the distractor. We propose that vertical saccades may be prone to greater distractor interference due to the superior colliculus, a midbrain region implicated in attentional and saccadic shifts, under-representing vertical target objects, which results in a relative over-representation of non-vertical distractor objects. In Experiment 3, we tested this hypothesis by having participants make saccades to vertical or horizontal targets in the presence or absence of bright or dim distractors. We reasoned that weaker representations for vertical targets would allow for greater interference from nearby distractors, which would be especially pronounced when distractors are highly salient. Consistent with this prediction, we found that only the trajectory of vertical saccades was modulated by distractor luminance.
Preface

All research reported was conducted at UBC’s Brain & Attention Research Laboratory, and was supervised by Dr. A. Kingstone. I was responsible for all program creation, completing or supervising data collection, performing data analysis and writing any work that resulted from the research. A version of the research reported in Experiments 1 and 2 has been published. Laidlaw, K.E.W, & Kingstone, A. (2010). The time course of vertical, horizontal and oblique saccade trajectories: Evidence for greater distractor interference during vertical saccades. *Vision Research, 50*, 829-837. I created the programs, ran much of the testing, wrote the drafts of the manuscript and edited the manuscript in collaboration with my co-author. Ethical approval for this research was provided by UBC’s Behavioural Research Ethics Board under the approval number of H04-80767 (see Appendix for certificate).
Table of Contents

Abstract ........................................................................................................................................... ii

Preface ............................................................................................................................................. iii

Table of Contents.......................................................................................................................... iv

List of Figures ................................................................................................................................... vii

Acknowledgments .......................................................................................................................... viii

Introduction....................................................................................................................................... 1

Brainstem Control of Saccades....................................................................................................... 1

Saccadic Curvature ............................................................................................................................ 4

Theories of Curvature and the Superior Colliculus .......................................................................... 6

Modulation of Saccadic Curvature .................................................................................................. 10

Purpose of Investigation .................................................................................................................. 14

Experiment 1: Effect of Target Location on Horizontal and Vertical Saccadic Trajectory .............. 18

Introduction....................................................................................................................................... 18

Methods.......................................................................................................................................... 18

Participants ...................................................................................................................................... 18

Stimuli and Procedure .................................................................................................................... 18

Data Handling ................................................................................................................................. 21

Results and Discussion ................................................................................................................... 21

Trial Exclusion ............................................................................................................................... 21
Experiment 2: Effect of Distractor Location on Oblique Saccade Trajectory

Introduction

Methods

Participants

Stimuli and Procedure

Data Handling

Results and Discussion

Trial Exclusion

Gap Effect

Trajectory Time Course – Effect of Distractor Location

Saccadic Reaction Time Analysis

Saccadic Trajectory Analysis

Comparison of Experiments 1 and 2

Discussion of Experiments 1 and 2

Experiment 3: Effect of Luminance on Saccadic Trajectory

Introduction

Methods

Participants

Stimuli and Procedure

Results

Trial Exclusion
Error Analysis – Effect of Distractor Luminance..................................................47

Gap Effect..................................................................................................................48

Trajectory time course – Effect of Target Location .................................................49
  Saccadic reaction time analysis.................................................................................49
  Saccadic trajectory analysis.......................................................................................50

Trajectory Time Course – Effect of Distractor Luminance.................................51

Discussion..................................................................................................................54

General Discussion....................................................................................................59

Experiment Summaries and Conclusions .............................................................59

Study Limitations..................................................................................................62

Future Directions ...................................................................................................65

Summary.....................................................................................................................68

Bibliography.............................................................................................................70

Appendix: Copy of UBC Research Ethics Board Certificate of Approval.............79
List of Figures

Figure 1. Spatial layout of saccade targets and distractors in Experiments 1-3.. ..........20

Figure 2. Mean saccadic reaction times (SRTs) for all subjects in Experiment 1........23

Figure 3. Mean saccadic curvature in Experiment 1 ..................................................26

Figure 4. Mean saccadic reaction times (SRTs) for all subjects in Experiment 2.........32

Figure 5. Mean saccadic curvature in Experiment 2. ..................................................34

Figure 6. Possible distractor activation pattern over time for Experiment 3 ............44

Figure 7. Mean saccadic reaction times (SRTs) for all subjects in Experiment 3 .......49

Figure 8. Mean saccadic curvature in Experiment 3 ..................................................51

Figure 9. Mean horizontal saccadic curvature in Experiment 3 ...............................53

Figure 10. Mean vertical saccadic curvature in Experiment 3 .................................54
Acknowledgments

Thank you to my supervisor, Dr. Alan Kingstone, for his remarkable ability to turn any problem into an opportunity. His constant optimism has helped to encourage me, and has kept me excited about research for the last two years. For their input and consideration, I would also like to thank my MA committee members, Dr. Jim Enns and Dr. Jason Barton. Thank you also to all members of the Brain and Attention Research Lab for all of the help along the way. Finally, endless thanks go out to my family for always supporting me.
Introduction

To compensate for the fact that our visual acuity is highest at the fovea of our retina (see Anstis, 1974), we spend our days making thousands of rapid eye movements, called saccades, to bring objects of interest into fixation. While it might be assumed that these extremely fast movements would travel in a straight line from one point in space to another, the reality is that saccades are rarely ever straight (Bahill & Stark, 1975, Yarbus, 1967). Viviani, Berthoz, and Tracey (1977) were the first to demonstrate that saccades often display a characteristic curvature to their trajectory, which changes depending on the direction of the eye movement. Starting from a central fixation point, participants were required to make saccades towards twelve points positioned in a circular array, each separated by 30 angular degrees. While both horizontal and vertical eye movements showed little obvious curvature, diagonal saccades showed consistent curvature away from the vertical meridian. Using a different procedure and eye tracking technique, Bahill and Stark showed that roughly 90% of all horizontal and vertical saccades were also comprised of transient orthogonal components, which tended to curve the saccade, however slightly. The presence of a curved saccadic trajectory during intentionally straight eye movements is thus the rule, rather than the exception. The aim of this thesis will be to investigate two of several factors known to influence saccadic trajectories, and in so doing, shed light onto how the brain represents visual space and initiates saccades.

Brainstem Control of Saccades

In order to appreciate how a saccade curves, one must first understand how an eye movement is generated within the brain, particularly within the brainstem. Once retinal
information is transferred and processed within visual cortex, signals are sent to the cortical eye fields (frontal and supplementary eye fields, FEF and SEF, respectively; see Hutton, 2008; Johnston & Everling, 2008). Although the cortical eye fields directly project to several brainstem areas implicated in the saccadic system (Shook, Schlag-Rey, & Schlag, 1990), these connections are sparse compared to those that project from the eye fields to the midbrain superior colliculus (SC) and cerebellum (Stanton, Goldberg, & Bruce, 1988). The SC is vital for saccade generation because it is thought that it may coordinate the discharge of downstream burst and omnipause neurons, which respectively send and inhibit the signals that drive the eye during a saccade (see Sparks, 2002).

Within the SC, the initial saccade direction is determined as a vector signal (Lee, Rohrer, & Sparks, 1988; Sparks, Lee & Rohrer, 1990), which is then sent to the brainstem. Popular models of saccade generation suggest that the vertical and horizontal components responsible for generating the saccadic movement are produced by separate pulse generators found within the brainstem (e.g. Becker & Jürgens, 1990). As most saccades consist of both a horizontal and vertical component (Bahill & Stark, 1975), the vector signal transmitted from the SC must be decomposed in the brainstem into its elements in order to generate a signal that can be transmitted to the motoneurons innervating the extraocular muscles (see Sparks & Mays, 1990, for a review). Premotor neurons in the pons and medulla are responsible for producing commands for horizontal movements, while the premotor neurons found in the rostral midbrain produce vertical movements (see Sparks, 2002). Activity in the paramedian zone of the paramedian pontine reticular formation has also been related to the control of horizontal saccades and the horizontal component of oblique saccades (Cohen & Komatsuzaki, 1972). The initial
burst of activity required to initiate a vertical eye movement is mediated by neurons in the rostral interstitial nucleus of the medial longitudinal fasciculus (Buttner, Buttner-Ennerver, & Henn, 1977). The phase signals are then sent to motoneurons, which innervate three pairs of extraocular muscles responsible for rotating the eye and generating the initial high-velocity movement typical of a saccade. The medial and lateral rectus muscles produce horizontal rotations, while superior and inferior rectus muscles work in coordination with the superior and inferior oblique muscle pairs to produce vertical movements (see Sparks, 2002). Thus, for saccades containing both vertical and horizontal components, all three muscle pairs are activated to varying degrees. A degradation of the pulse, or the burst of initial activity, follows. The step signal that stabilizes the eye once the desired rotation is achieved is also generated within the brainstem by the tonic discharge of neurons in the nucleus prepositus hypoglossi and medial vestibular nucleus for horizontal components, or the interstitial nucleus of Cajal for vertical components. The step signal does not appear to be generated by the colliculus (see Sparks & Mays, 1990).

As most saccades consist of both vertical and horizontal components, when signals are sent to the muscle pairs controlling the eye, the separated component signals must once again be coordinated. Normally, pontine omnipause neurons inhibit the burst neurons innervating the motoneurons, but once a trigger signal is sent, the omnipause neurons are momentarily inhibited and a saccade is initiated (see Moschovakis, Scudder, & Highstein (1996), for an extensive review). The omnipause neurons are thought to synchronize the onset of the horizontal and vertical components. The duration of the displacements is roughly equated by temporally stretching the smaller component, or
reducing its velocity by decreasing the discharge frequency of the excitatory burst neurons (King & Fuchs, 1979). If the onsets or offsets of the horizontal and vertical controllers are asynchronous, curved saccades will result.

**Saccadic Curvature**

It has only been recently discovered that the magnitude of saccadic curvature can be modulated by the presence of nearby distracting objects, without necessarily influencing the endpoint of the saccade (Quaia, Optican, & Goldberg, 1998). In various studies, when a distracting object is positioned near enough to a target object, a saccade aimed toward the target will often show a characteristic deviation towards the distractor, as though the eye is being lured towards the distracting stimulus. For example, significant curvature towards a distracting stimulus can be observed during double-step paradigms. In a double-step study, a participant is asked to saccade to a target, which after a variable delay, will shift from its initial position to a new target location (Westheimer, 1954; Wheeless, Boynton, & Cohen, 1966). When delays are short and the difference in initial and final target position is large (Van Gisbergen, Van Opstal, & Roebroek, 1987), participants often make what are called turn-around saccades. Initially, participants will execute a saccade towards the original target position, but will change directions mid-flight, correctly landing on the target after it is displaced. For these tasks, the target at its initial position can be considered the ‘distractor’, whereas the ‘goal’ is considered to be the target object at its final location. A more gradual curvature towards a distractor can be thought of as a less extreme form of a turn-around saccade, and is also observed in simple visual search paradigms, both in humans (McPeek, Skavenski, & Nakayama, 2000) and monkeys (McPeek & Keller, 2001). In fact, turn-around and curved saccades can be
observed within the same study. For instance, in a paradigm used by McPeek and Keller, monkeys were trained to make single saccades to colour-singleton targets. In each trial, the target could be red or green, while all distractors were the opposite colour. The colour of the target and distractors could switch randomly with each trial. On trials where the colour of the target switched, turn-around saccades were often observed, such that saccades were initially aimed to a distractor, but switched directions to land correctly at the target. Amongst these errors, less obvious ‘turns’ were observed, such that the saccade appeared to curve smoothly towards the distractor while on its way to the target. Deviations toward a distractor thus appear to be the result of a particularly salient distracting stimulus biasing initial saccade direction towards it.

