7-30-2014 12:00 AM

Statistical Summaries in Action: Evidence from the Antisaccade Task

Caitlin Gillen, *The University of Western Ontario*

Supervisor: Dr. Matthew Heath, *The University of Western Ontario*

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

Recommended Citation

Gillen, Caitlin, "Statistical Summaries in Action: Evidence from the Antisaccade Task" (2014). *Electronic Thesis and Dissertation Repository*. 2346.
https://ir.lib.uwo.ca/etd/2346

STATISTICAL SUMMARIES IN ACTION: EVIDENCE FROM THE ANTISACCADE TASK

(Thesis format: Integrated Article)

by

Caitlin Gillen

Graduate Program in Kinesiology

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

The School of Graduate and Postdoctoral Studies
The University of Western Ontario
London, Ontario, Canada

Abstract

Antisaccades require the top-down process of decoupling a stimulus and a response and executing a saccade mirror-symmetrical to a target. Notably, research has yet to characterize the endpoint properties of antisaccades. Experiment One had participants antisaccade in two trial blocks that contained the same number of target eccentricities but differed in respect to their magnitudes. Experiment Two manipulated the frequency that individual target eccentricities were presented within a block of trials. Notably, Experiments One and Two were designed to determine whether the top-down control of antisaccades renders the processing of target features via a strategy of perceptual averaging. Results showed that antisaccades endpoints were biased in the direction of the central target (i.e., the statistical summary) within a block of trials (Experiment One), and in the direction of the most frequently presented target (Experiment Two). Therefore, I propose that antisaccade endpoints are mediated via a perceptual averaging strategy.

Keywords: Antisaccades, amplitude, perceptual averaging, prosaccades

Co-Authorship

The author, under the supervision and mentorship of Dr. Matthew Heath, conducted the work in this master's thesis. Dr. Matthew Heath provided valued guidance in the experimental design, data- collection, analysis, and interpretation, and manuscript preparation. This master's thesis contains material from a published manuscript (Experiment One) as well as submitted manuscript (Experiment Two). On both manuscripts, Caitlin Gillen was the first author and Matthew Heath served as co-author. Additionally, content in the General Introduction and General Discussion contains similar content from the Introductions and Discussions of Experiment One and Two.

Acknowledgments

It is my pleasure to thank the individuals and funding agencies that have made my research possible. My research was supported by Western Graduate Research Awards from The University of Western Ontario, as well as an Ontario Graduate Scholarship. I would like to extend a warm thank-you to each and everyone one who participated in my experiments; your commitment and patience during data collection is greatly appreciated.

I would like to provide a special thank-you to my graduate advisor, Dr. Matthew Heath, who demonstrates strengths in every aspect of academia. He is a talented teacher and was crucial to my development as a writer and researcher. He is passionate and supportive and provides guidance and encouragement for all future endeavors. Dr. Heath provided mentorship and support throughout my graduate degree, and I am sincerely grateful for his commitment and dedication to my work throughout my time as a graduate student.

I would also like to thank my friends and family for their unwavering support throughout the years. Your support always served as encouragement to continue through the obstacles that are encountered with research. I would especially like to thank my mother, Cindy Gillen. She always showed love and support in every aspect of my life. She believes that I can achieve and be successful in whatever I choose and she has supported me throughout every decision I have made. Mom, I would like to dedicate this work to you.

Table of Contents

List of Tables

List of Figures

List of Appendices

General Introduction

Everyday humans make up to 100,000 voluntary eye movements that bring a target of interest into central vision (i.e., prosaccade) (Irwin and Carlson-Radvansky, 1996). Prosaccades are highly effective (i.e., accurate) and efficient (i.e., fast) movements mediated via absolute visual information in the retinotopic maps of the superior colliculus (Wurtz and Albano, 1980) and are executed largely independent of top-down processes (Dafoe et al., 2007). For example, the presentation of a peripheral target (e.g., 20°) activates neurons in the caudal region of the colliculus, whereas a more central target (e.g., 3°) activates neurons in the rostral region (Munoz and Wurtz, 1995). Notably, and although prosaccades are mediated via direct and absolute visual information, they are characterized by an undershooting bias such that primary prosaccades cover only 90% of veridical target amplitude (Abrams et al., 1989; Becker and Fuchs, 1969; Gerardin et al., 2011; Gillen et al., 2013; Weber and Daroff, 1972;). Moreover, the undershooting bias characterizes not only primary saccades but also secondary (i.e., corrective) saccades and increases as a function of increasing target eccentricity (Abrams et al., 1989; Gerardin et al., 2011). The basis for the undershooting bias has been linked to an invariant control strategy that is designed to minimize saccade flight time (Harris, 1995) and/or the energy requirements of the response (Becker, 1989; see also Oliveiria et al., 2005).

Although prosaccades predominant our day-to-day lives, individuals can volitionally decouple the spatial relations between a stimulus and a response and saccade in a direction other than a target stimulus (i.e., non-standard task). The study of non-standard tasks represents an important area of inquiry because if provides a framework by which to investigate how top-down cognitive control influences the oculomotor system. The most frequently examined non-standard task is the antisaccade paradigm wherein an individual is required to saccade mirror-symmetrical to a target. Extensive work has shown that antisaccades produce longer reaction times (RTs) and more directional errors than their prosaccades counterparts (Hallet, 1978; Fischer and Weber, 1992). The aforementioned antisaccade behavioural ‘costs’ have been linked to the top-down and two-component processes of inhibiting a stimulus-driven prosaccade (i.e., response suppression) and inverting a target’s spatial coordinates (180° sensory transformation) to a mirror-symmetrical location (for review see Munoz and Everling, 2004). More specifically, neuroimaging and electrophysiology evidence in humans and non-human primates has linked the evocation of an antisaccade to an increased activation of the classic saccade networks (i.e., frontal and supplementary eye fields, and lateral interpatietal area) and a respective increase and decrease in the activity of collicular fixation and burst neurons (Munoz and Everling, 2004; Munoz and Wurtz, 1993; Zhang and Barash, 2000).

As mentioned above, the two-component process of antisaccades results in longer RTs than their prosaccade counterparts. Moreover, it is not surprising that antisaccade endpoints differ from prosaccades. Indeed, instead of relying on a direct retinotopic mapping between stimulus and response the top-down nature of antisaccades requires that participants evoke their response based on a relative and perceived target location (i.e., a visual percept). Consequently, antisaccades exhibit an eccentricity-specific endpoint bias and increased variability relative to prosaccades (Amador et al., 1998; Bell et al., 2000; Dafoe et al., 2007; Evdokimidis et al., 2006; Heath et al., 2010; Heath et al., 2011; Krappmann et al., 1998; Weiler and Heath, 2012). For example, Evdokimidis et al. (2006) and Dafoe et al. (2007) employed a block of target eccentricities that ranged from 0.5°-10.0°. Both studies reported a respective over- and undershooting bias for the 'proximal' and 'distal' targets. In accounting for this finding, Evdokimidis et al. and Dafoe et al. proposed that the relative percept supporting antisaccade sensorimotor transformations is governed by a range effect (Poulton 1981; see also Kapoula, 1985).

The oculmotor range effect hypothesis asserts that participants can be made to over- and undershoot the proximal and distal targets contained *within* a stimulus-set (Kapoula 1985; see also Kapoula and Robinson 1986). For example, Kapoula had participants execute prosaccades in two blocks that included the same number of eccentricities but differed with regard to their magnitudes. In the first block, Kapoula (1985) employed eccentricities of 2.7°, 4.4°, 6.1°, 7.8°, and 9.5° (i.e., proximal block) and in the second block eccentricities were 7°, 10.9°, 14.7°, 18.3°, and 21.9° (i.e., distal block). Kapoula reported an undershooting bias for the more ‘distal’ (i.e., 7.8° and 9.5°) targets in the proximal block, whereas the ‘proximal’ targets (i.e., 7.0° and 10.9°) in the distal block produced an overshooting bias. As such, Kapoula proposed that the oculomotor system can be made to respectively under- or overestimate the ‘distal’ and ‘proximal’ targets contained within a stimulus-set. Notably, however, subsequent work (Gillen et al., 2013) using a methodology similar to Kapoula's found that: (1) prosaccades undershot veridical target location independent of the range and magnitude of the target eccentricities from within the block of trials in which they were performed, and (2) eccentricities common to each block elicited a reliable undershooting bias. What is more important, Kapoula employed a small sample size of four and two participants for the proximal and distal blocks, respectively, and a(n) (re)examination of the participant-specific data reported by Kapoula (1985: see Table 1 of that work) revealed no statistical evidence for a range effect in prosaccade amplitudes (see Gillen et al. 2013). Thus, Kapoula’s work does not support a range effect for prosaccade endpoints and therefore does not provide a viable framework for understanding the endpoint properties of antisaccades (see work by Evdokimidis et al., 2006; and also Dafoe et al., 2007).

