The antisaccade task: Visual distractors elicit a location-independent planning 'cost'

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Kinesiology

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THE ANTISACCADE TASK: VISUAL DISTRACTORS ELICIT A LOCATION-
INDEPENDENT PLANNING ‘COST’

(Thesis format: Monograph)

by

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**ABSTRACT**

Prosaccades are rapid eye movements with direct stimulus and response relations and are designed to bring the fovea onto a target or area of interest. In contrast, antisaccades require the inhibition of a prosaccade and the evocation of a saccade to a target’s mirror-symmetrical location. Previous work has shown that a remote (i.e., midline, contralateral) – but not proximal (i.e., ipsilateral) – task-irrelevant distractor relative to a visual target delays prosaccade reaction times (RT) (i.e., remote distractor effect: RDE). To my knowledge, however, no work has examined whether antisaccade RTs are similarly influenced by a RDE. Accordingly, I sought to determine whether planning costs for antisaccades are similarly dependent on the location-specific presentation of a distractor. In Chapter Two, I demonstrate increased antisaccade RTs independent of the spatial location of a distractor. Based on this result, I concluded that distractor-related antisaccade costs reflect the top-down evocation of explicit response-selection rules.

**Keywords:**
- Antisaccade
- Distractor
- Oculomotor
- Prosaccade
- Reaction time
- Remote distractor effect
- Response-selection
- Top-down control
CO-AUTHORSHIP

The author (J. DeSimone), under the supervision and mentorship of Dr. Matthew Heath, conducted the work in this master’s thesis. This encompasses experimental conception, design, and implementation; data collection, analysis and interpretation; and manuscript preparation. The author received support from one volunteer undergraduate research assistant in the data collection phase of this experiment.

This master’s thesis contains material from a manuscript presently under peer-review in which Jesse C. DeSimone is the first author and Drs. Matthew Heath and Stefan Everling serve as co-authors.
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<tr>
<td>ANOVA</td>
<td>analysis of variance</td>
</tr>
<tr>
<td>CDD</td>
<td>contralateral distal distractor</td>
</tr>
<tr>
<td>CIM</td>
<td>competitive integration model</td>
</tr>
<tr>
<td>CPD</td>
<td>contralateral proximal distractor</td>
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<tr>
<td>ID</td>
<td>ipsilateral distractor</td>
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<tr>
<td>MD</td>
<td>midline distractor</td>
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<tr>
<td>RDE</td>
<td>remote distractor effect</td>
</tr>
<tr>
<td>RT</td>
<td>reaction time (ms)</td>
</tr>
<tr>
<td>SC</td>
<td>superior colliculus</td>
</tr>
<tr>
<td>SR</td>
<td>stimulus and response</td>
</tr>
<tr>
<td>TO</td>
<td>target-only (distractor-free)</td>
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CHAPTER ONE

General Introduction
Oculomotor Control of Pro- and Antisaccades

Eye movements (i.e., saccades) are supported via six extraocular muscles that specify the rotation of the eye within horizontal, vertical, and torsional axes. In particular, the medial and lateral rectus muscles enable horizontal gaze shifts toward (i.e., adduction) and away (i.e., abduction) from the nose, respectively; the superior and inferior rectus muscles enable vertical eye movements in an upward (i.e., elevation) and downward (i.e., depression) direction, respectively; and the superior and interior oblique muscles enable torsional rotations toward (i.e., intorsion) and away (i.e., extorsion) from the nose, respectively. Moreover, the extraocular musculature is innervated by three groups of cranial nerves that originate in the brain stem. Cranial nerve III (i.e., the oculomotor nerve) innervates the superior rectus, medial rectus, inferior rectus, and inferior oblique muscles, whereas cranial nerves IV (i.e., the trochlear nerve) and VI (i.e., the abducens nerve) innervate the superior oblique and lateral rectus muscles, respectively (Kandel et al., 2000).

The activation of the ocular musculature is mediated by cortical and subcortical saccade structures that provide information related to the desired position and speed of the upcoming response. In particular, the cortical structures associated with saccades encompass – but are not limited to – the supplementary eye fields, frontal eye fields, dorsolateral pre-frontal cortex, lateral intraparietal area, and the anterior cingulate cortex. These cortical areas project directly or indirectly (via basal ganglia) to subcortical saccade mechanisms in the superior colliculus (SC) and eventually to the pre-motor circuit in the reticular formation. An important area of interest in the visual neurosciences is how the intricate ensemble of neural saccade mechanisms functions to adapt to unique
task-rules. In particular, a functional dissociation in task-rules is highlighted throughout this master’s thesis via contrasting the movement planning and execution properties of pro- and antisaccades. In particular, prosaccades entail a rapid eye movement that brings a peripheral target or area of interest onto the region of the retina that has the highest visual acuity (i.e., the fovea). Notably, the direct spatial overlap between stimulus and response (SR) (so-called standard task) associated with prosaccades enables dedicated retinotopic motor maps in the SC to specify a maximally efficient (i.e., rapid) and effective (i.e., accurate) response (Wurtz and Albano, 1980) that is largely independent of top-down cognitive control (Milea et al., 2005; Pierrot-Deseilligny et al., 1995). Notably, however, a salient visual stimulus need not reflexively capture one’s gaze; rather the oculomotor system can decouple the normally direct SR relations and saccade to a volitional area of interest (so-called non-standard task). The most frequently studied non-standard task involves the execution of a saccade mirror-symmetrical (i.e., 180° spatial transformation) to the location of a single and exogenously presented target (i.e., the antisaccade task). Extensive evidence has shown that antisaccades produce longer reaction times (RT) (Hallett, 1978; Hallett and Adams, 1980), increased directional errors (Fischer and Weber, 1992) and less accurate and more variable endpoints (Dafoe et al., 2007; Heath et al., 2011) than prosaccades. As well, the aforementioned behavioral ‘costs’ have been related to a top-down and two-component process requiring the inhibition of a stimulus-driven prosaccade (i.e., response suppression) and the visual remapping of the target’s spatial properties to mirror-symmetrical space (i.e., vector inversion) (Munoz and Everling, 2004). Moreover, extensive human and non-human primate neuroimaging and electrophysiological evidence has linked the preparatory phase
of the antisaccade task to increased activity within the frontal and supplementary eye fields, dorsolateral pre-frontal cortex, lateral intraparietal area, and anterior cingulate cortex (i.e., the classical saccade networks: Brown et al., 2007; Curtis and D’Esposito, 2003; DeSouza et al., 2003; Ford et al., 2005). As well, antisaccades are related to an increase and decrease in the activity of fixation and buildup neurons in the SC, respectively (Everling et al., 1999). In summary, the modulation of oculomotor networks associated with the preparation of an antisaccade supports a neural pre-setting that provides sufficient time to implement the constituent elements of the task (i.e., response suppression and vector inversion).