Although saccades can curve towards a distractor, perhaps more likely in humans is for the distractor to cause a saccade to curve away. In a now classic study by Sheliga, Riggio, and Rizzolatti (1995), participants made vertical saccades to targets either above or below fixation. To determine which direction they were required to move, the participants had to covertly attend to a peripheral cue located in the upper or lower visual field, either slightly to the left or right of the potential target location. Sheliga and colleagues found that when attention was directed to the cue on the right, saccades aimed at the target tended to curve to the left, while saccades curved to the right if attention was initially covertly shifted to the cue located on the left. In an oculomotor capture study by Doyle and Walker (2001), participants were asked to saccade to a target while ignoring a simultaneously presented, task-irrelevant distractor. Similar to that found by Sheliga and colleagues, participants consistently showed curved saccades away from the distractor, regardless of whether the saccade was reflexive (i.e. initiated based on the onset of the
target) or voluntary (i.e. initiated based on a central directional cue). Importantly, there was no significant effect of distractor presence on saccadic curvature if the distractor was presented in the opposite hemifield from the target, far away from the target location, which suggests that only proximal objects influence saccadic trajectories. From these studies, it has been shown that the act of attending to a nearby distracting object, be it either overtly or covertly, causes a saccade aimed towards a target to deviate away from a distractor.

**Theories of Curvature and the Superior Colliculus**

The dominant theory proposed to explain why distractors influence saccadic trajectories actually originated from the manual movement literature. Tipper’s population coding theory (Howard & Tipper, 1997; Tipper, Howard & Houghton, 2000; Tipper, Howard, & Jackson, 1997) was first proposed as an explanation for why reaching movements curved in response to obstacles. Shortly thereafter, this model was adopted with few changes to account for saccadic curvature. Although similar theories previously existed in the saccadic literature to explain deviation towards non-target objects (e.g. Glimcher & Sparks, 1993; Lee, Rohrer, & Sparks, 1988), Tipper is credited with developing a coherent theory of both deviation towards and away.

According to the population coding theory, possible target objects are processed and represented in parallel by large neuronal populations whose peak activity encodes a movement vector aimed at the target. The strength of the population code is directly related to the saliency of the object it represents (Tipper et al., 1997). Each object’s representation recruits a broad array of neurons, such that any two objects (for example a target and a distractor) that are nearby in space will activate overlapping neuronal
populations. As only one eye movement can be made at a time, the overlapping codes will be combined into one mean distribution that will code for a vector aimed at an intermediate location between the objects, as derived from the weighted average of the two populations (see Port & Wurtz, 2003; Robinson, 1972). Thus, when population codes of a target and distractor are combined, the resulting saccade will initially deviate towards the distractor.

Curvature away from a distractor appears to be contingent on inhibition being applied to the distracting object’s representation. This inhibition may occur via a suppression of an unwanted saccade program (for example, during covert attentional orienting, when a saccade is undesired; e.g. Sheliga et al., 1995), or may be based on a need to resolve competition between two neural codes (e.g. Tipper et al., 1997). As nearby objects are theorized to partially share neural populations, inhibition of the distractor’s code is thought to shift the peak activity of the target’s neural population slightly, thereby coding for a vector that is directed away from the distractor location.

There are two ways in which inhibition is thought to be applied to the distractor’s representation. When distractor activity is low, then lateral inhibition from the target’s representation may successfully reduce the impact that the distractor has on saccadic curvature. Tipper and colleagues (1997) stated that each neuron might have excitatory connections to nearby neurons, and inhibitory connections to those further away, consistent with an on-center, off-surround model (Georgopoulos, 1995). If the target’s representation is stronger than that of the distractor, as would often occur due to representational boosting from goal-driven mechanisms, then the target neurons’ inhibitory connections could suppress most or all of a distractor’s activation, given that
the distractor’s representation is sufficiently weak. This lateral inhibition is argued to be too weak to cause deviation away, however, but rather will decrease the degree of deviation towards the distractor. If a distractor’s activity is too strong to be suppressed via lateral inhibition, a saliency-modulated ‘reactive feedback’ system comes into play. This selective, goal-mediated inhibitory system is capable of inhibiting stronger distractor representations, and can push distractor activation below baseline levels (Houghton & Tipper, 1994). Thus, when saliency of a distracting object is high, deviation away is produced, such that the more salient the distractor, the greater the inhibition imposed, and thus the more deviation away observed.

As written, Tipper’s original theory has its flaws. Crucially, it predicts that weakly distracting objects will cause deviation towards, while strongly distracting objects will cause deviation away. In practice, however, it is typical that a more distracting object will actually result in greater deviation towards it (e.g. Deubel, Wolf, & Hauske, 1984; Godijn & Theewes, 2002). If one includes time as a factor in the model, however, and assumes that these inhibitory processes take time to develop, such that lateral inhibition comes online slightly before or at the same time as reactive inhibition, then the model can explain many saccadic behaviours. Thus, very rapid saccades will show deviation towards the distractor, as stronger forms of inhibition have not yet come online; while slower saccades will reveal deviation away from a distractor. Very recently, these predictions have been tested and confirmed (Campbell, Al-Aidroos, Pratt, & Hasher, 2009; McSorley, Haggard & Walker, 2006; Mulckhuyse, Van der Stigchel, & Theeuwes, 2009).

While a modified version of the population coding theory may do well at
explaining the behavioural and neurological results observed when it is extended to oculomotor behavior, it is reasonable to think that oculomotor behavior is not being guided by representations in the motor cortex. In the case of saccades, it is believed that an oculomotor map capable of representing potential saccade goals and determining an initial saccade direction is located within the intermediate layers of the SC (Robinson, 1972; Schall, 1991; Sparks & Hartwich-Young, 1989). The SC is a midbrain laminar structure that has been implicated in both eye movements and shifts of attention (Schall, 1991). Activity within this region consistently precedes saccade onset, emitting a pulse of activity about 20 ms before the start of a saccade (Sparks, 1978). In addition, its direct connections to the brainstem saccade generators make it a perfect candidate for the region critical in determining a saccade’s initial direction. Although not discussed here\(^1\), the cerebellum is thought to mediate online correction that occurs during saccadic movements (McSorley, Haggard, & Walker, 2004, Quaia, Lefèvre, & Optican, 1999).

Thus, under normal circumstances, the two regions work together to generate and control saccades.

As described above, the SC receives information from frontal and parietal regions, such as the FEF and lateral interparietal area (Munoz, 2002). The SC also receives direct retinal input; it must therefore act as an integrator of bottom-up and top-down information. In so doing, a topographic oculomotor map of visual space is

---

\(^1\) According to McSorley, Haggard, and Walker’s (2004) model of saccadic curvature, the SC, along with the FEF and visual inputs from other regions, determines the initial direction and amplitude of the saccade. The SC feeds this information to the brainstem saccadic generator. Quaia, Lefèvre, and Optican (1999) suggested that the cerebellum receives indirect input from the SC, FEF and SEF regarding the target’s position in space. The cerebellum thus inputs a drive signal that controls the saccade online via a feedback loop with the brainstem saccadic generator, which the SC is not involved in. The drive signal compares the desired and actual eye position in order to keep the saccade moving towards its desired endpoint.
generated, with each half of the observer’s visual field being represented within the contralateral half of the SC (Cynader & Berman, 1972; DuBois & Cohen, 2000; Hall & Moschovakis, 2003; Schneider & Kastner, 2005). Horizontal saccades therefore depend upon representations within only one colliculus, while saccades made in a vertical direction will be based on object representations present in both halves of the SC. It is upon this motor map that inhibition is thought to be imposed in a goal-directed manner, perhaps via inputs from the FEFs (Godijn & Theeuwes, 2002; McPeek, Han, & Keller, 2003; McSorley et al., 2004). Evidence that inhibition is imposed on this motor map comes from a study by McPeek and colleagues (2003), who used a unique-colour visual search task with monkeys and found that when two objects were presented on the screen, saccades were directed towards the object that generated the greatest pre-saccadic activity within the SC. Importantly, saccades also curved towards the other object (i.e. the distractor) and the magnitude of this curvature was correlated with the level of activity at the distractor’s representation. Further, when non-target locations were stimulated below threshold levels, saccades were found to curve towards the location of stimulation.

**Modulation of Saccadic Curvature**

Models of saccadic curvature imply that two factors should be critical in determining the magnitude and direction of curvature observed: distractor saliency and planning time. Saliency should directly influence the initial strength of the distractor’s representation, which itself determines the amount of inhibition that must be imposed to suppress it. Planning time, on the other hand, should influence the opportunity for inhibition, and thus the degree of inhibition that can be imposed before saccade execution.
The first critical factor, distractor saliency, has been investigated primarily by varying the similarity between target and distractor, with distractors that are more similar to the target being considered as more salient. In a study by Ludwig and Gilchrist (2003), participants had to make vertical saccades in the presence of horizontally positioned distractors that could be presented in the same colour as the target, or in a different colour. Saccades to a no-onset target were found to curve away more from a distractor that onset with the same colour as the target than one that onset with a different colour. Although object onset appeared to capture the attention of the participants in all conditions, such that saccades always curved away from an irrelevant distractor, the distractor’s similarity to the target modulated the magnitude of the curvature observed. In a similar task, Mulckhuyse and colleagues (2009) had participants make saccades to targets in the presence of same-colour distractors or same-colour-and-shape distractors. When saccadic reaction times (SRTs) were short, saccades made in the presence of dissimilar distractors showed greater deviation away than those made in the presence of similar distractors. When SRTs were longer, this difference disappeared and seemed to reverse at the longest SRTs, although this effect only reached significance when the distractor was always a unique shape but could share the same colour as the target. Regardless of how salience is manipulated, a more salient distractor appears to generate greater interference to a saccade aimed towards a nearby target.

Evident in Mulckhuyse and colleague’s (2009) findings is the importance of the second factor that should influence saccadic curvature: the amount of time available to plan the saccade. In 2006, a research group headed by McSorley demonstrated definitively that the amount of time available to plan a saccade prior to execution alters
the magnitude and direction of saccadic curvature observed. In their study, a gap paradigm (Ross & Ross, 1980; Saslow, 1967) was included in order to increase the variability of SRTs that participants would produce. Briefly, when a fixation point is removed, this releases the saccadic system from the inhibition that is applied by the fixation neurons within the rostral pole of the SC (Munoz & Wurtz, 1993), enabling saccades to be executed faster once a go-signal is presented shortly afterwards. If a fixation point remains on during target presentation, then SRTs are considerably slower. As the gap effect has been shown to have an independent effect on SRTs than those attributed to distractor presence (Walker, Kentridge, & Findlay, 1995), this manipulation allowed the authors to plot the time course of distractor influences on saccadic trajectories. At varying gap or overlap stimulus onset asynchronies, participants were required to make oblique saccades in the presence or absence of nearby distracting stimuli. When trajectory deviations were binned based on SRT and plotted as a time course, it was apparent that deviation changed as a function of SRT. When SRTs were rapid, deviation towards the distractor was observed. As SRTs increased, deviation towards decreased. At latencies of about 200 ms, deviation towards transitioned to away from the distractor, increasing linearly as reaction times increased. The authors suggested that inhibitory processes that suppress the distractor’s representation are relatively slow, and cannot successfully return distractor activity to baseline levels if saccades are executed faster than about 200 ms. These findings are consistent with the proposed modified model by Tipper and colleagues (1997, 2000), which states that inhibition takes some time to develop.
Interestingly, it appears that distractor inhibition can be initiated even before the distractor onsets, indicating that this effect is not entirely driven by visual features, but is also contingent on attentional allocation. When a cue is presented at fixation to indicate the location of an upcoming target or distractor, deviation away from the distractor is generally observed (e.g. Walker, McSorley & Haggard, 2006; Van der Stigchel & Theeuwes, 2006; 2008). However, when a central cue produces expectation of the onset of a distractor but the distractor does not actually appear, deviation away from the expected distractor location may reverse to deviation towards, or will at least be reduced in magnitude compared to when the distractor is presented (Walker et al., 2006; Van der Stigchel & Theeuwes, 2006). That expectation can influence saccadic curvature is further evidence of the importance of planning time in determining the direction and magnitude of deviation.