As an alternative to the range effect, my thesis proposes that the visual percept governing antisaccades renders the processing of perceived target location, in part, via a statistical summary of the individual target eccentricities included within a stimulus-set. Such a proposal is drawn from the perceptual averaging literature and the contention that top-down and obligatory judgments associated with the properties (e.g., size, extent, brightness, loudness) of a range of target stimuli are based on an averaged approximation of all the stimuli *within* a set (Albrecht et al., 2012; Ariely, 2001; Chong and Treisman, 2003; Corett and Oriet, 2011; Davarpanah Jazi and Heath, 2014). For example, Ariely (2001) showed that participants were able to accurately judge the average circle size of an array of circles with varying diameters; however, the same participants were unable to reliably identify an individual circle contained within the set (see also Chong and Treisman, 2003). Similarly, Corbett and Oriet (2011) presented participants with a sequence of circles with varying diameters. Following the sequence, participants were shown a test circle in which they had to identify it as a set-member, distinct member (i.e., largest circle) or as representing the mean diameter of all circles. Corbett and Oriet demonstrated that participants were better able to identify the test circle as representing the mean diameter in a stimulus-set. Further, Albrecht et al. (2012) reported that participants were able to report the average pitch associated with a series of auditory tones without being able to reliably report whether an individual tone was a member of a stimulus-set. Thus, a direct corollary from the perceptual averaging literature is the top-down control of antisaccades is based, in part, by a statistical summary and that such a summary influences the visual percept supporting antisaccade endpoints (i.e., the perceptual averaging hypothesis).

The goal of my thesis project was to examine whether antisaccade endpoints are influenced by an oculomotor range effect or a strategy of perceptual averaging. To accomplish that objective, Experiment One adopted a paradigm similar to that originally developed by Kapoula (1985; see also Gillen et al. 2013) in which participants completed antisaccades – and complimentary prosaccades - in separate blocks (i.e., proximal and distal) that included an equal number of targets but differed with respect to the magnitude of their target eccentricities. Specifically, in the proximal block target eccentricities were 3.0°, 5.5°, 8.0°, 10.5°, and 13.0°, whereas in the distal block target eccentricities were 10.5°, 13.0°, 15.5°, 18.0°, and 20.5°. If a range effect characterizes antisaccade endpoints, then the magnitude of eccentricities within a block of trials is predicted to produce an over- and undershooting bias to the 'proximal' and 'distal' targets in each block. Moreover, a direct prediction of the range effect hypothesis is that the targets common to each block (i.e., 10.5° and 13.0°) will produce an undershooting bias in the proximal block and elicit an overshooting bias in the distal block. Alternatively, if a strategy of perceptual averaging characterizes antisaccade endpoints then the bias associated with the each block’s central target (i.e., 8.0° or 15.5°) is predicted to influence the *magnitude* and *direction* of the bias associated with the other targets within each stimulus-set. For example, the perceptual averaging hypothesis asserts that endpoint bias associated with the central target in the distal block (i.e., 15.5°) will influence the magnitude and direction of the endpoint bias to the other targets contained within the set (i.e., 10.5°, 13.0°, 18.0°, and 20.5°). Thus, a large magnitude undershooting bias associated with the central target is predicted to produce an undershooting bias across the other targets within the stimulus-set.

Experiment Two of my thesis required that participants complete antisaccades in three separate blocks that contained identical target eccentricities (i.e., 10.5°, 15.5° and 20.5°) but differed with respect to the frequency that individual target eccentricities were presented. The specific goal of this experiment was to test the theoretical predictions of the perceptual averaging hypothesis. Indeed, perceptual averaging contends that the manipulation of target frequency will influence the statistical summary representing a stimulus-set and result in an endpoint bias in the direction of the most frequently presented target. Specifically, Experiment Two employed three weighting conditions. In the control condition, antisaccades were completed to each to target eccentricities with equal frequency. In turn, in the proximal- and distal-weighting conditions the 'proximal' and 'distal' targets were respectively presented five times as often as the other target eccentricities included within the set. If perceptual averaging characterizes antisaccade endpoints, then the visual percept supporting antisaccades will be influenced by a statistical summary that is biased in the direction of the most frequently presented target. As such, the statistical summary would be represented by the central target (i.e., 15.5°) in the control condition but would be biased toward the 10.5° or 20.5° target eccentricities in the proximal- and distal-weighting conditions, respectively. More specifically, antisaccade amplitudes in the proximal-weighting condition are predicted to undershoot more than the control condition, whereas a decreased undershooting is predicted for the distal-weighting condition.

Experiment One

Introduction

Prosaccades are rapid eye movements that bring the fovea onto a target of interest. Notably, the dimensional overlap between stimulus and response allows for the sensorimotor transformation supporting prosaccades to be mediated via *absolute* visual information specified by direct and retinotopically organized motor maps within the superior colliculus (Wurtz and Albano, 1980). In spite of the direct nature of the aforementioned sensorimotor transformations, prosaccades do not always land on the veridical location of a target; rather, prosaccades frequently exhibit an undershooting bias. For example, prosaccades completed across a range of target eccentricities (i.e., 5° through 40°) have been shown to elicit a 10% undershooting of veridical target location (Becker and Fuchs, 1969; Deubel et al., 1986; Robinson, 1964; Weber and Daroff, 1971). Additionally, the undershooting bias characterizes both primary and secondary (i.e., corrective) trajectories and has been shown to increase with increasing target eccentricity (Abrams et al., 1989; Gerardin et al., 2011; Gillen et al., 2013; Prablanc and Jeannerod, 1975). As such, it has been proposed that prosaccades are governed by an invariant oculomotor strategy that minimizes saccade flight time (i.e., saccade flight time hypothesis: Harris, 1995) and/or energy expenditure (i.e., energy minimization hypothesis: Becker, 1989). Indeed, both accounts provide a parsimonious interpretation for the undershooting bias because each limits the possibility of an overshooting error and the temporal and/or energy costs associated with implementing a secondary saccade in a direction opposite the primary trajectory. Moreover, it is important to recognize that the expanse of central vision for a target in peripersonal space (~2° through 4°) allows for the attainment of task goals even when a prosaccade reliably undershoots target location (Robinson, 1971).