**Distractor-related Influences in Oculomotor Control**

The daily environments in which humans interact rarely comprise a single stimulus. Accordingly, the successful execution of common goal-directed movements such as a prosaccade, walking, or reaching to grasp an object requires that we allocate cognitive resources toward a particular sub-set of task-relevant visual information while simultaneously placing less attentive emphasis on information that bears little or no importance to the response (Pashler, 1998). For example, consider riding a bike along a paved path through a park with hundreds of people. In order to reduce the risk of a collision the rider will generally restrict gaze shifts to the people or objects that are contained along the bike path in front of him/her and place less attentive emphasis on the patrons who occupy the distant grass-covered regions of the park. Thus, extracting task-relevant information from the visual properties contained along the bike path permit the rider to steer his/her bike in a manner that appropriately adapts to the ever-changing environment.
A central theme in the visual neurosciences is how the spatial properties of task-irrelevant visual information (i.e., a distractor) influence the oculomotor system’s efficiency and effectiveness. In particular, one methodology used to address the influence of task-irrelevant visual information on the planning and control of saccades is the remote distractor paradigm (e.g., Lévy-Schoen, 1969; Walker et al., 1997). For example, Walker et al. (1997) reported that the onset of a remote distractor (i.e., a distractor contralateral to a target or at the visual midline) concurrent with target presentation produced longer RTs than when a target was presented alone or when presented with a proximal distractor (i.e., ipsilateral to a target) (i.e., the remote distractor effect: RDE). The RDE has been attributed to the motor-related properties of neurons in the intermediate layers of the SC. In particular, the competitive integration model (CIM: Godijn and Theeuwes, 2002) contends that the visual information supporting a target and distractor are concurrently transformed into motor programs on a common retinotopic motor map in the SC. Consequently, if a distractor is presented distal (i.e., remote) to the location of the intended saccade goal, the motor-related activity of the distractor delays the activation of motor-related buildup neurons encoding the target via a long-range inhibitory pathway (see Takahashi et al., 2005) – thereby resulting in longer RTs (i.e., the RDE). Moreover, previous work has shown that homologous neural ensembles in the frontal eye fields are influenced by the presentation of a distractor and support target selection in a visual search task (Lee and Keller, 2008; McPeek and Keller, 2002). Although a number of studies have examined the basis of the RDE for prosaccades (Benson, 2008; Casteau and Vitu, 2012; Findlay and Walker, 1999; Honda, 2005; Lévy-Schoen, 1969; McSorley et al., 2012; Walker et al., 1995; 1997; Weber and Fischer, 1994), to my knowledge no
previous work has examined whether the motor-related properties of a target and distractor similarly influence antisaccade RTs.

As an alternative to the RDE, my thesis proposes that distractor-related planning costs for antisaccades may relate to a top-down evocation of response-selection rules independent of the distractor’s spatial location. Such a proposal is drawn from previous literature showing that increasing the number of SR alternatives (i.e., distractors) associated with antisaccades – but not prosaccades – results in a log-linear increase in RT as defined by Hick’s law (Hick, 1952; Kloft et al., 2012; Kveraga et al., 2002). In particular, distractor-related antisaccade RT costs are considered an index of response-selection uncertainty that relates to the top-down adoption of the task-rules necessary to decouple SR relations. In turn, prosaccades do not conform to the law because of the highly efficient retinotopic mapping of the SC that directly couples SR spatial relations (i.e., SR compatibility: see Fitts and Seeger, 1953). In other words, localization of the target stimulus in the prosaccade task serves as the imperative for an automatic response-selection process (see also Wright et al., 2007).

**Thesis Objectives**

The principal objective of my master’s research program was to determine whether – and to what degree – the spatial location of a distractor relative to a visual target influences antisaccade RTs. Indeed, such a question represents an important issue in the oculomotor control literature because the decoupling of SR relations provides a basis for determining whether sensory (i.e., target)- and/or motor (i.e., goal)-related features of a distractor influence response planning. To accomplish my objective, in Chapter Two I adopted the remote distractor paradigm employed by Walker et al. (1997)
and had participants complete pro- and antisaccades in a condition that entailed a single and briefly (i.e., 50 ms) presented target. In addition, pro- and antisaccades were completed in conditions wherein a target was concurrently presented with a distractor at a remote (i.e., midline, contralateral) or proximal (i.e., ipsilateral) spatial location. Specifically, the target was 8° left and right of fixation, whereas distractors were located: (1) ipsilateral to the target at an eccentricity of 4° from the fixation cross, (2) at the location of the fixation cross (i.e., visual midline, 0°), and (3) contralateral to the target at eccentricities of 4° and 8° from the fixation cross. If a RDE characterizes the planning of antisaccades, then a proximal – but not remote – distractor is predicted to selectively delay antisaccade RTs. The basis for this prediction stems from the fact that although a proximal distractor in an antisaccade task is in the same visual field as the target stimulus, the goal-location of the response is mirror-symmetrical to the target’s veridical (i.e., sensory) location (i.e., remote to the saccade generating neurons supporting the goal-location). Thus, in accord with the CIM – a proximal distractor is predicted to induce a long-range attenuation of motor-related buildup neurons in the SC that serve the antisaccade response. Alternatively, if increasing the number of SR alternatives (i.e., target only versus target and distractor) results in increased response uncertainty, then the decoupling of SR relations necessary for the antisaccade task should result in a distractor-related cost that is independent of the distractor’s spatial location.
References