Recently, an additional third factor has been proposed which should also have a significant impact on the degree of curvature observed: the manner by which inhibition is applied upon the colliculus. Although many studies have investigated curvature during vertical, horizontal and oblique saccades, few have directly investigated the effect that target location may have on the SC’s representations of these objects and the inhibition that can be applied to them. To understand why target location may have an effect on trajectory deviations, one must recall two points. First, horizontal objects are represented within one half of the SC, while vertical objects are represented across the two halves of the SC. Second, inhibition does not spread across the two halves of the SC. An efficient but not particularly specific inhibitory system would apply inhibition to a distractor’s representation in the broadest manner possible that does not completely eliminate the
target’s activation distribution. Indeed, some earlier research has suggested that inhibitory processes are broad and not very sensitive to the distractor’s position (McSorley et al., 2004; 2005; Van der Stigchel, Meeter, & Theeuwes, 2007; Van der Stigchel & Theeuwes, 2006). Thus, in the case of a vertical target and nearby (oblique) distractor, inhibition can be applied coarsely to one half of the SC, negating the target’s activity there, but leaving the remaining target’s representation in the other half of the SC untouched. In contrast, coarse inhibition cannot be achieved when the target object is on the horizontal, as it would suppress the entire target’s representation in the same half of the SC as the distractor. It is therefore predicted that a more selective, less effective type of inhibition might be applied to a distractor’s representation in such a circumstance. Behaviourally, these differences in the application of inhibition would manifest in greater deviation away from the same oblique distractor when a target is presented on the vertical than when it is presented on the horizontal. This is precisely what Van der Stigchel and Theeuwes (2008) found. The effect is also observed when attention is covertly and voluntarily shifted to a peripheral location (Sheliga, Riggio, Craighero, & Rizzolatti, 1995).

**Purpose of Investigation**

The purpose of the studies that follow was to further characterize what factors influence the curvature of a saccade. Although several factors have already been shown to modulate the effect a distracting stimulus has on a saccade made to a target, several questions remain.

Experiments 1 and 2 investigate the effect that target location has on the time course of saccadic inhibition. In Van der Stigchel and Theeuwes’ (2008) study where it
was observed that vertical saccades showed greater deviation away from an identical
distractor than did horizontal saccades, a 100% predictive cue was always presented to
indicate where the target would appear 800-1200 ms later. This advanced warning is
particularly important given the results of McSorley et al.’s (2006) work, which
implicated planning time as having dramatic effects on the magnitude and direction of
trajectory deviations. It is possible that the advanced warning provided by the cue could
have substantially increased the amount of inhibition that participants were able to apply.
As such, the presumed difference in inhibition levels during horizontal and vertical
saccades may represent the upper boundary of inhibition that can be imposed by using a
selective or coarse inhibitory strategy. When lengthy preparation time is unavailable,
inhibitory processes may not reach their peak, and as a result curvature away from a
distractor during horizontal and vertical saccades may appear similar. In other words,
during more typical conditions, when one executes a saccade as soon they are as able, no
behavioural difference in deviation would be observed. Indeed, a study by Walker and
colleagues (2006) compared deviation observed from horizontal, vertical and oblique
saccades when participants were provided with no advanced information regarding the
target’s location. Interestingly, no significant differences were observed in deviations
across saccade directions, although the small sample size (n = 6) may have prevented the
trend of the horizontal saccades showing the least amount of deviation from reaching
statistical significance.

In Experiment 1, we aimed to determine whether distractor-based trajectories
differences would be observed between horizontal and vertical saccades when
participants were not given advanced planning time. To accomplish this, participants
performed a modified version of the paradigm employed by McSorley and colleagues (2006), where saccades were made to vertical or horizontal targets in the presence or absence of nearby distractors. Thus, the response was identical to what Van der Stigchel and Theeuwes (2008) employed, but the planning time was restricted to the latency of the saccadic response.

For completeness, Experiment 2 asked whether any differences might be observed during oblique saccades based on the location of the distracting stimulus. While an oblique target and a horizontal distractor might be expected to rely on the same selective inhibitory mechanism used when the locations of the target and distractor are reversed (as per Van der Stigchel & Theeuwes, 2008), it is unclear whether splitting a vertical distractor’s representation across the two halves of the SC would have the same effect observed when a vertical target’s representation is split. Inhibition may be selectively applied to each distractor representation in each half of the SC, in which case we would anticipate no differences in trajectory based on distractor position. Alternatively, the portion of the distractor that does not share its half of the SC with the target’s representation could be inhibited coarsely (while the other portion remains selectively inhibited), thereby producing more deviation away when distractors are on the vertical than when they are on the horizontal. Although McSorley et al. (2006) reported no differences based on distractor location, it may be that the authors simply never analyzed their data in this manner.

Finally, we hoped to characterize the time course of these inhibitory effects, both later on when deviation away is often observed, as well as when SRTs are rapid and deviation towards typically dominates. While Van der Stigchel and Theeuwes’ (2009)
inhibition-based hypothesis can successfully explain target location differences in trajectories when deviation is away from a distractor, they make no predictions for what may occur when deviation towards is observed. If it is to be believed that greater deviation away is directly related to the initial strength of the distractor representation on the oculomotor maps, then it is possible that deviation towards may also differ based on target location. If this is the case however, an explanation concerning only differences in the efficacy of inhibition would be insufficient to account for initial deviation towards at very fast SRTs, as presumably the inhibitory processes would not yet have come online.

The focus of Experiment 3 was to test one proposed theory to account for the effects found in the previous experiments. To preface our results, it was found that greater deviation due to a nearby distractor is evident in vertical saccades not only during deviation away, as has previously been reported, but also during deviations towards the distractor. While theories based on inhibition can explain why deviation away differs based on target location, it cannot account for why deviation towards is also initially greater for vertical saccades. Here, we suggest that the efficiency by which objects are represented by the SC may account for the observed results, and to test this hypothesis we manipulated the relative salience of nearby distractors to the targets. The implications of Experiment 3 are important not only for understanding why vertical saccades show greater distractor interference, but also for understanding how salience influences saccade planning.
Experiment 1: Effect of Target Location on Horizontal and Vertical Saccadic Trajectory

Introduction

To determine whether differences in inhibition would be present for vertical and horizontal saccades, we used a paradigm similar to that employed by McSorley et al. (2006), with the exception that target and distractor locations were switched. Participants were asked to saccade to targets presented on the vertical or horizontal meridians, while distractors could be presented on the obliques. Thus, we were able to compare equivalent eye movements to Van der Stigchel and Theeuwes (2008) while using a paradigm that permitted us to analyze the time course of saccadic inhibition.

Methods

Participants

After giving informed written consent, 10 volunteers from the University of British Columbia participated in exchange for course credit or $10. Six participants were female; nine were right-handed. All participants reported normal or corrected to normal vision. The mean age was 25.50 years.

Stimuli and Procedure

Stimuli were displayed on a 17-inch monitor. Viewing distance was held constant at 65 cm by a chin rest. Eye movements were recorded with an EyeLink 1000 desktop-mounted eye tracker (SR Research, Mississauga, Ontario, Canada) recording at 1000 Hz.
At the start of each block of trials and whenever a drift check failed, participants completed an eye tracker calibration and validation, as per standard system settings. All stimuli were white and were presented on a grey background (17.95 cd/m²; RGB: 102, 102, 102). Saccades were made from a central fixation dot (0.38° x 0.38°) to a target ‘X’ or ‘O’ (all 0.8° x 0.8°) located in one of four positions on the cardinal axes (0, 90, 180, or 270 angular degrees), 7.4° from center. In two thirds of the trials, a distracting ‘X’ or ‘O’ was presented 45 angular degrees away from the target (i.e. at 45, 135, 225, or 315 angular degrees, depending on the target position; either to the left or the right of the target). Target and distractor assignment (i.e. X or O) was randomly selected for each participant. Figure 1 illustrates the spatial location of saccade targets and distractors.

There were eight possible distractor-present conditions (four target locations with the distractor to the left or right of the target), and four possible distractor-absent (baseline) conditions. A target occurred on every trial. In the distractor-present trials, the target and the distractor onset simultaneously. The fixation point offset at a stimulus onset asynchrony (SOA) of -200, -100, -50, 0, 50, 100, or 200 ms, relative to target onset. Negative values indicate gap conditions in which the fixation point offset before target onset; positive values indicate overlap conditions in which the fixation point offset after target onset. The inclusion of a fixation offset manipulation was important in order to generate a greater variability in SRTs, and has been used previously in other trajectory studies (e.g. McSorley et al., 2006; Campbell et al., 2009). Across target positions, participants completed 40 distractor trials and 20 no-distractor trials for each of the seven SOA intervals, totaling 420 trials. All trial-types were randomized, with the stipulation that the program could not present two successive trials with both the same
Each participant completed 10 practice trials, which were excluded from analysis.

![Spatial layout of possible saccade targets (T) and distractors (D) in Experiments 1 and 3 (Figure 1a) and Experiment 2 (Figure 1b). In Experiments 1 and 3, targets were always on the horizontal or vertical, and distractors were always on the oblique. For Experiment 2, the locations of the target and distractors were reversed compared to that used in Experiment 1. For Experiments 1 and 2, if the target was an ‘X’, then the distractor was an ‘O’, and vice versa. In Experiment 3, the target was always an ‘X’ while the distractor was always an ‘O’. The identity of the target and distractor was constant for each participant. Targets could appear alone (1/3 of the trials) or simultaneously with a single distractor flanked on the left or right (2/3 of the trials).]

Each trial began with the participant fixating a central fixation point. After a pseudo-random foreperiod of 800-1200 ms, participants were instructed to make one eye movement from the center of the fixation dot to the center of the target as soon as they
detected its onset. If the trial contained a distractor, participants were instructed to ignore it and treat the trial as if only the target object were present. If a participant failed to maintain central fixation at the start of the trial, the trial ended, calibration was checked, and the trial restarted. A 600 ms inter-trial interval separated each trial. Trials were divided into seven blocks of 60, separated by self-paced breaks.

**Data Handling**

Saccadic curvature was calculated using the quadratic fit method detailed in Ludwig and Gilchrist (2002). Each saccade was rescaled so that the eye movements traveled a common absolute distance, and the best fitting quadratic polynomial was determined for each saccade. The quadratic coefficient was taken as a measure of the amplitude of the saccade’s curvature, and is reported here in degrees of visual angle. To compensate for minor deviations in baseline trajectories, the average trajectory during distractor absent trials was found and the value was subtracted from the trajectories collected from distractor present trials. Because saccade trajectories are known to vary depending on the saccade direction (Viviani et al., 1977), baseline trajectory subtraction was specific to each saccade direction. Trajectories deviating away from the distractor were assigned negative values; trajectories deviating towards the distractor were assigned positive values.

**Results and Discussion**

**Trial Exclusion**

Trials were excluded from further analysis if the participant’s first saccade went to the distractor (3.64% of all trials), if the first saccade fell short of the target or did not
land at a target or distractor location (9.19%), if SRTs were below 100 ms (0.07%) or greater than 500 ms (0.10%), or if saccade curvatures were greater or less than three standard deviations away from the individual’s mean before baseline correction (1.33%).