In contrast to prosaccades, antisaccades entail the intentional process of decoupling the spatial relationship between stimulus and response and require a saccade to a target's mirror-symmetrical location (i.e., 180° spatial transformation). Thus, the study of antisaccades provides insight into how top-down and cognitive control influences the nature of the visual information supporting oculomotor planning and control mechanisms. Indeed, extensive work has shown that antisaccades produce longer reaction times and more directional errors than their prosaccade counterparts (e.g., Fischer and Weber, 1992; Hallett, 1978). These behavioural 'costs' have been tied to a top-down and two-component process requiring the suppression of a stimulus-driven prosaccade (i.e., response suppression) and the *visual* remapping of a target's spatial properties in mirror-symmetrical space (i.e., vector inversion) (for review see Munoz and Everling, 2004). As well, vector inversion does not allow for a target's spatial properties (i.e., extent) to be mediated via direct retinotopic motor maps within the superior colliculus. Rather, the sensorimotor transformations mediating antisaccades requires the activation of an extensive fronto-parietal network (Kimmig et al., 2001; Moon et al., 2007; Nyffeler et al., 2008; Zhang and Barash, 2000) and the mediation of target extent via a *relative* target percept. Thus, it is not surprising that antisaccades exhibit amplitudes that are distinct from their prosaccade counterparts. Specifically, Dafoe et al. (2007) and Evdokimidis et al (2006) found that antisaccades elicit a respective over- and undershooting bias for the 'proximal' and 'distal' targets included within a stimulus-set (Dafoe et al. = 0.5°, 1°, 2°, 4°, and 8°; Evdokimidis et al. = 2°, 3°, 4°, 5°, 6°, 7°, 8°, 9°, and 10°), whereas the central target exhibited a null endpoint bias. One account for the eccentricity-specific bias is that the relative visual information supporting antisaccade sensorimotor transformations may overestimate small eccentricities and underestimate larger eccentricities *within* a stimulus-set (i.e., *the oculomotor range effect hypothesis*: Poulton, 1981; Kapoula, 1985). Alternatively, the indirect mapping between stimulus and response may engender increased uncertainty regarding the spatial parameters of a target and thereby elicit a perceptual averaging strategy. Indeed, perceptual averaging is a well-documented phenomenon wherein participants judge a target property (e.g., extent, size, luminance) based on an abstract approximation of the averaged properties of all stimuli contained within a set (Albrecth et al., 2012; Ariely, 2001; Corbett and Oriet, 2011; Chong and Treisman, 2003, Davarpanah Jazi and Heath, 2014). Thus, a corollary to the *perceptual averaging hypothesis* is that the magnitude and direction (i.e., under- or overshooting) of the endpoint bias associated with the central target in a stimulus-set determines, in part, the bias associated with the near and far targets contained within the set.

Previous studies examining antisaccade amplitudes have used a single stimulus-set (e.g., Dafoe et al., 2007; Evdokimidis et al., 2006) and/or have included a limited number (i.e., ≤ 2) of target eccentricities (Heath et al., 2010; Krappmann et al., 1998; Weiler and Heath, 2012). Moreover, the aforementioned studies were not designed to contrast the theoretical predictions of the range effect and perceptual averaging hypotheses. To address that issue, I adopted a paradigm developed by Kapoula (1985) wherein saccades were performed across separate blocks involving an equal number of targets but differing with respect to the magnitude of their eccentricities (see also Gillen et al. 2013)[1]. In particular, participants completed antisaccades - and complementary prosaccades - to exogenously presented targets located left and right of a central fixation in two blocks. In the *proximal block*, target eccentricities were 3.0°, 5.5°, 8.0°, 10.5° and 13.0°, whereas in the *distal block* target eccentricities were 10.5°, 13.0°, 15.5°, 18.0° and 20.5°. If a range effect characterizes antisaccade endpoints, then the magnitude of the target eccentricities within a block of trials (and not veridical target eccentricity) should influence endpoint bias. More specifically, the target eccentricities common to the proximal and distal blocks (i.e., 10.5° and 13.0°) should produce a respective under- and overshooting of veridical target location: a prediction that is drawn directly from the range effects' assertion that small and large target eccentricities within a stimulus-set are over- and underestimated, respectively (Kapoula, 1985; Poulton, 1981). Alternatively, if antisaccades are governed by perceptual averaging, then the bias associated with the individual targets contained within the proximal and

---

[1] I recognize that Kapoula's (1985) work reported that prosaccades elicit a range effect. Importantly, however, Gillen et al's (2013) re-examination of Kapoula's data provides no evidence of a reliable range effect. As well, Gillen et al's empirical findings provide direct evidence that prosaccades reliably undershot veridical target location independent of the magnitude and range of target eccentricities from within the block in which they are performed. In other words, Gillen et al's findings support extensive evidence that prosaccades are governed by an invariant oculomotor strategy that minimizes saccade flight time (Harris, 1995) or the energy requirements of the task (Becker, 1989).

distal blocks should be influenced by the magnitude and direction of the under- or overshooting bias associated with the block's central target (i.e., the target representing the average amplitude). For example, if the central target in the distal block (i.e., 15.5°) elicits a large magnitude undershooting bias then a perceptual averaging strategy would result in all targets contained within the block similarly demonstrating an undershooting bias. Last, and as mentioned above, I included matched proximal and distal block prosaccades to contrast how direct versus indirect spatial relations between stimulus and response and their respective use of absolute and relative visual information influences endpoint bias.

Methods

Participants

Sixteen participants from the University of Western Ontario community volunteered for the present study (7 females and 9 males; age range = 19-31 years). Participants had normal or corrected-to-normal vision. This research was conducted in accordance with the Declaration of Helsinki and all participants signed a consent form approved by the Office of Research Ethics, The University of Western Ontario.

Apparatus and Procedures

Participants were seated in a comfortable chair in front of a normal table-top (height = 770 mm) with their head placed in a head-chin rest for the duration of data collection. Visual stimuli were presented on a 30-inch monitor (60 Hz, 8 ms response rate, 1,280 x 960 pixels; Dell 3007WFP, Round Rock, TX, USA) centred on participants midline and placed at a viewing distance of 550 mm. The gaze location of the participant's left eye was sampled at 360 Hz using a video-based eye recording system (Eye-Trac6: Applied Sciences Laboratories, Bedford, MA, USA). Two monitors that were visible only to the experimenter provided real-time point of gaze location, trial-by-trial saccade kinematics (e.g., displacement, velocity), and information related to the accuracy of the eye tracking system (i.e., to perform a recalibration when necessary). Computer events and the presentation of visual stimuli were controlled via MATLAB (7.8.0: The MathWorks, Natick, MA, USA) and the Psychophysics Toolbox extensions (ver 3.0; see Brainard, 1997). The lights in the experimental suite were extinguished throughout data collection.

Visual stimuli were presented against a high-contrast black background. The stimuli included a white fixation cross (1°) centered horizontally at the participant's eye level. In addition, yellow crosses served as targets (1°) and were presented 3.0°, 5.5°, 8.0°, 10.5°, 13.0°, 15.5°, 18.0°, and 20.5° left and right of the fixation cross and in the same horizontal plane as the fixation cross. Each trial began with the presentation of the fixation cross which alerted the participant to direct their gaze to its location. When a stable gaze was achieved (±1.5° for 420 ms), a randomized foreperiod (1,000 - 2,000 ms) was introduced during which time the fixation cross remained visible. Following the foreperiod, a target stimulus was briefly (i.e., 50 ms) presented at one of the aforementioned eccentricities and its onset served as the cue to initiate an instructed pro- or antisaccade "as quickly and as accurately as possible". The fixation cross remained visible during target presentation (i.e., no-gap paradigm). Prosaccades required saccades to the veridical target location, whereas antisaccades required saccades mirror-symmetrical to the target location. Each participant completed his or her pro- and antisaccade trials in separate and counterbalanced sessions that were separated by 24 hours. Prior to each session, participants were provided written instructions as to the required task (i.e., pro- vs. antisaccade). As indicated above, targets were presented for 50 ms. The brief presentation represents a classic antisaccade task ensuring that the target was extinguished prior to the completion of response planning; that is, the brief presentation required vector inversion as opposed to a longer presentation period wherein antisaccades could be supported via reorientation of attention from a (visible) target to a homologous region in space.

Within each pro- and antisaccade session, the different target eccentricities were arranged into two separate blocks. The first block involved eccentricities of 3.0°, 5.5°, 8.0°, 10.5°, and 13.0° (i.e., the proximal block), whereas the second block involved eccentricities of 10.5°, 13.0°, 15.5°, 18.0°, and 20.5° (i.e., the distal block). Notably, the 10.5° and 13.0° targets served as common eccentricities in each block. For both the proximal and distal blocks, target eccentricity and visual field (i.e., left vs. right) were randomized, and participants completed 12 trials to each target eccentricity and visual field combination. Thus, each participant completed 240 trials in each of the separate pro- and antisaccade sessions for a total of 480 trials. The proximal block was completed prior to the distal block and was done to match the methods of Kapoula (1985; see also Gillen et al. 2013). As well, the results of a recent study show that block ordering does not influence pro- and antisaccade amplitudes (Gillen and Heath, 2014a).