CHAPTER TWO

The Antisaccade Task: Visual Distractors Elicit a Location-Independent Planning ‘Cost’
Introduction

Prosaccades are rapid eye movements that bring a target of interest into central vision. The majority of work involving prosaccades has employed an experimental paradigm wherein a target is presented in an impoverished (i.e., empty) visual environment. Results from this work have shown that prosaccades are characterized by short latencies and accurate endpoints – a finding attributed to their mediation via dedicated retinotopic motor maps in the superior colliculus (SC) (Wurtz and Albano, 1980). It is, however, important to recognize that the visual environments in which humans interact are rarely comprised of a single stimulus; rather, successful prosaccades require disentangling the location of a target from task-irrelevant visual cues. As an experimental corollary, the visual distractor paradigm requires that participants ignore the presentation of a task-irrelevant visual distractor and complete a saccade to a visual target. A number of studies have shown that the location of a distractor relative to a target differentially influences prosaccade reaction times (RT) and amplitudes. For example, Walker et al. (1997) reported that the onset of a remote distractor (i.e., a distractor contralateral to a target or at the visual midline) concurrent with target presentation produced longer RTs than when a target was presented alone or when presented with a proximal distractor (i.e., ipsilateral to the target) (i.e., the remote distractor effect: RDE) (see also Casteau and Vitu, 2012; Lévy-Schoen, 1969). In turn, distractor location elicits a converse effect on prosaccade amplitudes such that proximal distractors bias amplitudes toward the distractor (i.e., the global effect), whereas a remote distractor does not influence amplitudes (Coren and Hoenig, 1972; Deubel et al., 1984; Findlay, 1982; Walker et al., 1997; for review see Van der Stigchel and Nijboer, 2011).
A number of studies have attributed the RDE and global effect to the motor-related properties of neurons in the SC. In particular, the competitive integration model (CIM) (i.e., Trappenberg et al., 2001; Godijn and Theeuwes, 2002) contends that the visual information supporting target and distractor are concurrently transformed into motor programs within a common retinotopic motor map in the intermediate layers of the SC. Given the common retinotopic mapping, target- and distractor-specific saccade neurons compete for a common threshold and create conflicting saccade generation commands that require additional time to resolve (see also Dorris et al. 2007). More directly, the CIM asserts that the RDE results from a long-range intercollicular inhibitory pathway in which saccade-related activity at one location inhibits the activation of distant locations within the motor map (Takahashi et al., 2005). Thus, active saccade neurons associated with a remote distractor delay the motor-related buildup properties serving a saccade to the target location (Trappenberg et al., 2001). In turn, when a distractor is presented proximal to a target the motor activity related to each stimulus merges into a single movement vector that represents a spatially averaged response (see also Van Gisbergen et al., 1987; Van Opstal and Van Gisbergen, 1989). Notably, although the spatially averaged response of a proximal distractor does not engender a cost to saccade latency it does result in a response that falls between the target and distractor (i.e., the global effect).

To my knowledge, previous work has not examined location-specific distractor effects for antisaccade planning times. In particular, antisaccades represent a non-standard motor task requiring that participants saccade mirror-symmetrical (i.e., 180° spatial transformation) to the location of an exogenously presented target. Extensive
evidence has shown that antisaccades produce longer RTs (Hallett, 1978; Hallett and Adams, 1980), increased directional errors (Fischer and Weber, 1992) and less accurate and more variable endpoints (Dafoe et al., 2007; Heath et al., 2011; Krappmann et al., 1998) than prosaccades. Moreover, human and non-human primate neuroimaging and electrophysiology findings have attributed the antisaccade planning ‘cost’ to a two-component process requiring the top-down inhibition of a stimulus-driven prosaccade (i.e., response suppression) and the visual remapping of target parameters to a mirror-symmetrical location in space (i.e., vector inversion) (for review see Munoz and Everling, 2004).

The present investigation sought to determine whether distractor location influences antisaccade planning times in a manner similar to prosaccades. Notably, the decoupled stimulus and response (SR) relations associated with the antisaccade task provide a basis for determining whether the sensory (i.e., target)- and/or motor (i.e., goal)-related features of a distractor influence response planning. In order to highlight this issue, Figure 1 shows that in an antisaccade task the sensory properties (i.e., veridical location) of a ‘proximal’ distractor are contained within the same visual field as the target stimulus; however, the goal-location of the response is in the mirror-symmetrical visual field (i.e., remote to the target’s veridical location). In other words, the sensory-related property of the distractor is proximal to the target, whereas the motor-related property of the distractor is remote to the target. In turn, Figure 1 shows the converse relationship associated with a ‘remote’ distractor. As such, a corollary prediction drawn from the CIM regarding antisaccades is that the saccade-related buildup properties serving a proximal – but not a remote – distractor should delay planning times. Indeed, a location-
specific increase in RT for a proximal distractor would support the contention that
distractor costs – in the antisaccade task – arise from a motor-related competition
between conflicting and directionally alternative saccade generation commands. More
directly, a proximal distractor would result in distractor- and saccade-related motor
activity that is encoded within remote areas of the retinotopic motor maps of the SC. As
such, a proximal – but not remote – distractor would induce a long-range attenuation of
motor-related buildup neurons serving antisaccade planning. As an alternative to
distractor-related antisaccade planning costs, it is possible that top-down response-
selection rule necessary for a response with decoupled SR relations influence planning
times independent of the distractor’s spatial location. The basis for this prediction stems
from a choice-RT study by Kveraga et al. (2002) showing that increasing the number of
SR alternatives (i.e., distractors) associated with an antisaccade – but not prosaccade –
task conforms to the log-linear increase in RT defined by Hick’s law (Hick, 1952).
According to Kveraga et al., antisaccades conform to Hick’s law because the top-down
nature of decoupling a SR requires: (1) an obligatory response-selection strategy that
entails the spatial transformation of the target vector, and (2) an increased response-
selection uncertainty related to the processing of each potential SR alternative. In turn,
Kveraga et al. proposed that prosaccades do not adhere to Hick’s law because localization
of the target among distractor(s) serves as the imperative to automatically map the
target’s spatially encoded visual activity into a motor response. As such, if response-
selection uncertainty underlies antisaccade distractor costs than RT delays should be
independent of the distractor’s spatial location.
Figure 1. Sensory- and motor-related spatial properties of a distractor in the antisaccade task. The top panel shows that although the sensory-related activity of a ‘proximal’ distractor in an antisaccade task is in the same visual field as the target stimulus, the goal-related activity is ‘remote’ (i.e., the opposite visual field). The bottom panel shows that the sensory-related activity of a ‘remote’ distractor in an antisaccade task is in the visual field opposite to the target (i.e., it is remote); however, the goal-related activity is proximal to the target (i.e., the same visual field).