**Gap Effect**

The mean SRTs across SOAs for distractor and no-distractor conditions are shown in Figure 2. A two-factor ANOVA was performed with distractor (present or absent) and SOA (-200, -100, -50, 0, 50, 100, 200 ms) as within-subject factors. For all analyses, if Mauchly’s test of sphericity was significant \( (p < .25) \), relevant degrees of freedom were adjusted using the Greenhouse-Geisser (if \( \varepsilon \leq .70 \)) or Huynh-Feldt (if Greenhouse-Geisser \( \varepsilon > .70 \)) adjustments. The main effect of distractor was significant, \( [F(1, 9) = 20.83, p = .001] \), indicating that SRTs were slower in the presence of a distractor than when the target onset alone, which is consistent with findings of a remote distractor effect (e.g. Walker, Deubel, Schneider, & Findlay, 1997). The main effect of SOA was also significant, \( [F(2.16, 19.42) = 47.21, p < .001] \), such that SRTs increased with increasing overlap between fixation point and target onset. The interaction between distractor and SOA was not significant, \( [F(6, 54) = .80, p > .50] \).
Figure 2. Mean saccadic reaction times for all subjects in Experiment 1 for distractor present and absent trials, for each SOA condition. Negative values indicate that the fixation point was extinguished before target onset; positive values indicate the fixation point was extinguished after target onset. Error bars for all figures represent 95% confidence intervals.

Trajectory Time Course – Effect of Target Location

Saccadic Reaction Time Analysis

To create a time course of trajectory deviation, each participants’ data was sorted based on SRT and divided into five equal-sized bins, with Bin 1 representing saccades with the fastest SRTs, and Bin 5 representing saccades with the slowest SRTs. As SRT has previously been shown to affect saccadic trajectory (McSorley et al., 2006), mean
trajectories produced for saccades directed to different target locations could only be directly compared through an analysis of variance if the mean SRT of each bin was comparable for saccades made to different target locations. If the mean SRTs for each bin were significantly different for saccades made to different target locations, then any direct comparison of trajectory would be confounded by differences in SRT.

To determine whether mean SRT bins were comparable across saccades made to different target locations, we ran a within-subjects ANOVA with target location (up, down, left, right) and SRT bin (1 through 5) as factors. As we had reason to believe that vertical saccades made to the upper and lower visual field might differ in mean SRT (see Honda & Findlay, 1992), we chose to compare the four target locations before collapsing across vertical and horizontal locations. Results showed a main effect of target location, $[F(2.05, 18.85) = 14.66, p < .001]$, and SRT Bin, $[F(1.26, 11.33) = 111.72, p < .001]$. Critically, the interaction was not significant, $[F < 1, p > .50]$, suggesting that the effect of target location did not influence SRTs differently across bins. Simple main effects analysis of target location was completed via pairwise contrasts using a Bonferroni correction for multiple comparisons with a corrected $p < .05$. As suspected, saccades made to targets in the lower visual field were slower than saccades made to any other targets, all $ps < .01$. No other contrasts were significant, all $ps > .50$. Importantly, as there was a main effect of target location on mean SRT, all trajectory analyses were completed using the value of the slope generated by plotting trajectory deviation over SRT bin. By using slope values, we were able to control for differences in SRT across target location conditions. Thus, any significant differences in conditions can be confidently attributed to differences in saccade trajectory, not SRT. Further, the use of slope as the dependent
variable allows easy investigation of the change in trajectory deviation over time, as steeper slopes directly indicate greater change.

Additionally, we compared the x-intercept, or the SRT at which the trajectory curvature equaled 0, for all analyses involving slope measures. If two conditions differ in their slope but not their x-intercept, then we can reasonably infer that the differences exist when SRTs are very fast or very slow, i.e. that the two conditions show different curvature towards and away. If two conditions differ in slope and x-intercept, then differences in curvature may be present only at certain time points but not others. If, however, the two conditions being compared do not differ in slope nor x-intercept, we can be confident that the condition manipulation had no differential influence on the magnitude of curvature either towards or away from the distractor. Finally, if the slopes do not differ but the x-intercepts are significantly different, then it is reasonable to infer that there was a main effect of the condition manipulation such that one condition has greater curvature away but less towards, or vice versa.

Saccadic Trajectory Analysis

The mean trajectory was determined for each SRT bin for vertical and horizontal target locations, regardless of SOA. Figure 3 displays saccadic curvature as a function of SOA for saccades made to vertical and horizontal target locations.
Figure 3. Mean saccadic curvature obtained during distractor present trials in Experiment 1, divided into five SRT bins for vertical and horizontal target locations. Negative values indicate curvature away from the distractor; positive values indicate curvature towards the distractor.

A two-tailed paired samples t-test comparing the slopes generated by making horizontal or vertical saccades revealed a significant difference, \( t(9) = 4.30, p = .002 \), such that the change in curvature of saccades made to vertical targets was much greater (i.e. the slope was steeper) than that found for saccades made to horizontal targets. Although saccades made to horizontal targets showed very little change in curvature in response to a nearby distractor, a one sample t-test comparing the slope generated by making horizontal saccades to a slope of 0 revealed a significant difference, \( t(9) = -4.18, p = .005 \).
indicating that the presence of a distractor did alter the curvature of the horizontal saccades. However, when the slope from the first three RT bins was compared against a slope of 0, no significant difference emerged, \[ t(9) = .26, \ p > .50 \], indicating that when RTs were rapid, the presence of a distractor did not significantly influence the curvature of horizontal saccades above what is demonstrated during the baseline condition (i.e. when no distractor was presented). Thus, the rate of change in saccadic curvature across SRTs was greater for saccades made to vertical targets than for saccade made to horizontal targets. The x-intercept did not differ for horizontal and vertical saccades, \[ t(9) = -1.56, \ p > .10 \]. Consistent with Van der Stigchel and Theeuwes (2008), vertical saccades demonstrated greater curvature away from the distractor than did horizontal saccades when SRTs were long. In addition, however, we found that vertical saccades demonstrated greater curvature towards the distractor than did horizontal saccades when SRTs were short. Thus, vertical saccades displayed greater overall interference from a distractor than did horizontal saccades.

As a secondary interest, a two-tailed paired samples t-test was run to compare the slopes from saccades made to targets in the upper versus lower visual fields. Given other known differences between saccades made to upper and lower visual field locations – for instance, SRT (Honda & Findlay, 1992) – we compared their trajectories to determine if any additional differences would be observed. They did not differ in their slopes, \[ t(9) = -.70, \ p > .50 \], or x-intercepts, \[ t(9) = 1.94, \ p > .05 \]. Thus, when differences in mean SRTs between upward and downward saccades are controlled for, the effect of a distractor on trajectory deviations is equivalent. For completeness, trajectory slopes of saccades made to left and right target locations were also compared with no significant differences.
found, \([t(9) = .46, p > .50]\). No difference was apparent in the x-intercepts of leftward or rightward saccades, \([t(9) = -1.04, p > .25]\).
**Experiment 2: Effect of Distractor Location on Oblique Saccade**

**Trajectory**

**Introduction**

Although McSorley et al. (2006) did not report any differences in curvature based on saccade direction, this may have been in part due to their use of oblique saccades rather than purely horizontal or vertical eye movements. To determine whether differences in distractor interference can also be observed in oblique saccades, we repeated the study with new participants but switched the target and distractor locations. In Experiment 2, participants were now asked to saccade to an oblique target and ignore a distractor presented either vertically or horizontally.

**Methods**

**Participants**

Ten volunteers from the University of British Columbia participated in exchange for course credit or $10. All gave informed written consent. Six participants were female; eight were right handed. All participants reported normal or corrected to normal vision. The mean age for all subjects was 21.50 years.

**Stimuli and Procedure**

The methods used for Experiment 2 were identical to Experiment 1 except that target and distractor locations were switched. The target (‘X’ or ‘O’) always appeared at one of four oblique locations (at 45, 135, 225, or 315 angular degrees). In two thirds of
the trials, a distracting ‘O’ or ‘X’ was presented 45 angular degrees away from the target (i.e. at 0, 90, 180, or 270 angular degrees, depending on the target position).

**Data Handling**

Unlike Experiment 1, the mean trajectory was determined for each bin for vertical and horizontal *distractor* locations, not target locations, irrespective of SOA condition. This change in analysis reflects the hypothesis that objects on the vertical meridian of visual space may be represented differently than objects elsewhere, which is supported by our findings in Experiment 1 as well as by Van der Stigchel and Theeuwes’ (2008) results. By dividing the data based on the objects that differ in vertical and horizontal space, analysis is kept consistent across studies.

**Results and Discussion**

**Trial Exclusion**

Trials were excluded from further analysis if the participant’s first saccade went to the distractor (13.74% of all trials), if the first saccade fell short of the target or did not land at a target or distractor location (14.34%), if SRTs were below 100 ms (0.05%) or greater than 500 ms (0.08%), or if saccade curvatures were greater or less than three standard deviations away from the individual’s mean before baseline correction (0.09%).

More saccades were erroneously directed to the distractor in Experiment 2 than in Experiment 1 (no other error rates were significantly different, all \( p > .05 \). In Experiment 2, significantly more saccades erroneously landed on horizontal than on vertical distractors [\( t(9) = 3.91, p = .004 \)], indicating that objects on the horizontal captured the participants’ attention more than objects on the vertical. Further, saccades to
the distractor were more common during gap than during overlap trials, \[t(9) = 4.83, p = .001\], indicating that more errors occurred when saccades were rapid and when saccades typically show greater curvature towards the distractor\(^2\). Saccades have a tendency to curve towards the horizontal, even in the absence of a distractor (Viviani et al., 1977). If this natural tendency to curve towards the horizontal is combined with a general deviation towards a horizontal distractor (when saccades are rapid), then this may have created so much deviation that online cerebellar correction was ineffective, and thus more errors to the distractor occurred in the horizontal distractor condition. In contrast, when the distractor is on the vertical, then the natural inclination to curve towards the horizontal would be offset by the saccade curving towards the distractor when reaction times are fast, thereby reducing the overall degree of curvature that must be compensated for in order to accurately land near the target. Although this is an interesting observation, our results investigated the effect of a distractor on saccade curvature, not endpoint, and as such, the remainder of our analyses focuses on these effects.

**Gap Effect**

The mean SRTs across SOAs for distractor and no-distractor conditions are shown in Figure 4. A two-factor ANOVA was performed with distractor (present or absent) and SOA (-200, -100, -50, 0, 50, 100, 200 ms) as within-subject factors. As in Experiment 1, the main effect of distractor was significant, \[F(1, 9) = 6.00, p = .04\]. The

\(^2\) In Experiment 1, the number of erroneous saccades made to the distractor were not significantly different based on target or distractor location, all \(ps > .10\). In Experiment 1, there were significantly more erroneous saccades directed to the distractor during gap trials than during overlap trials, \[t(9) = 3.88, p = .004\]. Consistent with a speed-accuracy trade-off, when saccades are speeded, more errors occurred.
The main effect of SOA was also significant, \([F(1.95, 17.52) = 14.64, p < .001]\), such that SRTs increased with increasing overlap between fixation point and target onset. The interaction between distractor and SOA was not significant, \([F(2.72, 24.49) = .92, p > .25]\).

Figure 4. Mean saccadic reaction times (SRTs) for all subjects in Experiment 2 for distractor present and absent trials, for each SOA condition. Negative values indicate that the fixation point was extinguished before target onset; positive values indicate the fixation point was extinguished after target onset.
Trajectory Time Course – Effect of Distractor Location

Saccadic Reaction Time Analysis

As in Experiment 1, an initial within-subjects ANOVA of distractor location (up, down, left, right) and SRT Bin (1 through 5) revealed a significant main effect of distractor location, \([F(3, 27) = 6.60, p = .002]\), as well as a significant main effect of SRT Bin, \([F(1.30, 11.65) = 119.41, p < .001]\). There was no interaction between distractor location and SRT Bin, \([F(3, 27) = 2.35, p = .10]\). Simple main effects analysis of distractor location was completed via pairwise contrasts using a Bonferroni correction for multiple comparisons with a corrected \(p < .05\). Only saccades made in the presence of the distractor in the upper visual field (i.e. up) were marginally but not significantly faster than saccades made in the presence of a distractor at any other location, all \(ps > .05\). As in Experiment 1, remaining analyses were performed on the slope generated by plotting saccade curvature over time.