Data Reduction and Dependent Variable

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 computed similarly via the velocity data. Saccade onset was marked when velocity and acceleration values exceeded 30°/s and $8{,}000°/s^2$, respectively. Saccade offset was marked when saccade velocity fell below a threshold value of 30°/s for 15 consecutive frames (i.e., 42 ms). The dependent variables were saccade amplitude in the primary (i.e., horizontal) movement direction and reaction time (time from stimulus presentation to saccade onset). Main effects and interactions ($p < 0.05$) were decomposed via simple effects and/or power-polynomials (i.e., trend analysis: see Pedhazur, 1997). For example, task (pro-, antisaccade) by target eccentricity interactions were decomposed by: (1) examining the trend (i.e., linear, quadratic etc.) best describing the scaling of pro- and antisaccades to target eccentricity, and (2) contrasting pro- and antisaccades at matched target eccentricities via paired-samples t-tests.

Results

Pro- and antisaccade amplitudes.

My first analyses contrasted pro- and antisaccade amplitudes separately for proximal and distal blocks via 2 (task: pro-, antisaccade) by 5 (target eccentricity: proximal block: 3.0°, 5.5°. 8.0°, 10.5° and 13.0°; distal block: 10.5°, 13.0°, 15.5°, 18.0°, and 20.5°) repeated measures ANOVAs[2]. Results produced main effects for target eccentricity, $Fs(4,60) = 673.12$ and 484.79 for proximal and distal blocks, respectively, $ps < 0.001$, and task by target eccentricity interactions, $Fs(4,60) = 243.80$ and 120.44 for proximal and distal blocks, respectively, $ps < 0.001$. As expected, pro- and antisaccade amplitudes in proximal and distal blocks increased with increasing target eccentricity (only linear effects significant: $Fs(1,15) > 780.00$, $ps < 0.001$). Notably, however, the task by target eccentricity interactions revealed an eccentricity-specific scaling of pro- and antisaccades. Results for the proximal block revealed that antisaccade amplitudes to the 3.0° and 5.5° targets were greater than their prosaccade counterparts, whereas the converse pattern was true for the 10.5° and 13.0° targets (a null difference was observed for

---

[2] Visual space (left, right) was included as an initial variable in our ANOVA model; however, it did not elicit a significant effect or interaction $Fs < 1.72$ (see also Gillen et al., 2013; Heath et al., 2011; Weiler and Heath, 2014). As such, visual space was included as a collapsed factor in my main analyses.

the 8.0° target) (Figure 1: see Table 1 for post hoc contrasts). Second, results for the distal block showed that anti- and prosaccade amplitudes to the 10.5° target did not reliably differ, whereas antisaccade amplitudes to the remaining targets (i.e., 13.0°, 15.5°, 18.0°, and 20.5°) were less than their prosaccade counterparts (Table 1). Additionally, I computed participant-specific slopes relating pro- and antisaccade amplitudes to target eccentricity for the proximal and distal blocks and examined those data via 2 (task: pro, antisaccade) by 2 (block: proximal, distal) repeated measures ANOVA. Results revealed a main effect of task, such that antisaccade slopes (0.32°, $CI_{95\%}= 0.12$) were shallower than prosaccades (0.93°, $CI_{95\%}= 0.12$), $F(1,15) = 493.98$, $p < 0.001$[3]. However, and as can be seen in Figure 1, the results did not yield a reliable effect for block or a task by block interaction, $Fs < 1$. Thus, prosaccade amplitudes scaled in relation to veridical target amplitude to a greater extent than antisaccades: a result that was not modulated across the proximal and distal blocks.

---

[3] I used Loftus and Masson's (1994) method for computing confidence intervals in a within-participant design.

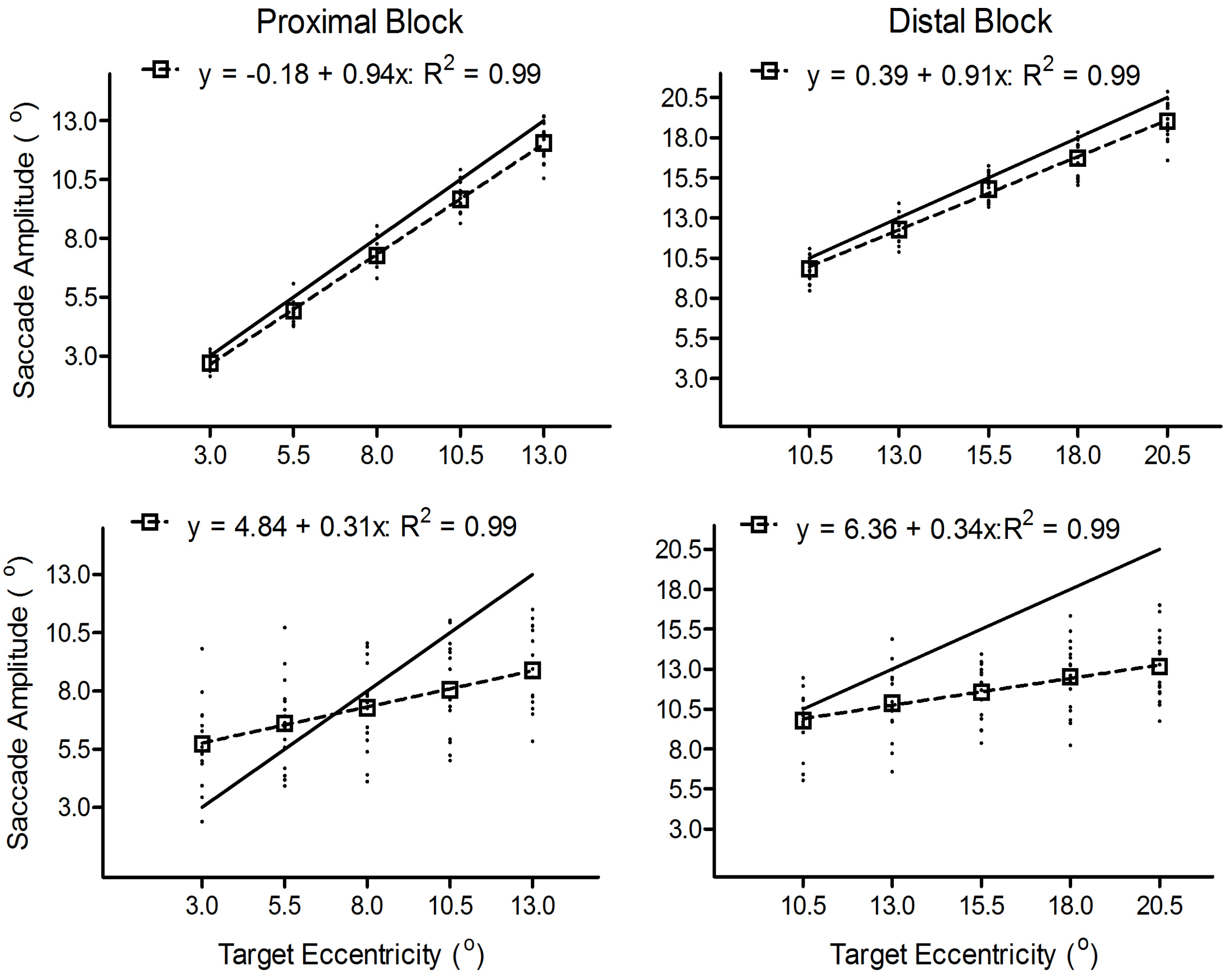


Figure 1. The top and bottom panels show pro- and antisaccade amplitudes (°), respectively, as a function of target eccentricity in the proximal and distal blocks. For each panel, filled circles represent the mean value for individual participants and the open squares represents the group mean. The hatched line represents the linear regression of mean amplitude to target eccentricity and the regression equation and associated R^2 value is presented at the top of each panel. The solid line in each panel represents veridical target amplitude.

Target Eccentricity (°)	Mean Saccade Amplitude (°)		t-ratio	P-value*
	Prosaccade	*Antisaccade*		
Proximal				
3.0	2.70 (0.20)	5.74 (0.32)	-7.29	0.001
5.5	4.91 (0.20)	6.62 (0.32)	-4.02	0.001
8.0	7.29 (0.20)	7.28 (0.32)	0.02	0.986
10.5	9.67 (0.20	8.06 (0.32)	3.61	0.003
13.0	12.05 (0.20)	8.90 (0.32)	8.76	0.001
Distal				
10.5	9.84 (0.24)	9.77 (0.40)	0.19	0.853
13.0	12.27 (0.24)	10.89 (0.40)	3.14	0.007
15.5	14.79 (0.24)	11.56 (0.40)	9.33	0.001
18.0	16.74 (0.24)	12.52 (0.40)	9.53	0.001
20.5	19.01 (0.24)	13.17 (0.40)	12.43	0.001

Table 1: Mean saccade amplitude (°) and 95% confidence intervals (in parentheses) for pro- and antisaccade amplitudes as a function of target eccentricity in proximal and distal blocks. Additionally, t-ratios and associated p-values are presented for paired-sample contrasts of pro- and antisaccades at each target eccentricity.