The present study sought to determine whether – and to what degree – the spatial location of a distractor relative to a visual target differentially influences pro- and antisaccade planning times. To that end, I employed the same general methodology used in Walker et al.’s (1997) examination of the RDE for prosaccades. In particular, pro- and antisaccades completed in a neutral visual background (i.e., target-only condition) were
contrasted with responses completed in conditions involving proximal (i.e., ipsilateral) and remote (i.e., midline and contralateral) distractors. In terms of potential research outcomes, if antisaccades are susceptible to the same long-range inhibition as prosaccades than the motor- and not the sensory-related location of the distractor should result in an increase in RT. More directly, the presentation of a proximal distractor should selectively lengthen antisaccade RTs because the encoded motor activity of the distractor and the required response are represented within distant retinotopic coordinates. In turn, if an obligatory process of response-selection influences in antisaccade planning then distractor-related RT costs should be location-independent.

Methods

Participants

Fifteen individuals (11 female and 4 male: age range 18 – 30 years) from the University of Western Ontario community volunteered for this experiment. All participants were self-declared right-hand dominant with normal or corrected-to-normal vision. Participants signed consent forms approved by the Office of Research Ethics, the University of Western Ontario, and all work was conducted in accord with the ethical standards outlined in the Declaration of Helsinki.

Apparatus and procedure

Participants were seated at a table (775 mm in height) with their head placed in a head-chin rest for the duration of the experiment. Visual stimuli were presented on a 30-inch LCD monitor (60 Hz, 8 ms response rate, 1280 × 960 pixels, Dell 3007WFP, Round Rock, TX, USA) placed 550 mm from the participant and centered on their midline. Point of gaze data were obtained from each participant’s left eye via a video-based eye-tracking
system (Eye-Trac 6: Applied Science Laboratories, Bedford, MA, USA) sampling at 360 Hz. Prior to data collection a nine-point calibration of the viewing space was performed and confirmed via an immediate follow-up calibration. Two additional monitors that were visible only to the experimenter provided: (1) real-time point of gaze information, (2) visual depiction of trial-to-trial saccade kinematics (i.e., displacement, velocity), and (3) information on the accuracy of the eye tracking system (i.e., to allow for drift correction or re-calibration when necessary). All computer events were controlled via MATLAB (Version 7.8.0, The MathWorks, Inc., Natick, MA, USA) and the Psychophysics Toolbox extension (version 3.0; see Brainard, 1997). The lights in the experimental suite were extinguished during data collection.

Visual stimuli included a white fixation cross (0.7°) centered horizontally on the monitor and at the eye level of the participant. White diagonal crosses (0.7°) served as target stimuli and were located 8° left and right of fixation. Additionally, unfilled white circles (0.7°) served as task-irrelevant stimuli (i.e., distractors) and were presented along the same horizontal axis as the fixation and target stimuli. Distractors were located (1) ipsilateral to the target at an eccentricity of 4° from the fixation cross (i.e., ipsilateral distractor: ID), (2) at the location of the fixation cross (i.e., 0° and henceforth referred to as the midline distractor: MD), (3) contralateral to the target at an eccentricity of 4° from the fixation cross (i.e., contralateral proximal distractor: CPD), and (4) contralateral to the target and at an eccentricity of 8° from the fixation cross (i.e., contralateral distal distractor: CDD) (see Figure 2). The different distractor locations were identical to those employed in Walker et al.’s (1997) initial examination of the RDE for prosaccades.

At the start of each trial, the fixation cross was presented and participants were
instructed to direct their gaze to its location. Once a stable gaze of the fixation cross was achieved (±1.5° for 420 ms), a randomized foreperiod (1,000 – 2,000 ms) was initiated during which time the fixation cross remained visible. Following the foreperiod, a target stimulus (i.e., target-only condition: TO), or target stimulus with distractor (i.e., ID, MD, CPD, CDD conditions) was presented for 50 ms (see Figure 2 for timeline of visual events). The onset of the target stimulus served as the cue to pro- or antisaccade “as quickly and accurately as possible” and to ignore the irrelevant distractor when present. Notably, prosaccades entailed a response to the target’s veridical location, whereas antisaccades entailed a response mirror-symmetrical to the veridical target location.
Figure 2. Timeline of visual events for a target presented in the right visual field. A white fixation cross was presented for a randomized foreperiod (1,000 – 2,000 ms). Following the foreperiod, the fixation cross was extinguished and a visual target was presented right of fixation for 50 ms. For 80% of trials, a visual distractor was presented concurrent with the target at a proximal (ID), or remote (MD, CPD, CDD) spatial location along the horizontal target axis. For the remaining trials a target was presented without a distractor (TO). The onset of the target (and distractor) served as the imperative to complete the instructed pro- or antisaccade.