Saccadic Trajectory Analysis

In order to investigate the effect of SRTs on saccadic trajectory, each participant’s data was sorted by SRT and divided into five SRT-based bins. Figure 5 displays the curvature as a function of SOA for saccades made to oblique targets made in the presence of vertical and horizontal distractor locations.
Figure 5. Mean saccadic curvature obtained during distractor present trials in Experiment 2, divided into five SRT bins for vertical and horizontal distractor locations. Negative values indicate curvature away from the distractor; positive values indicate curvature towards the distractor.

A two-tailed paired samples t-test comparing the trajectory slopes generated by saccades made in the presence of horizontal distractors versus those made in the presence of vertical distractors revealed a non-significant difference in slope, \( t(9) = -.57, p > .50 \), indicating that the location of the distractor had no significant impact on the trajectory slope of the saccade. In addition, the x-intercepts for saccades made in the presence of horizontal versus vertical distractor did not differ, \( t(9) = .31, p > .75 \). No differences
were found for saccades made in the presence of distractors in the upper versus lower visual field, either for slope \([t(9) = 1.73, p > .05]\) or x-intercept, \([t(9) = 2.14, p > .05]\); nor were there any differences for left versus right distractors in slopes, \([t(9) = -0.136, p > .75]\), or x-intercept, \([t(9) = .68, p > .50]\).

**Comparison of Experiments 1 and 2**

Since there was no difference in curvature over time based on distractor location in Experiment 2, we collapsed horizontal and vertical slopes to generate an average change of oblique saccade curvature over time irrespective of distractor location. We then compared this measure with curvature over time when making a vertical or horizontal saccade in Experiment 1. For vertical saccades, a two-way, independent samples t-test revealed a significant difference in slopes between experiments, \([t(12.91) = -2.46, p = .03]\), but no difference in x-intercept, \([t(18) = .24, p > .75]\), indicating that distractor interference was greater during vertical versus oblique saccades. A two-way independent samples t-test comparing the slopes generated from Experiment 2 to the slopes from Experiment 1 when a horizontal saccade was made revealed a trend towards a significant difference, \([t(18) = 1.92, p = .07]\). For horizontal saccades compared to oblique saccades, there was no difference in x-intercept, \([t(18) = 1.46, p > .10]\), which together with the slope analysis suggests that oblique saccades showed marginally greater interference from a distractor than did horizontal saccades.
Discussion of Experiments 1 and 2

The results from Experiments 1 and 2 show that vertical saccades are unique in their susceptibility to greater distractor interference than either horizontal or oblique saccades. In both experiments, our results replicated the time course of curvature previously reported by McSorley et al. (2006). At fast reaction times, curvature towards the distractor was observed, and this decreased with increasing SRTs until it transitioned to curvature away at the longest SRTs. When horizontal and vertical saccades made in Experiment 1 were analyzed separately, we also replicated Van der Stigchel and Theeuwes’ (2008) finding that after longer planning times, vertical saccades curved away from the distractor more so than did horizontal saccades.

A potentially major difference between our study and that of Van der Stigchel and Theeuwes’ (2008) paradigm was that our participants were not given an informative precue indicating where the target would occur 800-1200 ms later. As it has been shown that planning time can dramatically influence how curvature in response to a distractor is manifested (McSorley et al., 2006), it is possible that the differences between horizontal and vertical saccades reported by the authors may not be present when the extra planning time is not available. Van der Stigchel and Theeuwes argued that the differences in deviation observed were due to the manner in which inhibition was applied in each condition. For horizontal saccades, the representations of the target and distractor fell within the same half of the SC, and thus inhibition of the distractor’s activation would occur selectively so as to not eliminate the target’s representation and thus also inhibit a saccade. In contrast, for vertical saccades, the target object was represented across both halves of the SC. As inhibition does not spread across the two halves of the SC, inhibition
could be applied more coarsely across the half of the SC containing the distractor’s representation without the risk of completely eliminating the target’s activation distribution. The greater deviation away during a vertical saccade was thereby a result of the coarser, more effective manner that inhibition was applied. It is possible, however, that the difference in efficacy of the two processes might not be observed behaviourally unless maximum inhibition is applied, as might be the case when participants are given an average of a second to plan a movement and inhibit possible distractor locations.

Our study excludes this alternative interpretation. Even though participants in Van der Stigchel and Theeuwes’ (2008) original study were given up to 1200 ms to plan their saccade and potentially apply inhibition to locations where a distractor may appear, our results show that this difference between horizontal and vertical curvature away from the distractor is observed even when planning is limited to that available during slower SRTs. In other words, this difference in inhibition is apparent as soon as curvature away from the distractor is observed, and increases with longer planning times.

When only deviation away is considered, our results are consistent with the differences in inhibitory processes proposed by Van der Stigchel and Theeuwes (2008). In Experiment 1, however, we also observed a difference between horizontal and vertical saccades during fast SRTs, such that vertical saccades curved towards the distractor more. It is important to note that the differences in inhibitory efficiency postulated by Van der Stigchel and Theeuwes (2008) are based on the process of applying inhibition (i.e. the strategy that is used). They do not mention that the relative strengths of the representations being inhibited would have any influence. As such, their hypothesis makes no clear predictions about what would be observed when saccades initially show
curvature towards the distractor, when inhibition has not yet been applied and differences in the magnitude of curvature are thought to reflect the relative strength of the distractor’s representation compared to that of the target (McPeek et al., 2003).

Based on the population coding theory of Tipper and colleagues (1997; 2000), since none of the qualities of the distractor varied between horizontal and vertical saccade conditions, there is no reason to believe that deviation towards would differ across conditions. However, if one presumes that the different mechanisms by which inhibition is applied selectively versus coarsely are initiated early on during saccade planning, then one may hypothesize that the rate of change in the magnitude of deviation towards the distractor would differ, as observed here.

In addition, however, there was a dramatic difference even at the fastest SRT bin, where inhibition is not yet thought to have come online (McSorley et al., 2006). The observance of differences in trajectory for horizontal and vertical saccades at the fastest time bin poses a problem for the population coding hypothesis. To maintain consistency with the model, one must presume that even before inhibitory processes have come online, the degree to which the distractor’s activation contributes to the weighted vector average differs when averaged with a vertical compared to a horizontal object. As the distractor used in each condition was identical, it is reasonable to conclude that this difference could only be produced by differences in the strength of vertical or horizontal target representations, such that the same visual stimulus produces varying levels of activation upon the oculomotor map based on its location.

The important question now becomes: what mechanism could drive such differences in activation? This question cannot be answered based on our results alone,
however recent neuroimaging techniques capable of imaging the SC may point to one plausible explanation. While human participants passively viewed contrast-reversing checkerboard patterns, Schneider and Kastner (2005) recorded BOLD responses within the SC. Strikingly, it was observed that stimulation falling along the vertical meridian of the visual field was significantly under-represented upon the SC relative to that shown for stimuli within the horizontal and oblique’s areas of the visual field. Although detailed neuroimaging results of the SC are still relatively uncommon and the findings by Schneider and Kastner should be supported with other neurological studies, it nevertheless suggests that in our study, a vertical target’s activation upon the SC could have been severely under-represented compared to those of targets or distractors at other locations in the visual field. As the initial saccade direction coded by the SC depends upon the relative strengths of activation of the target and distractor, a distractor nearby an under-represented vertical target would exert greater influence on the saccade direction. This would produce greater curvature towards the distractor location compared to conditions where the target is not under-represented upon the SC (i.e. during horizontal and oblique trials), which is consistent with the findings in Experiment 1.

Under-representation of the vertical meridian in the SC may also be helpful in explaining findings from previous studies that reported a difference between vertical and horizontal saccadic curvature. For example, Sheliga and associates (1995) asked participants to voluntarily orient their attention to distractor locations before making a saccade to a nearby target location, and found that vertical saccades showed greater deviation in response to a distractor than did horizontal saccades.
Based on the above account, it might be hypothesized that a vertical distractor would generate *less* interference during an oblique saccade than would a horizontal distractor, as the vertical distractor would now be the object that is under-represented. Following this, it would be predicted that overall, oblique saccades would not differ in their x-intercept compared to vertical or horizontal saccades, but would show intermediate curvature slopes compared to vertical or horizontal saccades, as results would be collected in the presence of distractors that introduced a lot (i.e. horizontal distractors) or a little (i.e. vertical distractors) competition with the target’s activation within the SC. Indeed, our results support this prediction: while the x-intercept did not differ across saccade directions, the curvature slopes from oblique saccades were significantly shallower than vertical curvature slopes, and marginally steeper than horizontal curvature slopes (page 35). At slower SRTs, oblique saccades made in the presence of a horizontal distractor appeared to show greater curvature away than those made in the presence of a vertical distractor, although this did not reach significance. Note, however, that no significant difference was found in the overall slopes of saccades made in the presence of horizontal or vertical distractors (see also, Walker et al., 2006). These results need not conflict with our account, however, as it is plausible that the under-representation of a vertical distractor may have a weaker influence on saccadic behavior than is seen if it is the target that is under-represented. For example, if the region of the SC representing the vertical locations of visual space under-represents objects because strong activations exceed its maximal level, then it is possible that a weaker representation from a task-irrelevant distractor may not tax this region to the same degree that a strong activation produced by a target might. In other words, the
under-representation of a distractor may be less severe than that of a target. It should be noted, however, that in Walker et al.’s study, they also found a trend for oblique saccades to show greater curvature overall than either vertical or horizontal saccades. Although this effect did not reach significance, it stands as a cautionary signal and stresses the importance of further research investigating our account of the present data.

If our interpretation of the results of Experiment 1 and 2 is correct, then the vertical under-representation hypothesis should successfully predict several behavioural consequences. One possible behavioural effect, the impact that distractor luminance changes would have on a saccade’s curvature, is investigated in Experiment 3.
**Experiment 3: Effect of Luminance on Saccadic Trajectory**

**Introduction**

The aim of Experiment 3 was to test one prediction based on the hypothesis that vertical saccades show greater distractor interference because vertical locations in the visual field are under-represented within the SC’s oculomotor map. To do so, we had participants complete a modified version of Experiment 1 in which the target was always on the vertical or horizontal, while the distractor could be presented on the major obliques. In Experiment 3, we added an additional manipulation: when a distractor was present, it was displayed with either the same luminance or a dimmer luminance than the target. When the target and distractor are of equal luminance, we anticipate a replication of Experiment 1, such that stronger distractor interference will be observed for vertical compared to horizontal saccades both in deviation towards and away from the distractor. When the distractor is dimmer than the target, however, we anticipate that it will cause less interference during saccadic planning. We reason that reducing the luminance of the distractor will reduce its salience, which will decrease the strength of the activation distribution that represents the distractor on the SC’s oculomotor map. Relative to the reduced representation of the dim distractor, an under-represented activation distribution of a vertical target should appear stronger, and will contribute more when the initial saccade direction is determined via a weighted vector average. Further, when inhibitory processes come online, less inhibition will be needed to suppress the distractor’s representation below baseline levels. As observed in Experiment 1, only vertical saccades showed strong interference from the distractor. For this reason, it is unlikely that reducing
the luminance of the distractor will have any significant impact on the curvature of horizontal saccades. A horizontal target’s representation is already much stronger than that of the distractor, and thus the distractor, no matter how salient it is, will contribute relatively little to the weighted vector average that determines the initial saccade direction.