Note (*): Confidence intervals were computed as per Loftus and Masson (1994) and were based on the mean squared error for target eccentricity determined via separate ANOVAs for task and block. As well, exact p-values are reported for non-reliable contrasts, whereas reliable effects are reported to the nearest digit less than 0.01.

The preceding analyses examined the scaling of pro- and antisaccades to target eccentricity and contrasted each task at matched target eccentricities. In the following analyses, I sought to specifically determine whether pro- and antisaccades for each target eccentricity and block combination elicited an under- or overshooting bias. As such, I contrasted mean pro- and antisaccade amplitudes for each target eccentricity to veridical target location via single-sample t-statistics. Figure 2 shows that prosaccade amplitudes in proximal and distal blocks undershot veridical target location across each target eccentricity, $ts(15) < -3.71$, $ps < 0.01$. In terms of antisaccades, results for the proximal block showed that the 3.0° and 5.5° targets overshot veridical target location, $ts(15) = 6.19$ and 2.36, and $ps = 0.002$ and 0.03, respectively, for the 3.0° and 5.5° targets, whereas the 8.0° target did not reliably differ from veridical, $t(15) = -1.58$, $p = 0.14$. In turn, the 10.5° and 13.0° target eccentricities undershot veridical target location ($ts(15) < -4.95$, $ps < 0.001$). Results for distal block antisaccades showed that amplitudes for the 10.5° target did not reliably differ from veridical, $t(15) = -1.53$, $p = 0.15$, whereas the remaining eccentricities (13.0°, 15.5°, 18.0°, and 20.5°) undershot veridical target location, $ts(15) < -3.86$, $ps < 0.002$.

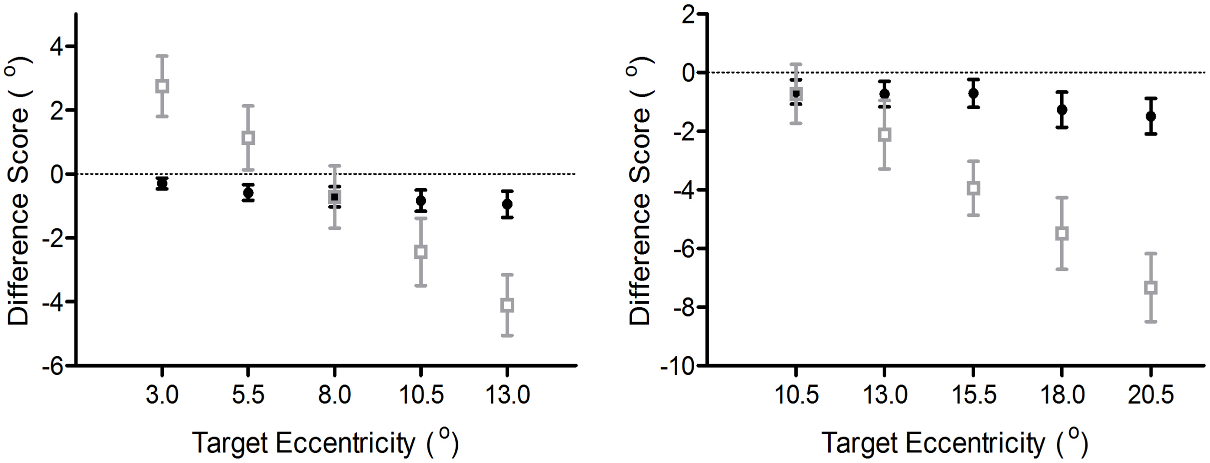


Figure 2. Pro- (filled circles) and antisaccade (open squares) amplitude difference scores (°: prosaccade [or antisaccade] minus veridical target amplitude) as a function of target eccentricity for proximal (left) and distal (right) blocks. The error bars for difference scores represent eccentricity-specific 95% confidence intervals (Cumming, 2013). The absence of overlap between a confidence interval and zero provide a graphical depiction of a reliable under- or overshooting bias, and can be interpreted independent of a test of the null hypothesis (Cumming, 2013).

Pro- and antisaccade reaction times and their relationship to saccade amplitude.

Reaction times were examined via the same ANOVA model used for saccade amplitudes. Results for the proximal and distal blocks elicited main effects for task, Fs(1,15) = 77.56 and 91.47 for proximal and distal blocks, respectively, ps< 0.001, such that antisaccade reaction times (proximal block = 317 ms, $CI_{95\%}$= 40; distal block = 286 ms, $CI_{95\%}$= 29) were longer than prosaccades (proximal block = 212 ms, $CI_{95\%}$= 40, distal block = 204 ms, $CI_{95\%}$= 29)[4]. As well, Figure 3 shows that the proximal block elicited a main effect for target eccentricity, Fs(1,15) = 9.75, $p < 0.001$, indicating that reaction times for the 3.0° target were longer than the other eccentricities within the block (significant quadratic effect: F(1,15) = 24.20, $p < 0.001$).

---

[4] Within-participant confidence intervals were computed separately for proximal and distal blocks via the mean squared error term for task (Loftus and Masson, 1994). For that reason, the confidence intervals for proximal pro- and antisaccades are the same as the confidence intervals for distal block pro- and antisaccades.

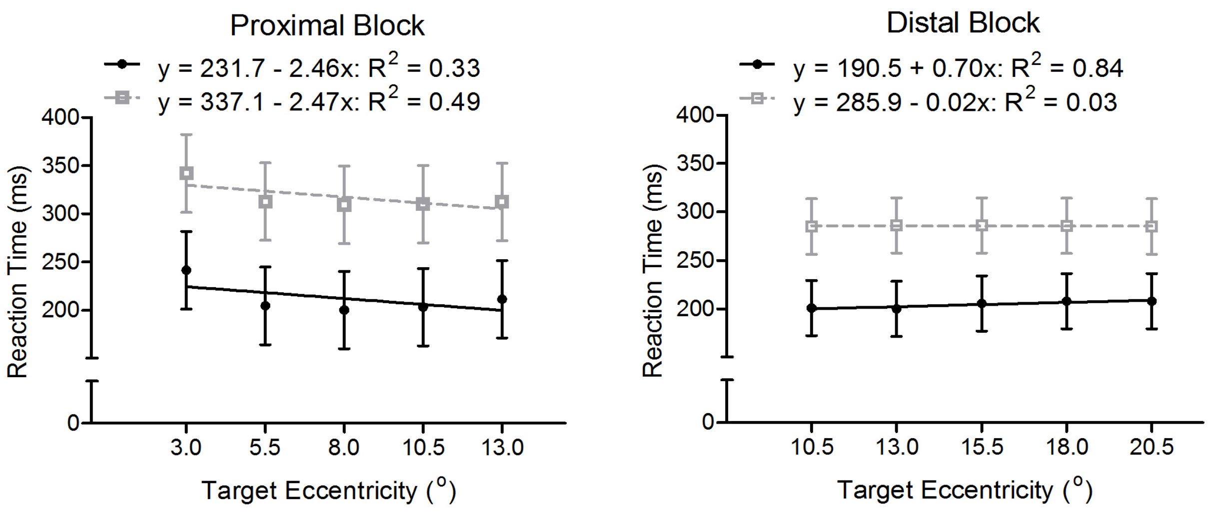


Figure 3. Mean pro- (filled circles) and antisaccade (open squares) reaction times (ms) for proximal (left) and distal (right) blocks as a function of target eccentricity. In addition, the panels present linear regression equations for each task and block combination. Error bars represent within-participant 95% confidence intervals (Loftus and Mason, 1994).