Participants completed pro- and antisaccades in separate and randomly ordered blocks. As noted above, responses were completed in target-only (TO) and four distractor conditions (ID, MD, CPD, and CDD) that were randomly interleaved within each block. In addition, the visual field (left, right) associated with the target stimulus was randomized within each block. For each block, participants completed 12 trials to each of the aforementioned trial-type by visual field combinations (i.e., 240 total experimental
Data analysis and dependent variables

Displacement data were filtered offline using a dual-pass Butterworth filter employing a low-pass cut-off frequency of 15 Hz. Filtered displacement data were used to compute instantaneous velocities via a five-point central finite difference algorithm. Acceleration data were similarly obtained from the velocity profiles. Saccade onset was determined on the basis of velocity and acceleration values that exceeded $30^\circ$/s and $8,000^\circ$/s$^2$, respectively. Saccade offset was marked when velocity fell below $30^\circ$/s for 15 consecutive frames (i.e., 42 ms). The dependent variables were reaction time (RT: time from target onset to movement onset) and saccade amplitude in the horizontal movement direction. Dependent variables were examined using 2 (task: prosaccade, antisaccade) by 5 (trial-type: TO, ID, MD, CPD, CDD) repeated measures ANOVAs. Post-hoc decomposition for trial-type were completed by contrasting each distractor condition to their respective TO condition counterpart via paired samples t-tests. Only directionally correct pro- and antisaccade trials were analyzed. Accordingly, for each participant an average of 3% and 10% of pro- and antisaccade trials were excluded, respectively. Furthermore, for each participant an average of 2% of trials were removed due to: (1) signal loss (i.e., blinking), (2) a RT greater than two standard deviations above the mean group performance (i.e., RT > 700 ms), and (3) an anticipatory response (i.e., RT < 85 ms).
Results

Reaction time

Results yielded main effects of task, $F(1,14) = 70.80, p < 0.001$, trial-type, $F(4,56) = 25.12, p < 0.001$, and their interaction, $F(4,56) = 5.64, p < 0.002$. As expected, Figure 3 shows that prosaccades (277 ms, SD = 37) produced shorter RTs than antisaccades (391 ms, SD = 72). Moreover, Figure 3 shows that RTs for prosaccades in the remote distractor conditions (i.e., MD, CPD, CDD) were longer than their TO condition counterpart, $t(14) > 7.97, ps < 0.001$, whereas the ID and TO conditions did not reliably differ, $t(14) = 1.35, p = 0.20$. For antisaccades, ID, MD, CPD, and CDD conditions produced longer RTs than the TO condition, $t(14) > 2.68, ps < 0.02$. Thus, prosaccade elicited a RDE, whereas antisaccade RTs were increased independent of the distractor’s spatial location.

To determine if distractor location differentially influenced the magnitude of the above-mentioned RT costs, I computed difference scores (i.e., distractor RT minus target-only RT) for those conditions that reliably differed from the TO condition. As such, for prosaccades I computed difference scores for MD, CPD, and CDD conditions, whereas for antisaccades I computed difference scores for each distractor condition (i.e., ID, MD, CPD, and CDD). Pro- and antisaccade difference scores were submitted to separate one-way ANOVAs. Results for prosaccades indicated that the magnitude of the distractor cost did not reliably differ across conditions (MD: 84 ms, SD = 40; CPD: 86 ms, SD = 39; and CDD: 82 ms, SD = 38), $F(2,28) = 0.25, p = 0.78$. Similarly, the magnitude of the antisaccade distractor cost did not reliably differ across conditions (ID: 20 ms, SD = 20;
MD: 25 ms; SD = 28; CPD: 45 ms; SD = 64; and CDD: 54 ms; SD = 70), $F(3,42) = 2.22$, $p = 0.10$ (see Figure 3).

**Figure 3.** The main panel depicts mean reaction time (ms) for pro (i.e., closed circles) and antisaccades (i.e., open squares) in target-only (TO), proximal distractor (ID), and remote distractor (MD, CPD, CDD) conditions. Error bars for this panel represent within-participant 95% confidence intervals (Loftus and Masson, 1994). Confidence intervals were computed based on the mean-squared error term for trial-type separately for pro- and antisaccades. The top-right and bottom-right offset panels show mean distractor RT difference scores for pro- and antisaccades, respectively. Error bars represent between-participant 95% confidence intervals (Cumming, 2011; 2013). The absence of overlap between error bars and zero (i.e., horizontal axis) provides a graphical depiction of a reliable difference that can be interpreted inclusive to a test of the null hypothesis.
Saccade Amplitude

Saccade amplitude data yielded main effects of task, $F(1,14) = 18.01$, $p < 0.002$, trial-type, $F(4,56) = 38.32$, $p < 0.001$, and their interaction, $F(4,56) = 9.82$, $p < 0.001$. As shown in Figure 4, prosaccade amplitudes (6.9°, SD = 0.9) were longer than antisaccades (5.8°, SD = 1.5) across each trial-type. As well, prosaccade amplitudes in the ID condition were less than the TO condition, $t(14) = 5.51$, $p < 0.001$, whereas MD, CPD, and CDD conditions were greater than the TO condition, $ts(14) > 2.23$, $ps < 0.05$. For antisaccades, ID and CDD conditions produced amplitudes that were less than and greater than the TO condition, respectively, $ts(14) > 4.14$, $ps < 0.002$. In turn, amplitudes for MD and CPD conditions did not reliably differ from their TO counterpart, $ts(14) = 0.79$ and 0.27, respectively, $ps > 0.44$. 
Figure 4. The main panel depicts mean saccade amplitude (°) in the horizontal direction for pro (i.e., closed circles) and antisaccades (i.e., open squares) completed in target-only (TO), proximal distractor (ID), and remote distractor (MD, CPD, CDD) conditions. Error bars for this panel represent within-participant 95% confidence intervals (Loftus and Masson, 1994). The top-right and bottom-right offset panels show mean distractor amplitude difference scores for pro- and antisaccades, respectively. Error bars represent between-participant 95% confidence intervals (Cumming, 2011; 2013).

Discussion

The present study sought to determine whether – and to what degree – the spatial location of a distractor relative to a visual target differentially influences pro- and antisaccade planning times. More specifically, I sought to determine whether putative distractor related costs for antisaccades relate to: (1) a long-range inhibitory pathway in the SC (i.e., the RDE; e.g., Trappenberg et al., 2001), or (2) a top-down evocation of
response-selection rules that are independent of the distractor’s spatial location (e.g., Kveraga et al., 2002). To that end, participants completed pro- and antisaccades left and right of a common fixation in a target-only condition (i.e., TO: distractor-free), and conditions wherein a distractor was presented at a proximal (i.e., ID) or remote (i.e., MD, CPD, CDD) spatial location.