Thus, for vertical but not for horizontal saccades, we anticipate a change in curvature based on distractor saliency. Based on previous findings, we predict that a saliency manipulation will influence vertical saccadic curvature in one of two manners. The first is based on findings from Mulckhuyse and colleagues (2009; described in the Introduction, page 11), which suggests that a bright distractor will cause more interference during saccadic planning than will a dim distractor. Based on this hypothesis, we anticipate that vertical saccades will show more deviation towards and away from a distractor that is the same luminance as the target than a distractor that is dimmer than the target. More explicitly, this model predicts that distractor salience will interact with SRT, such that the rate of change in curvature based on SRT will be slower when the saccade is made in the presence of a dim distractor.

The second possibility is based on a recent model of neural activation during saccade planning proposed by McSorley, Haggard, and Walker (2009). This model assumes that the rate of inhibition is constant regardless of distractor salience, and that the initial strength of the objects’ representation determines how long it will take for inhibition to suppress activity to baseline levels. Thus, compared to a weakly salient distractor, a strongly salient distractor that produces a stronger activation distribution will take longer to inhibit below baseline activation levels. In other words, a stronger initial
activation of the distractor will push the inhibitory process back in time relative to that which would be observed for a distractor with a weaker activation on the SC. This model is illustrated in Figure 6. If we sample a time period between peak activation and peak inhibition, then a more salient distractor will elicit saccades that show greater deviation towards the distractor initially, but less deviation away from the distractor at longer SRTs. This model predicts that manipulating distractor salience should not interact with reaction time, but rather have a main effect on saccadic curvature.

Figure 6. Possible distractor activation pattern across time for Experiment 3, based on the model proposed by McSorley, Haggard, and Walker (2009). Initially, each object creates an activation peak, although a strongly salient distractor will elicit a stronger peak in activity. As inhibition is applied, this activation is reduced and eventually is pushed below baseline levels, until such a point where inhibition is removed and activity returns to baseline. An initially stronger activation peak, as would be produced by a salient object, demands greater inhibition to push to baseline levels; the time needed to reach baseline will be extended relative to that necessary to suppress a weakly salient distractor to baseline. Similarly, the return to
baseline levels will be longer for a very salient distractor than for a weakly salient distractor. The shaded region represents the time block that we anticipate our study would measure, such that we would expect to observe a main effect of distractor saliency for vertical saccade trajectories. Although it is depicted that a stronger initial activation will eventually be suppressed below baseline activation levels more so than would a less strong activation, it is not known for certain whether this is the case. The possibility remains that regardless of initial activation strength, all representations are inhibited to the same extent below baseline activation. Regardless, the predictions derived from this model for our study are the same.

**Methods**

**Participants**

Fifteen volunteers from the University of British Columbia participated after giving informed written consent in exchange for course credit or $10. Eleven participants were female, 14 were right-handed. All reported normal or corrected-to-normal vision. The mean age was 21.53 years.

**Stimuli and Procedure**

The apparatus and procedures used were identical to Experiment 1 with the following exceptions. Participants sat 60 cm from the screen. All objects were resized so that they encompassed the same visual degrees as detailed in Experiment 1. The identity of the target was always ‘X’, while the distractor was always ‘O’. Distractors could be presented as the same luminance as the target (same condition), or substantially dimmer
than the target (dim condition). Same distractors and targets were white (148.52 cd/m²; RGB: 255, 255, 255); dim distractors were light grey (28.42 cd/m²; RGB: 128, 128, 128); the background was the same light gray colour as used in Experiments 1 and 2 and was darker than the dim distractor. Luminance of the distractor was chosen randomly on each trial, with half of the distractor-present trials consisting of a same distractor and half of the distractor-present trials consisting of a dim distractor. In an attempt to complete the study within a single one-hour session, the number of SOA conditions was reduced to three: -200, 0, and 200 ms. Thus, there were three SOAs (-200, 0 and 200 ms), four possible target locations (up, down, left, and right, herein collapsed and referred to as vertical or horizontal), two distractor-present conditions (same and dim), and three possible distractor positions (to the left or right of the target, no distractor). Participants completed 10 practice trails that were later discarded, and 360 test trials, divided into six blocks of 60.

**Results**

**Trial Exclusion**

Trials were excluded from further analysis if the participant’s first saccade went to the distractor (2.35% of all trials), if the first saccade fell short of the target or did not land at a target or distractor location (9.74%), if RTs were below 100 ms (0.09%) or greater than 500 ms (0.22%), or if saccade curvatures were greater or less than three standard deviations away from the individuals mean before baseline correction (1.19%). To avoid exceptional between-subject variability that might mask any significant effects, a criterion of no more than 1/3 errors per bin per saccade direction per distractor
luminance was set. Any subject who exceeded this criterion was eliminated from analysis, leaving the 15 participants reported above.

**Error Analysis – Effect of Distractor Luminance**

As our predicted effects of saccadic curvature are dependent on our manipulation of distractor salience, it was important for us to establish that our selected luminance values for the distractor did in fact change the participants’ perception of their luminance. Therefore, we analyzed all errors made in Experiment 3 to determine whether distractor luminance had an effect on error rates, either for saccades erroneously landing at the distractor, or for ‘saccade to nothing’ eye movements, in which an eye movement was made but did not reach either the target or distractor.

A within-subjects ANOVA of errors made to the distractor was conducted with distractor luminance (dim or same), saccade direction (horizontal or vertical) and lag between target onset and fixation offset (-200, 0, 200 ms) as factors. Distractor luminance had a significant main effect on number of erroneous saccades made to the distractor, \[ F(1,14) = 40.30, p < .001 \], such that more errors were made when the distractor was the same luminance as the target compared to when it was dimmer. Consistent with findings from Experiments 1 and 2, the gap condition also had a main effect, \[ F(1.94, 27.01) = 6.03, p = .007 \]. Simple main effects analysis of gap condition revealed that significantly more errors were made in the 0 ms and -200 ms gap conditions, when compared to error

---

3 Participants were run by the author and an undergraduate student with no previous eye-tracking or experimental experience. A total of 34 participants were run originally. Of those tested by the author (n = 15), 4 participants were excluded: 3 due to excessive errors and 1 due to an incomplete data set. Of those tested by the undergraduate assistant (n = 19), 15 participants were excluded: 11 due to excessive errors, and 4 due to mechanical problems.
rates in the 200 ms overlap condition, both $p < .05$. No other effects or interactions reached significance, all $p > .05$.

A within-subjects ANOVA of ‘saccade to nothing’ errors with the same three factors also revealed a significant main effect of distractor luminance, $[F(1,14) = 7.21, p = .02]$, with more errors when the distractor was the same luminance as the target. More errors were made in gap trials, $[F(2, 28) = 12.73, p < .001]$, as revealed by simple main effects analysis in which trials in both gap conditions of -200 ms and 0 ms had more errors than trials with overlap condition 200 ms, both $p < .05$. In addition, the target location during the trial also had a main effect on error rates, such that more ‘saccade to nothing’ errors were made when the target was on the vertical than when the target was on the horizontal, $[F(1, 14) = 24.93, p < .001]$. No other main effects or interactions reached significance, all $p > .05$.

**Gap Effect**

Figure 7 shows the mean SRTs across SOAs for distractor-absent and distractor-present conditions for bright and dim distractors. A three-factor ANOVA was performed on SRTs with distractor presence (present or absent), distractor luminance (same or dim) and SOA (-200, 0, 200 ms) as within-subject factors. Consistent with Experiments 1 and 2, there was a main effect of distractor presence, $[F(1, 14) = 52.56, p < .001]$. There was also a main effect of SOA, $[F(1.37, 19.14) = 41.39, p < .001]$, such that SRTs increased with increasing overlap between fixation point and target onset. There was no significant effect of distractor luminance, $[F(1, 14) = 0.62, p > .25]$, nor were any two-factor or three-factor interactions significant, all $p > .20$. 
Figure 7. Mean saccadic reaction times (SRTs) for all subjects in Experiment 3 for distractor present (dim and same luminance) and absent trials, for each SOA condition. Negative values indicate that the fixation point was extinguished before target onset; positive values indicate the fixation point was extinguished after target onset.

**Trajectory time course – Effect of Target Location**

**Saccadic reaction time analysis**

An initial three-factor within-subjects ANOVA on SRTs with target location (horizontal, vertical), distractor luminance (dim, same), and SRT Bin (1-5) as factors revealed a significant main effect of target location, \([F(1, 14) = 19.54, p = .001]\), such that vertical saccades were slower overall than horizontal saccades. As anticipated, there was also a significant main effect of SRT Bin, \([F(1.08, 15.18) = 84.53, p < .001]\), such
that all SRT bins were significantly different from all others, all $ps < .001$. Distractor luminance did not have a significant effect on SRT, $[F(1,14) = 1.75, p > .15]$, and no interactions reached significance, all $ps > .05$. To avoid confounding differences in SRT with differences in saccade direction, the effect of saccade direction was completed on the slopes of the trajectory change over time, while all analyses involving distractor salience were completed separately for horizontal and vertical saccades. Consistent with Experiments 1 and 2, analyses of the x-intercept were also completed.

**Saccadic trajectory analysis**

To investigate the effect of saccade direction on saccadic trajectory, we determined the slope for each participant’s trajectory time course (i.e. trajectory curvature over time) for vertical and horizontal saccades and submitted these values to a two-tailed paired samples t-test. Consistent with Experiment 1, and apparent in Figure 8, results revealed a significant difference in slope, $[t(14) = 4.72, p < .001]$, such that vertical saccades showed a greater effect of distractor interference (i.e. showed a steeper slope, or greater change over SRT bins) than did horizontal saccades. Similarly, the x-intercept of the trajectory time course for horizontal and vertical saccades did not differ, $[t(14) = -1.74, p > .10]$, which suggests that vertical saccades showed greater curvature towards the distractor at rapid SRTs and more curvature away from the distractor at slower SRTs. Similar to Experiment 1, the horizontal trajectory time course was significantly different from zero, based on a one-sample t-test, $[t(14) = 4.84, p < .001]$. Also similar to Experiment 1, the curvature towards a distractor when making a horizontal saccade at the first three SRT Bins (where a numerical curvature towards the distractor was observed) was not significantly different from zero, $[t(14) = 1.22, p > .20]$. 
Figure 8. Mean saccadic curvature obtained during distractor present trials in Experiment 3, divided into five SRT bins for vertical and horizontal target locations. Negative values indicate curvature away from the distractor; positive values indicate curvature towards the distractor.

Trajectory Time Course – Effect of Distractor Luminance

As it was previously determined that saccade direction had an effect on SRT, thus confounding our SRT Bins with saccadic direction, the effect of distractor luminance was investigated independently for horizontal and vertical saccades. For horizontal saccades, a two-factor repeated measures ANOVA with trajectory bins (1-5) and distractor luminance (same or dim) showed that, predictably, there was a main effect of trajectory bin, \(F(3.64, 50.97) = 8.37, p < .001\]. There was no effect of distractor luminance, \(F(1, 14) = .59, p > .25\], nor was there a significant interaction, \(F(2.10, 29.43) = 1.13, p > .25\]. Additionally, the x-intercept for horizontal saccades made in the presence of dim
distractors was not significantly different from the x-intercept for horizontal saccades made in the presence of same-luminance distractors, \[ t(14) = -0.27, p > .75 \]. Thus, distractor luminance did not influence saccadic trajectory for horizontal saccades.