I employed correlation analyses relating reaction time and saccade amplitude to determine if target eccentricity effects were related to a speed-accuracy trade-off. Thus, I computed correlation coefficients based on mean participant pro- and antisaccade amplitude and reaction time values separately for each target eccentricity within the proximal and distal blocks. Table 2 shows that prosaccades elicited a null relationship for each target eccentricity. In turn, antisaccades elicited a null relationship for each target eccentricity with the exception that the 10.5° and 13.0° targets in the proximal block yielded a decrease in reaction times with increasing amplitude (r = -0.56 and -0.58, for the 10.5° and 13.0° targets respectively, ps = 0.02). Thus, findings suggest that planning times were neither consistently nor reliably related to saccade amplitudes.

Target Eccentricity (°)	Prosaccade		Antisaccade	
	R	*p*	*R*	*p*
Proximal				
3.0	0.02	0.96	-0.46	0.07
5.5	-0.44	0.09	-0.36	0.17
8.0	-0.25	0.34	-0.33	0.21
10.5	0.01	0.98	-0.56	0.02
13.0	0.02	0.95	-0.58	0.02
Distal				
10.5	-0.41	0.12	-0.44	0.09
13.0	-0.37	0.15	-0.29	0.28
15.5	-0.17	0.53	-0.22	0.42
18.0	0.09	0.73	-0.16	0.54
20.5	0.01	0.98	-0.10	0.71

Table 2. Correlation coefficients (R) and p-values for the relationship between reaction time and saccade amplitude for pro- and antisaccades as a function of each target eccentricity in the proximal and distal blocks.

Discussion

The primary objective of this study was to determine whether a range effect or a strategy of perceptual averaging governs the relative visual percept mediating antisaccade sensorimotor transformations. Prior to addressing that objective, I first describe the results for pro- and antisaccade reaction times and the general properties of prosaccade amplitudes.

Pro- and antisaccade reaction times and the effect of target eccentricity

Antisaccades produced longer reaction times than their prosaccade counterparts. This well-documented finding has been linked to the time-consuming and top-down demands associated with suppressing a stimulus-driven prosaccade (i.e., response suppression) and inverting a target's coordinate to mirror-symmetrical space (i.e., vector inversion) (for review see Munoz and Everling, 2004). As well, the reaction time analysis showed that pro- and antisaccades in the distal block did not vary with target eccentricity; however, the 3.0° target in the proximal block produced longer reaction times (pro- and antisaccades) than the other target eccentricities within the block. This result has been reported elsewhere (Bell et al., 2000; Dafoe et al., 2007; Kalesnykas and Hallett, 1994) and has been attributed to a continuum of saccade-related and fixation neurons across the superior colliculus' motor map. In particular, targets proximal to a fixation create conflicting saccade generation and fixation commands that require additional time to resolve (Bell et al., 2000).

Prosaccades amplitudes are characterized by an invariant undershooting bias.

Prosaccades (see below for antisaccades) were completed across separate blocks that contained an equal number of target eccentricities but differed with respect to their magnitudes. In particular, participants completed prosaccades to targets presented in proximal (3.0°, 5.5°, 8.0°, 10.5° and 13.0°) and distal (10.5°, 13.0°, 15.5°, 18.0° and 20.5°) blocks. Results shown in

Figures 1 and 2 indicate that proximal and distal block prosaccades across each target eccentricity elicited a reliable undershooting bias: a finding replicating earlier work by my group (Gillen et al., 2013). These results provide no evidence to support a range effect. Indeed, had a range effect influenced prosaccades then the target eccentricities common to each block (i.e., 10.5° and 13.0°) would have produced an under- and overshooting bias in the proximal and distal blocks, respectively. Further, that amplitudes were not influenced by the magnitude of the endpoint bias for the central target in each block (i.e., proximal block = 8.0°, distal block = 15.5°) indicates that prosaccades were not influenced by a strategy of perceptual averaging. These findings are in keeping with evidence that prosaccades operate independent of relational target properties; that is, prosaccades are mediated via absolute visual information (i.e., retinotopic motor maps in superior colliculus: see Wurtz and Albano, 1980). Moreover, my findings support the contention that prosaccades are governed by an oculomotor strategy that minimizes movement time (Harris, 1995) and/or the energy requirements of the response (Becker, 1989).

It is possible that online target vision and/or a putative speed-accuracy tradeoff influenced the prosaccade undershooting bias. Indeed, because the present study entailed a brief (i.e., 50 ms) target presentation it is possible that the undershooting bias observed here may relate to the absence of target vision for on- or offline error reduction (Gaveau et al., 2003; Harris and Wolpert, 1998; Heath et al., 2011). Although the design of the present study precludes a direct examination of this issue, earlier work by my group using the same methodology as used here demonstrated that prosaccade undershooting is independent of target vision (Gillen et al., 2013). As well, a number of studies have shown that primary and secondary prosaccades to visual targets produce an undershooting bias (Becker and Fuchs, 1969; Gerardin et al., 2011). As such, evidence suggests that the prosaccade undershooting bias is independent of concurrent target vision. In terms of a speed-accuracy trade-off, some work has shown that response planning times are related to saccade endpoint bias (Kowler and Blaser, 1995). Notably, however, the results presented here indicated a null relationship between reaction time and amplitude across each target eccentricity (see also Gillen et al., 2013). In other words, prosaccade planning times were independent of the target eccentricities within the block of trials in which they were performed.

Antisaccades amplitudes are characterized by perceptual averaging.

Figures 1 and 2 show that proximal block antisaccades to the 3.0° and 5.5° target eccentricities (i.e., the ‘proximal’ targets within the block) elicited an overshooting bias, whereas the 10.5° and 13.0° target eccentricities (i.e., the ‘distal’ targets within the block) produced an undershooting bias (the central 8.0° target did not produce a reliable bias). As outlined in the Introduction, Dafoe et al. (2007) and Evdokimidis et al. (2006) also reported that the 'proximal' and 'distal' targets in their stimulus-sets elicited an over- and undershooting bias, respectively, and that their central targets did not differ from veridical. Thus, results from the proximal block as well as previous work provides tentative evidence that the relative and perceived target representation supporting antisaccades engenders a range effect. Of course, if a range effect represents a systematic feature of antisaccades then the target-specific over- and undershooting bias should similarly characterize distal block antisaccades. Notably, however, the distal block showed that the 10.5° target eccentricity (i.e., the ‘nearest’ target in the block) did not reliably differ from veridical target location, whereas the remaining eccentricities (i.e., 13.0°, 15.5°, 18.0° and 20.5°) produced a systematic undershooting bias. As well, although the 10.5° target did not demonstrate a reliable bias, Figure 2 shows that its mean amplitude was less than veridical.

Furthermore, the target eccentricities common to the proximal and distal blocks (i.e., 10.5° and 13.0°) produced an undershooting bias independent of the block in which they were performed (see above for 10.5° target in the distal block). This represents a salient finding because it directly counters the range effect hypothesis' assertion that the target eccentricities common to the proximal and distal blocks respectively under- and overshot veridical target location.

As an alternative to the range effect, perceptual averaging contends that the stimuli contained within a set are most reliably represented as a statistical summary (Ariely, 2001: see also Chong and Treisman, 2003; Corbett and Oriet, 2011; Davarpanah Jazi and Heath, 2014). For example, Ariely reported that participants were unable to reliably identify the metrical property (i.e., circle size) of individual stimuli within a set but were able to represent the average of the set. Thus, a corollary prediction drawn from the perceptual averaging literature contends that the relative nature of the visual information supporting antisaccades is, in part, based on a statistical summary (i.e., the average) of the combined target percepts included in a set. In the context of the present investigation then, perceptual averaging holds that bias associated with the percept for the central target (i.e., the target representing the statistical summary) determines the direction and magnitude of the bias to individual targets in the block. I believe that the antisaccade results support perceptual averaging for three reasons. First, the proximal block showed a null endpoint bias for the central target (i.e., 8.0°), whereas the 'proximal' (i.e., 3.0° and 5.5°) and 'distal' (10.5° and 13.0°) targets in the block respectively over- and undershot veridical target location. In turn, the distal block produced a reliable - and large magnitude (see Figure 1) - undershooting bias that characterized not only the central target (15.5°) but also the other targets (10.5°, 13.0°, 18.0° and 20.5°) within the block (see above for description of the 10.5° target). Second, Figure 1 shows that slopes relating target eccentricity to saccade amplitude were shallower for antisaccades than prosaccades: a finding that was consistent across proximal and distal blocks. Third, proximal and distal block antisaccades produced equivalent slopes. Taken together then, results show that: (1) the scaling of response amplitudes to perceived target eccentricity was independent of the magnitude of target eccentricities included in a block, and (2) the direction and magnitude of endpoint bias for individual targets was influenced by the bias (or absence thereof) associated with the central target within the block. In other words, the sensorimotor transformation supporting antisaccades are based on a statistical summary of the range of perceived amplitudes included in a stimulus-set.