*Prosaccade RTs: A replication of Walker et al. (1997)*

The target and distractor conditions employed here were the same as those used by Walker et al. (1997). Figure 3 shows that remote distractor (i.e., MD, CPD, CDD) conditions elicited longer prosaccade RTs than the TO condition, whereas the proximal distractor (i.e., ID) and TO conditions did not reliably differ. Moreover, the average cost of a remote distractor was 84 ms and the magnitude of this effect did not vary across the different remote distractor locations. Thus, the results demonstrate a reliable RDE in line with Walker et al. (1997) and I interpret this result to evince that remote distractors delay prosaccade planning times via a long-range attenuation of target-related buildup neurons in the SC (i.e., the CIM).

*Prosaccade amplitudes are influenced by proximal and remote distractors*

Prosaccades in the ID condition landed between the target and distractor. This result reported previously by Walker et al. (1997) and others (Coren and Hoenig, 1972; Deubel et al., 1984; 1988; Findlay, 1982; Ottes et al., 1985) has been interpreted to reflect that the motor representation of target and distractor locations on a common short-range motor map within the intermediate layers of the SC results in the spatial averaging of motor-related saccade activity (i.e., the global effect). Notably, however, I also observed that amplitudes for remote distractor conditions were longer than their TO condition.
counterpart. This finding counters Walker et al. who reported a null amplitude effect of remote distractors. One possible explanation for the between-experiment discrepancy is that the current study employed a brief (50 ms) target presentation, whereas the target (and distractor) used in Walker et al’s study was available throughout response execution. As such, the continuous target (and distractor) vision associated with Walker et al. may have served to support on- or offline corrections to the primary saccade trajectory (Gaveau et al., 2003; Heath et al., 2011; West et al., 2009). To address this issue, I completed a supplemental experiment involving 10 participants (7 female and 3 male: age range 18 – 30 years) and used the same procedures as the main experiment with the only difference being that the target (and distractor) was available throughout response execution. In other words, the supplemental experiment provided the same online target (and distractor) vision as employed by Walker et al. The results for the supplemental experiment are presented in Figure 5 and provide a direct replication of the main experiment – amplitudes for the ID condition landed between the target and distractor ($t(9) = 10.32, p < 0.001$), whereas amplitudes for the remote distractor conditions (MD, CPD, and CDD) were longer than the TO condition ($ts(9) > 3.17, ps < 0.002$). Thus, the presence of target and distractor vision throughout response execution does not account for the discrepancy between the current results and Walker et al. As an alternative account, I note that Walker et al. employed six participants, whereas the main and supplemental experiments used here employed 15 and 10 participants, respectively. It is therefore possible that the detection of remote distractor effects may relate to statistical power. In addressing this issue I created 20 unique and pseudo-randomly sampled data sets involving six participants from each of the main and supplemental experiments and
contrasted amplitudes for the TO and CDD condition amplitudes via paired-samples t-tests. Results showed that the probability of statistically equivalent endpoints for CDD and TO conditions were 100% (20/20) and 60% (12/20) for the main and supplemental experiments, respectively. Given these findings, I propose that the null remote distractor effect reported in previous work relates to an exiguous replication sample size.

**Figure 5.** Data for the supplemental experiment wherein target and distractor were visible throughout response execution. The main panel depicts mean saccade amplitude (horizontal °) for prosaccades completed in target-only (TO), proximal distractor (ID), and remote distractor (MD, CPD, CDD) conditions. Error bars represent within-participant 95% confidence intervals (Loftus and Masson, 1994). The right panel shows the mean distractor amplitude difference scores. Error bars represent between-participant 95% confidence intervals (Cumming, 2011; 2013).

In explaining the longer amplitudes in the remote distractor conditions I note that previous work has shown that manual and saccade trajectories ‘curve’ away from the
location of a distractor in pursuit of the response goal (Doyle and Walker, 2001; Tipper et al., 2000; 2001; Walker and McSorley, 2008). In particular, Tipper and colleagues’ population coding model contends that the top-down inhibition of exogenous distractor-related activity in the saccade map of the SC biases the mean vector of saccade-related activity in a direction contralateral to the distractor. Thus, the results may relate to a spatial bias wherein the programmed amplitude of a prosaccade moves further away from the location of a remote distractor to avoid capture of task-irrelevant visual information.

*Antisaccade RTs: Planning costs are independent of a distractor’s spatial location*

Antisaccade RTs in each distractor condition were longer than the TO condition, and the magnitude of the distractor cost (average of 36 ms) was independent of the distractor’s spatial location. As such, antisaccades RTs do not elicit a RDE commensurate with prosaccades. Moreover, results demonstrate that distractor-related saccade activity at a remote area of the collicular motor map does not selectively inhibit saccade-related motor activity. Instead, results suggest that distractors influence antisaccade RTs due to the top-down demands of evoking the response-selection rule necessary for decoupling SR spatial relations. In accord with this view, previous work has shown that antisaccades – but not prosaccades – adhere to Hick’s law (Kloft et al., 2012; Kveraga et al., 2002; see also Lawrence, 2010). According to Kveraga and colleagues, prosaccades violate Hick’s law because an automatic response-selection process couples the location of a target stimulus with a motor response. Indeed, the fact that humans complete upwards of 100,000 prosaccades in the course of their daily activities (Irwin and Thomas, 2007) highlights the fact that the prosaccade response-selection process efficiently attenuates task-irrelevant visual information (see Pashler, 1998, p. 357; Teichner and Krebs, 1974).
In turn, Kveraga et al. contend that antisaccades adhere to Hick’s law because the location of a target stimulus cannot be automatically mapped onto the direction of an ensuing response. Instead, the decoupled SR relations engender a cost related to the processing of each potential SR alternative. Moreover, electrophysiological evidence from non-human primates has shown that distinct neural ensembles serve the visual selection of a target stimulus and the selection of an appropriate antisaccade endpoint. For example, Sato and Schall (2003) recorded single-cell activity from the frontal eye fields (FEF) of macaques during the planning of pro- and antisaccades to a target stimulus presented within an array of three distractors. Results showed that pro- and antisaccade RT differences were not linked to stimulus identification within the FEF (i.e., disentangling target from distractor); rather, the increase in antisaccade RTs was linked to the onset of FEF activity supporting the selection of the task-rule necessary for decoupling SR relations. Notably, my work adds to previous literature insomuch as it demonstrates that the spatial location of a distractor does not differentially influence the planning time required to adopt an appropriate antisaccade task-rule.