For vertical saccades, a similar two-factor ANOVA revealed a significant main effect of trajectory bin, \[ F(2.70, 37.79) = 14.92, \ p < .001 \]. Further, there was also a significant main effect of distractor luminance, \[ F(1, 14) = 4.79,\ p = .05 \]. The interaction of the two factors was not significant, \[ F(3.74, 52.34) = 1.51,\ p > .20 \]. Thus, for vertical saccades, distractor luminance significantly influenced saccade trajectory such that overall, a distractor that was dimmer than the target created more deviation away than did a distractor with the same luminance as the target. Consistent with this, the x-intercept for vertical saccades made in the presence of dim distractors was significantly different than the x-intercept for vertical saccades made in the presence of same-luminance distractors, \[ t(14) = -2.57, \ p = .02 \]. Figure 9 and 10 show the trajectory time course for horizontal and vertical saccades based on distractor luminance.
Figure 9. Mean saccadic curvature obtained during horizontal saccades during distractor present trials in Experiment 3, divided into five SRT bins for same and dim distractor luminance. Negative values indicate curvature away from the distractor; positive values indicate curvature towards the distractor.
Figure 10. Mean saccadic curvature obtained during vertical saccades during distractor present trials in Experiment 3, divided into five SRT bins for same and dim distractor luminance. Negative values indicate curvature away from the distractor; positive values indicate curvature towards the distractor. Note the change in the Y-axis scale from that in Figure 8.

Discussion

Experiment 3 was designed to test one predicted effect of the hypothesis that vertical objects may be under-represented within the SC’s oculomotor map. Through manipulating the luminance of the distractor stimulus, we aimed to shift the relative strengths of the target and distractor activations within the SC’s map. We hypothesized that a dim distractor would create a weaker representation, and thus it was anticipated that it would contribute less to the weighted vector average that determined the initial saccade direction. As such, we anticipated that dimmer distractors would produce less interference in the trajectory of vertical saccades aimed at nearby targets. We predicted
that any luminance effects would only be observable for vertical saccades since horizontal saccades were relatively unaffected by the presence of a bright distractor in Experiment 1. Thus, we did not anticipate that the reduction in interference from a dimmer distractor would have significant behavioural consequences for horizontal saccades.

As predicted, we observed an effect of distractor salience only in the trajectory of vertical saccades. Initially, we proposed two possible ways in which vertical saccade trajectories could be influenced by distractor luminance. The first was based on findings from Mulckhuyse and colleagues (2009), which suggested that a bright distractor would cause more deviation towards and away from its location than would a dimmer distractor. The second possibility, based on a model recently proposed by McSorley and colleagues (2009), predicted that a dim distractor would require less inhibition and thus would take less time to reach baseline and below-baseline activation levels than would a bright distractor. Based on this model, we predicted that manipulating distractor luminance would have a main effect on saccadic trajectory. Our results clearly support this latter hypothesis: luminance had a main effect on saccade curvature, such that a dimmer distractor created less deviation towards its location but also more deviation away. In other words, deviation away was greater overall for dimmer distractors than for distractors that were the same luminance as the target. Importantly, we also replicated our effects of target location that were observed in Experiment 1, such that vertical saccades showed greater distractor interference than did horizontal saccades.

Although the supported model was based on work by McSorley and colleagues (2009) in which distractor position, rather than target-distractor similarity, was
manipulated, we believe that this manipulation nevertheless influenced the saliency of the distractor. Varying whether the distractor appeared at a possible target location would have changed the spatial similarity of the distractor to the target, and thus would have produced conditions in which the distractor’s saliency varied. As such, it is reasonable to treat the study by McSorley and colleagues as a test of the role of salience on curvature. Thus, our hypothesis that other manipulations of distractor saliency, such as through varying luminance, would modulate curvature in a similar manner is justified. Our findings are consistent with the idea that the initial activation of the same-luminance distractor was greater than the activation of the dim distractor. According to the proposed model, this initial boost in activation of the same-luminance distractor delayed the time at which inhibition was able to suppress activity to, and below, baseline levels. In contrast, inhibition of the dim distractor, whose initial activation was not as strong, would have suppressed activity to baseline levels quicker. Thus, when trajectories were sampled at the same time points for saccades made in the presence of distractors of varying salience, it would appear as though the dim distractor elicited less deviation towards, and more deviation away from its location than would be produced by the same-luminance distractor.

Interestingly, the results of McSorley’s group showed a decrease in inhibition at the latest time points in their less salient condition, suggesting that peak inhibition was reached under these conditions, and inhibition was now being removed from the distractor’s representation. Results from our dim distractor condition did not show this, likely because the SRTs sampled in Experiment 3 were substantially faster than those recorded by McSorley’s group. If we were to sample later time points, it would be
hypothesized that eventually, inhibition of the dim distractor would peak, and then begin to decrease, while inhibition of the same-luminance distractor would delayed and would continue to increase for some time before eventually also decreasing.

Although our results support the work of McSorley and associates (2009), they seem to be in direct opposition to the findings by Mulckhuyse and colleagues (2009). There are, however, reasons to believe that the results of Mulckhuyse’s group may be exceptional and potentially not replicable. First, although the SRTs recorded in their study are comparable to those reported in our Experiment 3, all deviations observed by Mulckhuyse were away from the distractor. This is puzzling, because the results of our study and those of other researchers (e.g. young adults in Campbell et al., 2009; McSorley et al., 2006) have consistently demonstrated that when SRTs are rapid, deviation is generally towards the distractor. Indeed, saccadic trajectory generally transitions to deviation away from the distractor once SRTs go beyond about 200-240 ms.

Due to this abnormally rapid implementation of inhibitory processes, the interaction between SRT and distractor luminance reported by Mulckhuyse resulted in the dissimilar distractor producing less deviation away from the distractor at rapid SRTs, but more deviation away at longer SRTs. Mulckhuyse and colleagues posit that their results are due to target-distractor similarity affecting the manner by which inhibition is imposed on the distractor’s representation, such that dissimilar distractors can be inhibited purely through lateral inhibition, whereas similar distractors require slower top-down inhibition to properly suppress. If this is true, then it must be explained why this ‘slow’ top-down inhibition can nevertheless suppress the distractor’s representation to below baseline levels before even the fastest saccades could be executed. Due to the
inconsistencies of the findings of Mulckhuyse’s group with other work present in the literature, we believe that the model proposed by McSorley and associates provides a better explanation of how the SC handles differences based on object saliency.

Although the effect of distractor salience has been investigated in several ways in the past (Ludwig & Gilchrist, 2003; McSorley et al., 2009; Mulckhuyse et al., 2009), ours is the first to show that only vertical saccades demonstrate any modulation of curvature based on salience, at least when salience is manipulated through luminance differences. This is consistent with our hypothesis that a reduction in distractor activity upon the oculomotor map would have a more dramatic effect on vertical saccadic trajectories than on horizontal trajectories because of the under-representation of vertical objects in the SC. A horizontal object is presumed to have a much stronger representation compared to that of a vertical object, as has been demonstrated via fMRI (Schneider & Kastner, 2005). As such, even a very salient distractor presented on the oblique would do little to effect the curvature of a horizontal saccade; in contrast, it should have a much larger impact on a vertical saccade. Thus, reducing the distractor’s contribution to the saccade vector by decreasing its salience would proportionally have a much larger influence on vertical rather than horizontal saccades.
General Discussion

Experiment Summaries and Conclusions

Experiment 1 and 2 determined whether the trajectory differences between vertical and horizontal saccades as reported by Van der Stigchel and Theeuwes (2008) would be evident without extensive planning. To accomplish this, we asked participants to complete a modified version of the task used by McSorley and colleagues (2006). In Experiment 1, participants made saccades to horizontal or vertical targets either in the presence or absence of a nearby distractor object. The offset of the fixation point was manipulated in order to increase the variability of SRTs, so that a time course of saccade curvature could be observed. Unlike Van der Stigchel and Theeuwes’ study, participants were not cued to the upcoming target’s location, but instead had to prepare and execute their saccade immediately upon target onset. Consistent with Van der Stigchel and Theeuwes’ findings, vertical saccades did show greater curvature away from a distractor than did horizontal saccades, if SRTs were long (i.e. greater than about 240 ms). Interestingly, when SRTs were fast, vertical saccades showed greater curvature towards a distractor than did horizontal saccades, an effect that has not been previously demonstrated. Taken together, this suggests that vertical saccades are prone to greater distractor interference than are horizontal saccades.

Experiment 2 explored whether greater interference effects were unique to vertical saccades by asking participants to make oblique saccades in the presence or absence of horizontal and vertical distractors. No significant difference in curvature was found in oblique saccades based on distractor location. Importantly, while the x-
intercepts did not differ across conditions, the trajectory slope (i.e. the slope produced by plotting curvature across SRTs) produced by oblique saccades was significantly flatter than that produced by vertical saccades, while there was a trend towards it being slightly steeper than that produced by horizontal saccades.

We theorized that the effects observed in Experiments 1 and 2 may be due to the SC under-representing objects that fall along the vertical meridian of space. Experiment 3 aimed to test one prediction of this theory, mainly that vertical saccades would be more affected than horizontal saccades to changes in distractor luminance. Under-representation of vertical objects would make vertical saccades more susceptible to interference from bright distractors. Conversely, vertical saccades should show reduced interference from dimmer, less salient distractors. We presented two manners by which saccadic curvature might be affected by distractor salience. One, based on the results of Mulckhuyse and colleagues (2009), proposed that a less salient distractor would create less deviation towards the distractor when saccades were rapid, as well as less deviation away when saccades were planned for a longer time. The other, based on McSorley and colleagues’ activation model (2009), suggested that at the saccadic latencies sampled in our study, a less salient distractor would show less deviation towards the distractor but more deviation away. Our results supported the latter group’s results: distractor salience had a main effect on saccadic curvature such that the dimmer distractor showed overall greater deviation away than was observed for the distractor that was the same luminance as the target. As predicted, distractor saliency only significantly modulated the curvature of vertical saccades. Horizontal saccades consistently showed little interference from a nearby distractor, and this effect did not vary based on distractor salience.
Taken together, the findings from our studies provide evidence for three main theories critical for understanding saccadic curvature and its relation to target selection within the saccadic system. First, the time courses of curvature that we report in all three experiments lend support to Tipper’s (2000) inhibition hypothesis of saccadic curvature (see Van der Stigchel, Meeter, & Theeuwes, 2006, for a review). Implicit in his theory is the assumption that the degree of curvature towards a distractor determines the degree of curvature away from it at longer saccadic latencies. Our time courses all follow roughly linear trends during the transition from deviation towards to away from a distractor. When deviation towards is strong, as is the case for our vertical saccades, then the ensuing deviation away from the distractor location is also strong. The opposite is true for horizontal saccades, while oblique saccades showed a trend for an intermediate amount of curvature that was less than what was observed for vertical saccades but slightly greater than what was observed for horizontal saccades.

Second, the results from Experiments 1 and 3 lend support to Van der Stigchel and Theeuwes’ (2008) finding for a difference between horizontal and vertical saccadic curvature. Our research extends this finding, however, to demonstrate that these differences are not only due to the manner by which inhibition is imposed upon distractor activity in either condition. Rather, differences between vertical and horizontal saccadic curvatures are evident even at the earliest time points recorded, when inhibition has presumably not yet come online. While we believe that an inhibition-based theory can explain why vertical saccadic curvature has a faster rate of change across SRTs than does horizontal saccadic curvature, we have posited an additional factor that can explain why these differences in curvature exist when inhibition should not yet be in play. Based on
neuroimaging work that shows that visual responses from the SC are predominantly from objects on the horizontal meridian (Schneider & Kastner, 2005), we suggest that objects requiring a vertical saccade to fixate may be under-represented within the SC. This under-representation would make saccade preparation more sensitive to nearby distractor activations, and thus greater initial deviation would be observed for vertical saccades compared to saccades made in other directions. The results of Experiment 3 are consistent with our theory, although further work will be necessary to investigate whether other ocular behaviours are compatible with our proposal.