Two issues require addressing. The first issue relates to why antisaccade amplitudes scaled in relation to target eccentricity. Indeed, one could argue that perceptual averaging should result in comparable amplitudes for each target eccentricity within a set. It is, however, important to recall that although a statistical summary provides the most *reliable* and predominant information to represent a set of items, perceptual averaging contends that an individual target property can also influence (albeit to a lesser extent) the formation of a visual percept. Certainly the modulation of antisaccade endpoints about the central target in each block and the equivalent slopes for proximal and distal block antisaccades support such an argument. The second issue relates to why the antisaccade undershooting bias increased with the more distal target eccentricities contained within a block (see also Evdokimidis et al., 2006; Dafoe et al., 2007). To begin, I note that such a finding is distinct from the theoretical prediction of the range effect. Recall that Poulton (1981) asserted that a range effect manifests as a respective over- and undershooting bias for the ‘proximal’ and ‘distal’ targets within a block (see also Kapoula, 1985). In contrast, the present results require an account for the monotonic decrease in antisaccade amplitudes with increasing target eccentricity. Additionally, the bias cannot be attributed to a difficulty detecting a briefly presented peripheral target given that prosaccades did not demonstrate a similar effect (see *Prosaccades amplitudes are characterized by an invariant undershooting bias).* Instead, I propose that the visual percept mediating antisaccades is compressed as a function of target eccentricity. In support of this view, memory-guided prosaccades (Sheth and Shimojo, 2001), propointing (Heath, 2005; Lemay and Proteau, 2001; Westwood et al., 2003) and walking responses (Knapp and Loomis, 2004) produce a monotonic rise in undershooting bias with increasing target eccentricity: a finding reminiscent of Helmholtz's (1962) seminal report that the perceived length of a peripherally presented line is inversely proportional to its eccentricity from a central fixation (see also Viguier et al., 2001). Moreover, increasing target eccentricity is tied to increased noise in perceived target location (i.e., Weber's law: see Baird and Noma, 1978). Thus, the top-down nature of antisaccades may have produced a compression of perceived target location that was amplified with increasing target eccentricity. It is also worthy to note that visual compression provides parsimonious explanation as to why antisaccades to the central target in the proximal block (8.0°) did not differ from veridical target location, whereas the central target in the distal block (15.5°) produced an undershooting bias. Indeed, it is proposed that the proximal block was associated with a reduction in visual compression and thereby rendered a statistical summary that provided an accurate percept for the central target (see also Dafoe et al., 2007; Evdokimidis et al., 2006).

A final question relates to the neural basis of perceptual averaging. To my knowledge, neuroimaging and electrophysiological work has not examined the putative neural mechanisms associated with the aforementioned hypothesis. It is, however, possible to derive a framework based on the distractor literature. Indeed, it has been shown that visual and motor signals related to target and distractor are combined to produce a spatially averaged prosaccade amplitude

(Walker et al., 1997). Moreover, non-human primate work has linked the spatial averaging of prosaccades to a spatial combination of target and distractor related visual and preparatory signals within the superior colliculus (Dorris et al., 2007). By extension then, it is possible that the top-down control of antisaccades drives a spatial averaging and leads to the integration of high- and low-level signals in the production of a visual percept (Cisek, 2007). Of course, I am aware that such a proposal awaits formal evaluation; however, it does offer a framework for understanding how high-level plans influence the representation of a visual percept (He and Kowler, 1989).

Conclusions

The present results show that endpoint bias for the central target in a block of antisaccades determines the direction and magnitude of the bias associated with the perceived location of individual targets. Based on this result, I propose that the relative and perceived nature of the visual information supporting antisaccades results in the mediation of endpoints via perceptual averaging.

Experiment Two

Introduction

The most frequent motor act that humans perform is an eye movement that brings the fovea to a target of interest (i.e., prosaccade). In fact, an individual can make upwards of 100,000 prosaccades on a daily basis (Irwin and Carlson-Radvansky, 1996). Notably, the direct spatial relations between stimulus and response permit absolute visual information to mediate prosaccade sensorimotor transformation via retinotopically organized motor maps within the superior colliculus (Wurtz and Albano, 1980). In spite of the direct spatial relations, primary and secondary (i.e., corrective) prosaccades typically undershot veridical target location (Abrams et al., 1989; Becker and Fuchs, 1969; Deubel et al., 1986; Gillen et al., 2013; Prablanc and Jeannerod, 1975; Robinson, 1964; Weber and Daroff, 1971). In particular, prosaccades exhibit a 10% undershooting bias that is thought to reflect an invariant control strategy that minimizes saccade flight time (i.e., saccadic flight time hypothesis: Harris, 1995) and/or the energy requirements of the response (i.e., energy minimization hypothesis: Becker, 1989). Indeed, undershooting represents an optimal strategy for prosaccades because it reduces the potential of an overshooting error and the time-consuming and energy-demanding requirements of implementing a corrective response in a direction opposite the primary saccade (Robinson, 1973; see also Elliott et al., 2004).

In contrast to prosaccades, antisaccades require decoupling the spatial relations between stimulus and response and implementing a saccade to a target's mirror-symmetrical location (i.e., 180° spatial transformation). As such, antisaccades provide a framework for understanding how top-down and cognitive control influences motor output. Extensive work has shown that antisaccades produce longer reaction times (RT) than prosaccades (Fischer and Weber, 1992; Hallett, 1978) - a behavioural 'cost' that has been related to the time-consuming processes of suppressing a stimulus-driven prosaccade (i.e., response suppression) and the *visual* remapping of a target's spatial properties (i.e., vector inversion) (for extensive review see Munoz and Everling, 2004). Moreover, it is not surprising that antisaccades are less accurate and more variable than prosaccades (Dafoe et al., 2007; Evdokimidis et al., 2006; Heath et al., 2011; Krappmann et al., 1998); after all, decoupling the spatial relations between stimulus and response does not permit sensorimotor transformation via retinotopically organized motor maps in the superior colliculus. Instead, vector inversion requires that a *relative* target percept support sensorimotor transformations. In other words, the top-down control of antisaccades influences the nature of the visual information supporting motor output.

As mentioned above, prosaccades exhibit an invariant undershooting bias; however, antisaccades elicit a target-specific bias based on the range of eccentricities included within a stimulus-set. For example, Dafoe et al. (2007) and Evdokimidis et al. (2006) reported that the 'proximal' and 'distal' targets within their stimulus-sets respectively over- and undershoot veridical target location, whereas the central targets in their stimulus sets exhibited a null bias (Dafoe et al. 0.5°, 1.0°, 2.0°, 4.0° and 8.0°; Evdokimidis et al. 2.0°, 3.0°, 4.0°, 5.0°, 6.0°, 7.0°, 8.0°, 9.0° and 10.0°) (see also Bell et al., 2000; Heath et al., 2011; Weiler et al., 2011). One interpretation of this finding is that the visual percept supporting antisaccades overestimates 'proximal' targets and underestimates 'distal' targets *within* a stimulus-set (i.e., the range effect hypothesis: see Poulton, 1981; Kapoula, 1985). Experiment One of my thesis sought to test the range effect hypothesis by having participants antisaccade in separate blocks (i.e., proximal and distal) that contained the same number of target eccentricities but differed with respect to their magnitudes. In the proximal block, target eccentricities were 3.0°, 5.5°, 8.0°, 10.5° and 13.0°, whereas in the distal block target eccentricities were 10.5°, 13.0°, 15.5°, 18.0° and 20.5°. In line with Dafoe et al. and Evdokimids et al., the proximal block showed that the 'proximal' (i.e., 3.0°, 5.5°) and 'distal' (i.e., 10.5°, 13.0°) targets respectively over- and undershot veridical target location, whereas responses to the central target (8.0°) did not reliably differ from veridical. In contrast, the distal block showed an undershooting bias that was independent of target eccentricity. Most notably, that the target eccentricities common to each block (i.e., 10.5° and 13.0°) produced an undershooting bias directly counters the range effect hypothesis' assertion that the 'proximal' and 'distal' targets within a stimulus-set respectively over- and undershoot veridical target location. As such, I proposed that the visual percept supporting antisaccades is based, in part, on a statistical summary of the perceived target eccentricities included within in a stimulus-set (e.g., *perceptual averaging hypothesis*). In particular, the perceptual averaging hypothesis asserts that the properties of a stimulus-set (i.e., extent, size, luminance) are rapidly summarized without precise information about individual targets (Albrecht et al., 2012; Ariely, 2001; Chong and Treisman, 2003; Davarpanah Jazi and Heath, 2014). For example, Ariely reported that although participants were unable to identify whether an individual circle was a member of a stimulus-set, they were able to accurately represent the average size of all circles included in the set. Thus, perceptual averaging provides a parsimonious account for the findings from the proximal and distal blocks because it contends that the percept for the central target in each stimulus-set (i.e., the statistical summary) determines the *direction* and *magnitude* of the endpoint bias associated with individual targets within the set.