*Effects of proximal and remote distractors on antisaccade endpoints*

Antisaccade amplitudes in the ID and CDD conditions were less than and greater than the TO condition, respectively. In turn, antisaccade amplitudes in the MD and CPD conditions did not reliably differ from the TO condition. In contrast to the present results, Viswanathan and Barton (2013) reported that antisaccade endpoints in a remote – but not proximal – distractor condition produced endpoints consistent with a global effect. Viswanathan and Barton interpreted their results to evince a spatial averaging of motor-related activity serving the response goal and distractor on a common short-range motor
map in the intermediate SC. Notably, however, my results do not support a global effect for remote distractors. Indeed, had the present results demonstrated a global effect then the CPD condition would have produced shorter amplitudes than the TO condition because the goal-location of the response is proximal to the distractor’s location (see Figure 1). To my knowledge, the present work and Viswanathan and Barton’s represents the only studies to have examined distractor-related influences on antisaccade amplitudes. As well, I am unable to identify a between-experiment methodological difference that might explain for the discrepant findings. Moreover, Viswanathan and Barton did not systematically report distractor-related antisaccade RT costs; and thus, I am unable to contrast planning and endpoint related differences between experiments. Taken together then, I propose that a global effect does not represent a reliable property of antisaccade amplitudes.

In accounting for the finding that ID and CDD conditions produced amplitudes that were distinct from TO trials I note that antisaccade sensorimotor transformation are mediated via a relative visual percept (Dafoe et al., 2007; Evodokimidis et al., 2006; Heath et al., 2001; Krappmann et al., 1998). Moreover, the antisaccade visual percept has been shown to be governed by a strategy of perceptual averaging such that the visual properties of a target are encoded relative to the properties of other stimuli (i.e., distractors) within a stimulus-set (Gillen and Heath, 2014a; 2014b). Thus, I propose that antisaccade amplitudes are based on a statistical summary of the visual location of the target and distractor. Indeed, for the ID condition the proximity between target and distractor would render a statistical summary and associated visual percept that leads to an increase in endpoint hypometria. In turn, because the target and distractor in the CDD
condition are in opposite visual fields, but have equal eccentricities, a statistical summary would render a more accurate target percept and therefore serve to reduce hypometria. Of course, I emphasize that the perceptual averaging proposal is distinct from the global effect as the former represents a statistical summary of the sensory-related properties contained within a stimulus-set (Ariely, 2001; Corbett and Oriet, 2011; Gillen and Heath 2014a; 2014b), whereas the latter is attributed to the weighted average of motor-related activity encoding target and distractor response goals (e.g., Godijn and Theeuwes, 2002).

Conclusions

Antisaccades showed a distractor-related increase in RT that was independent of the distractor’s spatial location. Such a finding indicates that motor-related activity associated with the distractor at a remote location from the intended saccade goal does not selectively attenuate the motor-related properties of buildup neurons serving the antisaccade response. Instead, I propose that distractor-related antisaccade RT costs reflect uncertainty associated with the top-down evocation of the task-rule necessary to decouple SR relations.
References


CHAPTER THREE

General Discussion
The primary objective of my master’s research program was to determine whether distractor-related antisaccade RT costs relate to: (1) a long-range inhibitory pathway in the SC (i.e., the RDE; e.g., Godijn and Theeuwes, 2002; Trappenberg et al., 2001), or (2) a top-down evocation of response-selection rules that is independent of the distractor’s spatial location (e.g., Kveraga et al., 2002). To accomplish my objective, Chapter Two employed the same general stimulus paradigm as Walker et al. (1997) wherein participants completed pro- and antisaccades in a condition that entailed the presentation of a single and briefly (i.e., 50 ms) presented target stimulus (i.e., TO), as well as conditions wherein a target was concurrently presented with a distractor at a proximal (i.e., ID) or remote (i.e., MD, CPD, CDD) spatial location along the horizontal target axis. Importantly, in synthesizing the present results it is important to recall that the sensory- and motor-related properties of a target in an antisaccade task are dissociable, whereas the properties overlap in a prosaccade task. In particular, the top panel of Figure 1 provides an example of a proximal distractor condition. In this condition, the sensory-related position of target and distractor are proximal (i.e., presented in the same visual); however, for an antisaccade task the motor-related activity of the response is remote to the distractor’s spatial location. In turn, the bottom panel of Figure 1 shows that for a remote distractor the motor-related activity associated with the antisaccade task is proximal to the distractor’s spatial location. Thus, antisaccades entail dissociable sensory- and motor-related target activity.

Chapter Two showed that prosaccade RTs were increased for the remote (i.e., MD, CPD, CDD) but not proximal (i.e., ID) distractor conditions (Figure 3). Thus, prosaccades elicited a reliable RDE – a result that I have interpreted as support for the
competitive integration model’s (CIM) assertion of an attenuation of motor-related buildup neurons in the SC via long-range inhibitory connections. In turn, antisaccade RTs in each distractor condition (i.e., ID, MD, CPD, CDD) were increased relative the TO condition and the magnitude of this effect was independent of the distractor’s spatial location (average RT cost 36 ms; see Figure 3). As such, I propose that the results for Chapter Two support the position that distractor-related antisaccade RT costs relate to implementing top-down task-rules associated with selecting a response with decoupled SR relations.