Finally, our findings from Experiment 3 support and extend the activation and inhibition model recently put forth (McSorley et al., 2009). Although originally proposed to explain why changes in distractor location would influence saccadic curvature, we show that other factors that increase the similarity between target and distractor, such as luminance, also follow the time course described. It should be noted that this model is also consistent with Tipper’s population coding and inhibition theories (1997; 2000), as they both suggest that more salient objects produce stronger activations within the oculomotor maps, and as a result require greater inhibition to suppress below baseline levels.

**Study Limitations**

Our work has shed light on several important factors involved in determining saccadic curvature and how curvature relates to the underlying neurological processes. Nevertheless, there are many unanswered questions that our paradigm cannot speak to. Although the results of Experiment 3 support our under-representation hypothesis, it is clear that future research must be undertaken to critically test our theory. If our
hypothesis is correct, then other manipulations besides adjusting distractor luminance values should have predictable effects on the observed curvature of saccades. All distractor saliency manipulations previously tested should also have a greater impact on the curvature of vertical saccades over horizontal, or even oblique saccades. For example, manipulations of distractor/target similarity based on colour (Ludwig & Gilchrist, 2003) or shape (Mulckhuyse et al., 2009) should either only influence vertical saccades, or at least influence vertical saccades to a greater extent. It is conceivable that one would be able to equate the deviation observed for vertical saccades with that observed for horizontal saccades by independently manipulating the relative salience of the distractor to the vertical and horizontal targets.

Perhaps the best test of our theory of under-representation would be to image the SC while human participants completed a task similar to that used in our experiments. Although this may be possible in the future, this is not yet feasible with current technology. The SC is a very small structure located deep within the brain, and imaging is very difficult due to nearby cardiac pulsatile noise (Poncelet, Wedeen, Weisskoff, & Cohen, 1992). Advances are being made to image the SC with better signal-to-noise ratios (e.g. Wall, Walker, & Smith, 2009), but current results have yet to reach the spatial specificity required to isolate activation from multiple objects within the SC (see DuBois & Cohen, 2000; Schneider & Kastner 2005; 2009; Sylvester, Josephs, Driver, & Rees, 2007, for examples of the resolution currently possible). For now, at least, our theories, as well as those of Tipper (1997; 2000) and McSorley and colleagues (2009) can only be tested indirectly.
A major limitation of not only our work but also all human behavioural work investigating saccadic curvature is our reliance on indirect evidence to support theories of brain function. While this is not a unique problem to this literature, it is one that warrants mention. The theories that currently drive our understanding of past literature and fuel our future predictions are primarily based on assumptions derived from single cell recordings from the SC in monkeys. Although it appears as though humans and monkeys share many behavioural similarities when it comes to saccadic curvature, (at least) one important difference exists. Without pharmacological intervention using the GABA agonist muscimol (Aizawa & Wurtz, 1998), there has been no recorded evidence of monkeys showing deviation away (Van der Stigchel & Theeuwes, 2006). As curvature away, rather than towards, a distractor is more commonly observed in humans (e.g. Ludwig & Gilchrist, 2003; McSorley et al., 2009; Van der Stigchel & Theeuwes, 2008; van Zoest, Van der Stigchel, & Barton, 2008; Walker, Techawachirakul, Haggard, 2009), this discrepancy between species serves as a cautionary note that any extrapolation from monkey to human brain function is little more than speculation, and must be supported by human neuropsychological evidence as soon as possible.

Another limitation common to many cognitive psychology studies relates to the generalizability of our results to more realistic situations and stimuli. The main goal of most saccadic curvature studies relates to how one particular object will influence the trajectory of a saccade made to another goal object; as such, the stimuli used are necessarily impoverished compared to what is experienced in everyday situations. Few studies have investigated the effect multiple stimuli have on trajectory (although see Inhoff, Seymour, Schad, & Greenberg, 2010; Sogo & Takeda, 2006, for somewhat more
complex studies of trajectory). It is an open question whether these effects would be observable when participants explore complex scenes such as pictures or videos of natural environments. One particular challenge would be to determine what constitutes a distractor in cluttered environments: does the brain treat certain stimuli as more task-relevant, and therefore more distracting based on the goals of the observer? Another particularly interesting question would be whether trajectory is influenced by objects that were salient for previous saccades but not necessarily the saccade under investigation. It is evident that there are numerous questions concerning how our results and those of the literature in general scale up, and future studies will hopefully reveal how our effects relate to real-life oculomotor behaviour and brain function.

**Future Directions**

Based on the limitations of our studies, it is clear that there are many directions that the saccadic curvature literature can take. Measures of curvature are extremely sensitive and can be used to test effects of attention (Sheliga, Riggio, Craighero et al., 1995; Sheliga, Riggio, & Rizzolatti, 1995) and visual orienting. As such, there is the potential for curvature to become a powerful dependent variable for a wide variety of studies concerning visual cognition and attention. Indeed, some researchers are already including saccadic curvature measures in their studies. For example, measures of saccadic curvature have been incorporated into studies of inhibition of return (IOR; relating to the finding that we are slower to respond to a target at a cued location if the time lag between cue and target is long; Posner & Cohen, 1984). Theeuwes and Van der Stigchel (2009) have demonstrated that the magnitude of saccadic curvature can be used to reflect the degree of attentional processing taking place at a particular location at a
given time and that, consistent with previous reports (Godijn & Theeuwes, 2004), IOR and curvature measures may reflect related by separate inhibitory processes working within the saccadic system. The use of saccadic curvature as a dependent measure is promising, although it may be premature. Until we know more about how curvature is influenced by different experimental manipulations, testing other effects using this measure may lead to uninterpretable results.

In the immediate future, more efforts should be focused on confirming some of the major assumptions that studies of saccadic curvature are founded on. Tipper’s (1997; 2000) model of inhibition states that both top-down and lateral inhibition are applied to the distractor’s representation. Evidence from primate studies support the existence of lateral inhibition (Georgopoulous, 1995), and possibly top-down inhibition (McPeek et al., 2003), however it is not well understood how these inhibitory processes work together. Originally, it was proposed that lateral inhibition was responsible for modulation of deviation towards, while goal-mediated inhibitory processes pushed the distractor’s activation below baseline levels and led to deviation away from a distractor. This claim has not been rigorously tested. It remains possible that both types of inhibition are applied at the same time. Efforts should be made to characterize the time course of the inhibitory processes, especially with relation to the initial onset of inhibition. Although this may prove difficult given the lack of evidence of top-down inhibition in monkey models, it will be critical for understanding how factors such as salience, expectancy, and location influence the onset, rate, and removal of inhibition to representations within the SC.
Although most of our research focuses on the initial direction or the peak curvature of a saccade, it is possible that saccadic curvature measures can also be used in relation to understanding endpoint error. Several researchers have suggested that the SC may not be heavily involved in online correction of trajectory (McSorley et al., 2004; Quaia et al., 1999), but newer evidence suggests that the initial and end points of saccades are well correlated, such that a stronger deviation away from a distractor leads to greater endpoint deviation (Van der Stigchel et al., 2007). While the SC may not determine the exact trajectory of the saccade, output from the SC may adjust the saccades trajectory continuously over the course of the movement (Meeter, Van der Stigchel & Theeuwes, 2010). Furthering our understanding of the role the SC plays throughout the course of a saccade may enable us to use other saccadic metrics besides curvature to study attentional effects on object processing.

Finally, one major area that must be further studied is that of individual variation. Although trends in saccadic curvature are observable and predictable, there nevertheless exists a great deal of individual and between-subject variability in the magnitude and even the direction of saccadic curvature. It remains very possible, considering the novelty of any investigations of trajectory that several factors that have dramatic effects on saccadic curvature have yet to be discovered. Personality factors may contribute substantially to between-subject variation. For example, participants who perform poorly on other measures of distraction, as might be tested with performance on an Erikson Flanker task (Erikson & Schultz, 1979) or scores on the Cognitive Failures Questionnaire (Broadbent, Cooper, FitzGerald, & Parkes, 1982) may show greater levels of deviation towards the distractor, or later transitions to deviation away. Similarly, susceptibility to
mind wandering may also contribute to both variations within and between participants. Factors influencing perception and attention, as well as those that influence processing within higher-level cortical levels could conceivably also contribute to the observed variability in saccadic curvature.

Clearly, there is a great deal that is as of yet unknown about why saccades curve and how object information is represented within the brain. Once we have a clearer understanding of the factors affecting curvature, its use as a dependent measure may help researchers studying a variety of cognitive effects. Similar to the investigations into the attentional processing involved during IOR, curvature measures could shed light onto the effects that different types of cues have on our attentional orienting. Paradigms involving visual search and attentional capture could also benefit substantially from incorporating such a sensitive measure.

**Summary**

Despite the many unanswered questions present in the literature, our work has nevertheless provided valuable information regarding why saccades curve and how objects are represented within the saccadic system. We have demonstrated that vertical saccades show overall greater distractor interference than either oblique (Experiments 1 and 2) or horizontal saccades (Experiments 1 and 3). Further, we have shown that only vertical saccades appear to be sensitive to changes of a distractor’s luminance (Experiment 3), which may suggest that other salience manipulations have a significantly greater impact on vertical saccade trajectories than on horizontal eye movements. Both of our findings support our vertical under-representation hypothesis, and suggest that the manner by which our visual environment is represented within the SC can have
measurable behavioural consequences. Our findings complement the work of McSorley et al. (2006; 2009) and Van der Stigchel and Theeuwes (2008), and have contributed to our understanding of how and why saccades often show characteristic curvature in response to nearby irrelevant objects. As we continue to test our model and investigate other effects on saccadic curvature, we move towards developing a sophisticated conceptualization of both the SC specifically, and our visual system in general.
Bibliography


Cynader, M., & Berman, N. (1972). Receptive-field organization of monkey superior


approaches for studying sensorimotor integration. Boca Raton: CRC Press.


Theeuwes, J., & Van der Stigchel, S. (2009). Saccade trajectory deviations and


Appendix: Copy of UBC Research Ethics Board Certificate of Approval

---

**CERTIFICATE OF APPROVAL - MINIMAL RISK RENEWAL**

<table>
<thead>
<tr>
<th>Principal Investigator:</th>
<th>Department:</th>
<th>UBC BREB Number:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alan Kingstone</td>
<td>UBC/Arts/Psychology, Department of</td>
<td>H04-50757</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Institution(s) Where Research Will Be Carried Out:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Institution</td>
</tr>
<tr>
<td>-------------</td>
</tr>
<tr>
<td>UBC</td>
</tr>
<tr>
<td>Other locations where the research will be conducted:</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Co-Investigator(s):</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thomas Foyleham</td>
</tr>
<tr>
<td>Kirsten Dalrymple</td>
</tr>
<tr>
<td>Joseph Chisholm</td>
</tr>
<tr>
<td>Evan Risko</td>
</tr>
<tr>
<td>Michael R. Maciasac</td>
</tr>
<tr>
<td>Katlin Laslaw</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sponsoring Agencies:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural Sciences and Engineering Research Council of Canada (NSERC) - &quot;Components of Human Selective Attention&quot; - &quot;Research in Cognitive Ethology&quot;</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Project Title:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Research in Cognitive Ethology</td>
</tr>
</tbody>
</table>

**Expiry Date of This Approval:** December 15, 2010

**Approval Date:** December 15, 2009

The Annual Renewal for Study have been reviewed and the procedures were found to be acceptable on ethical grounds for research involving human subjects.

Approval is issued on behalf of the Behavioural Research Ethics Board:

Dr. M. Judith Lynam, Chair  
Dr. Ken Craig, Chair  
Dr. Jim Rupert, Associate Chair  
Dr. Laurie Ford, Associate Chair  
Dr. Anita Ho, Associate Chair

---

1 of 1  
4/29/2010 5:53 PM