In light of the findings of Chapter Two, it is important to highlight the extensive body of work demonstrating that planning efficiency is influenced by the adoption of an appropriate task-set related to a set of $N$ possible SR alternatives. In particular, Merkel’s (1885; cited in Keele, 1973; Woodworth, 1938) classic work was the first to show that choice-RT increases linearly as a function of doubling the number of SR alternatives. Specifically, Merkel asked subjects to perform a key-press task where the number of SR alternatives was varied between one and 10 within different sets of trials. Participants were presented with a set of Arabic (i.e., 1 to 5) and Roman (i.e., I to V) numerals and were required to press a key with a corresponding finger on the left (i.e., Roman) and right (i.e., Arabic) hands. For example: the Roman numeral III corresponded to a key press using the left middle finger, whereas the Arabic numeral 2 corresponded to a key press using the right ring finger. Moreover, the seminal papers of Hick (1952) and Hyman (1953) developed a logarithmic formula to quantify choice-RT as a function of
the number of SR alternatives (i.e., Hick’s or Hick-Hyman law\(^1\): for reviews see Teichner and Krebs, 1974; Welford, 1968). Hick’s law asserts that the rate of gain in stimulus information (i.e., SR alternatives) conforms to an increased index of uncertainty and duration of response-selection. More specifically, Hick’s law states a response-selection ‘cost’ arises from the serial processing of each SR alternative (i.e., bits of sensory information) until a correct decision is made.

In keeping with the preceding paragraph, an important issue in the visuomotor control literature is how the rate of gain in stimulus information influences the planning of standard and non-standard motor tasks. Indeed, literature in this area has shown that increasing the number of SR alternatives selectively increases RTs for motor tasks that require an explicit rule-based (i.e., endogenous) response-selection strategy. In particular, an endogenous response-selection strategy is required for tasks in which the spatial location of the motor response is not spatially congruent with the location of the target stimulus. For example, Kveraga et al. (2002; see also Kloft et al., 2012) demonstrated that antisaccades – but not prosaccades – adhere to Hick’s law (see also Lawrence, 2010; Lawrence and Gardella, 2009; Lawrence et al., 2008; Lawrence and Weaver, 2011). In particular, Kveraga et al. proposed that prosaccades violate Hick’s law because of the highly efficient retinotopic mapping of the SC that directly couples the location of the

\(^1\) Hick-Hyman law – A logarithmic quantification of choice-RT (CRT) as a function of the rate of gain in stimulus information: \(\text{CRT} = a + b \log_2 N_A\), where \(a\) and \(b\) represent empirical constants and \(\log_2 N_A\) represents time to process the number of equal probability SR alternatives (i.e., log to the base of two represents the number of bits required to reduce response-selection uncertainty by half).
target stimulus and motor response (i.e., SR compatibility). In other words, localization of the target stimulus in the prosaccade task serves as the imperative for an *automatic* response-selection process (see also Wright et al., 2007). Conversely, that antisaccades adhere to Hick’s law has been taken to evince an increased index of response-selection uncertainty because the incoming target signal cannot be directly transformed into a motor command via direct retinotopic pathways. Thus, the adoption of appropriate task-rules for antisaccades is associated with a cost related to the processing each potential SR alternative and the spatial transformation of the target vector (i.e., vector inversion) necessary for the obligatory decoupling of SR relations. Moreover, recent work has shown that arrow-cued (Kloft et al., 2012; Lawrence, 2010) and number-cued saccades (Kloft et al., 2012) adhere to Hick’s law – findings supporting the assertion that endogenous control increases response-selection uncertainty. For example, in the number-cued task participants are presented with a number corresponding to different locations on an analogue clock (i.e., the number 3 would entail a horizontal saccade in a rightward direction, whereas the number 12 would entail a vertical saccade in an upward direction). Notably, in this task the location of the stimulus is indirectly tied to the location of the motor response. Thus, a correctly executed response requires an explicit response-selection strategy that entails the spatial transformation of an arbitrary central cue. It is, however, important to recognize that previous literature has not examined how the spatial relationship between a target and a distractor influences the adoption of the appropriate task-rules for antisaccades. Thus, the results from Chapter Two are important because they demonstrate that the planning time – and therefore uncertainty – associated
with decoupling SR relations is independent of the distractor’s spatial location (i.e., ipsilateral, midline, contralateral).

A final issue I address relates to Sato and Schall’s (2003) single-cell recording work in non-human primates demonstrating that the selection of pro- and antisaccade endpoints are supported by distinct neural ensembles in the frontal eye fields (FEF). In particular, their work showed that longer RTs for antisaccades in a visual search paradigm (compared to prosaccades) were linked not to the onset of FEF activity supporting stimulus identification; rather, increased antisaccade RT costs were attributed to FEF activity related to the selection of the task-rules necessary for decoupling SR relations (i.e., endpoint selection). Thus, Sato and Schall’s findings coupled with the results of Chapter Two provide behavioral evidence that the planning time associated with adopting an appropriate antisaccade task-rule is independent of the distractor’s spatial location. It is, however, important to bear in mind that I am unaware of any current neuroimaging or electrophysiology work that has examined the neural mechanisms supporting response-selection for antisaccades as a function of the distractor’s spatial location. Thus, future work may disentangle antisaccade RT costs as a function of the distractor’s spatial location in order to identify the putative contributions of cortical and subcortical saccade networks supporting response-selection.

**General Conclusions**

The results of my master’s thesis show that the distractor-related increase in antisaccade RTs is not accounted by the CIM’s assertion of a long-range inhibition of motor-related saccade activity within in the SC. Thus, I propose that the location-independent planning cost associated with visual distractors evinces the time required to
implement the top-down task-rules associated with selecting a response with decoupled SR relations.
References


APPENDIX A

Use of Human Participants - Ethics Approval Notice

Principal Investigator: Dr. Matthew Heath
File Number: 103523
Review Level: Delegated
Protocol Title: Kinematics of pro- and antisaccade trajectories
Department & Institution: Health Sciences/Kinesiology, Western University
Sponsor:
Ethics Approval Date: April 18, 2013 Expiry Date: February 28, 2015

Documents Reviewed & Approved & Documents Received for Information:

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This is to notify you that the University of Western Ontario Research Ethics Board for Non-Medical Research Involving Human Subjects (NMREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the applicable laws and regulations of Ontario has granted approval to the above referenced revision(s) or amendment(s) on the approval date noted above.

This approval shall remain valid until the expiry date noted above assuming timely and acceptable responses to the NMREB’s periodic requests for surveillance and monitoring information.

Members of the NMREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussions related to, nor vote on, such studies when they are presented to the NMREB.

The Chair of the NMREB is Dr. Riley Hinson. The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 0000941.

Signature

Ethics Officer to Contact for Further Information

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