The goal of the present investigation was to test the assertion that perceptual averaging provides a direct account for the nature of the visual information supporting antisaccades. To accomplish that objective, participants completed antisaccades - and complementary prosaccades - to three target eccentricities (10.5°, 15.5°, and 20.5°) located left and right of a central fixation in conditions that differed with regard to the frequency that individual target eccentricities were presented. In the *control condition*, target eccentricities were presented with equal frequency. In the *proximal-weighting* condition the ‘proximal’ target eccentricity (10.5°) was presented five times as often as the other target eccentricities, whereas in the *distal-weighting* condition the ‘distal’ target eccentricity (20.5°) was presented five times as often as the other target eccentricities. Of course, I am aware that previous work has shown that probabilistic information related to the spatial location of a target (i.e., left or right and/or above or below a central fixation) influences pro- and antisaccade reaction times – a finding that has been linked to improved target detection and increased pre-saccadic collicular buildup neuron firing rates in the receptive field of the frequently presented target (Dorris and Munoz, 1998; Geng and Behrmann, 2005; Liu et al., 2010; see also Gmeindl et al. 2005). Notably, however, the current study differs from previous work in that I was interested in determining whether the frequent presentation of a target eccentricity influences the statistical summary used to represent individual targets within a stimulus-set. Indeed, if the perceptual averaging hypothesis is correct, then the proximal- and distal-weighting conditions should render statistical summaries - and associated visual percepts - that are biased in the direction of the most frequently presented target. More specifically, it is predicted that amplitudes for each target eccentricity in the proximal- and distal-weighting conditions will under- and overshot, respectively, their matched target eccentricities in the control block. Last, and as indicated above, I included prosaccades to the same target eccentricities and conditions as used for antisaccades. Prosaccades were included to demonstrate that responses mediated via absolute visual information are refractory to context-dependent manipulations (i.e., frequency) of target eccentricity.

Methods

Participants

Twenty participants from the University of Western Ontario community volunteered for the present study (11 females and 9 males; age range = 19-29 years). All participants had normal or corrected-to-normal vision. This research was conducted in accordance with the Declaration of Helsinki and all participants signed a consent form approved by the Office of Research Ethics, The University of Western Ontario.

Apparatus and Procedures

Participants sat comfortably at a normal tabletop (height = 770mm) with their head placed in a head-chin rest for the duration of data collection. Visual stimuli were presented on a 30-inch monitor (60 Hz, 8 ms response rate, 1,280 x 960 pixels; Dell 3007WFP, Round Rock, TX, USA) located at a viewing distance 550 mm from the participant and centered on their midline. The gaze location of the participant's left eye was sampled at 360 Hz using a video-based eye recording system (Eye-Trac6: Applied Sciences Laboratories, Bedford, MA, USA). Prior to data collection, a nine-point calibration of the participant's viewing space was completed. Two computer monitors that were visible only to the experimenter provided real-time point of gaze information, trial-by-trial saccade kinematics (e.g., displacement, velocity), and information related to the accuracy of the eye tracking system (i.e., to perform a recalibration when necessary). Computer events and the presentation of visual stimuli were controlled via MATLAB (7.8.0: The Math Works, Natick, MA, USA) and the Psychophysics Toolbox extensions (ver 3.0; see Brainard, 1997). The lights in the experimental suite were extinguished throughout data collection.

Visual stimuli were presented against a high-contrast black background and included a white fixation cross (1°) and yellow target crosses (1°) presented 10.5° (i.e., ‘proximal’ target), 15.5° (‘middle’ target), and 20.5° (i.e., ‘distal’ target) left and right of fixation. Stimuli were located on the horizontal meridian and at the participant’s eye level. Each trial began with the presentation of the white fixation cross which alerted the participant to direct their gaze to its location. After a stable fixation was achieved (±1.5° for 420ms), a randomized foreperiod (1,000 – 2000 ms) was introduced during which time the fixation cross remained visible. Following the foreperiod, a target stimulus was briefly (i.e., 50 ms) presented and its onset cued participants to pro- or antisaccade "as quickly and as accurately as possible." The fixation cross and target were concurrently extinguished (i.e., no-gap paradigm). Prosaccades required a response to veridical target location, whereas antisaccade required a response mirror-symmetrical to the target. Prior to each block participants received written instructions related to the nature of the task (prosaccade, vs. antisaccade). The 50 ms target presentation was used so that the target was unavailable throughout response planning and execution – a method requiring visual vector inversion for antisaccades as opposed to a continuous target presentation wherein antisaccades may be mediated via an obligatory shift of attention from the target to a homologous region in space (Olk and Kingstone, 2003).

Pro- and antisaccades were completed across conditions that differed with respect to the weighting of target eccentricity. In the *control condition*, an equal number of trials (i.e., 10) were completed to each target eccentricity by visual space combination (i.e., 60 pro- and antisaccade trials). In the *proximal-weighting* condition, the ‘proximal’ target (i.e., 10.5°) was presented five times as often as the ‘middle’ (i.e., 15.5°) and ‘distal’ (i.e., 20.5°) target eccentricities. Thus, 50 trials were completed to each left and right visual field ‘proximal’ target, and 10 trials were completed to each left and right visual field ‘middle’ and ‘distal’ target. In the *distal-weighting* condition, the ‘distal’ target was presented five times as often as the ‘proximal’ and ‘middle’ target eccentricities. As such, 50 trials were completed to each left and right visual field ‘distal’ target, whereas 10 trials were completed to each left and right visual field ‘proximal’ and ‘middle’ target. Therefore, for each weighting condition participants performed 140 pro- and antisaccade trials.

The three weighting conditions (i.e., control, proximal-weighting, distal-weighting) were completed in separate sessions with each separated by a minimum of 24 hours. I employed the separate sessions in order to minimize eye strain and mental fatigue. All participants performed the control condition during the first session, whereas the ordering of the proximal- and distal-weighting conditions was counterbalanced across the remaining sessions. The ordering of pro- and antisaccade blocks within each session was counterbalanced, and for all blocks target presentation (visual space by target eccentricity) was randomized.

Data Analysis

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 data. Saccade onset was marked when velocity and acceleration values exceeded 30°/s and $8{,}000/s^2$, respectively. Saccade offset was marked when saccade velocity fell below a threshold value of $30^o/s$ for 15 consecutive frames (i.e., 42 ms).

Dependent Variables and Statistical Analyses

The dependent variables were saccade amplitude in the primary (i.e., horizontal) movement direction and reaction time (RT: time from stimulus presentation to saccade onset). Post hoc decompositions for pro- and antisaccades were completed via paired-samples t-tests, whereas the decomposition of target eccentricity was computed via power polynomials (i.e., trend analysis: see Pedhazur, 1997). Only significant effects are reported below ($p < 0.05$).

Results

Pro- and antisaccade amplitudes

My first analysis examined amplitudes via 2 (task: pro-, antisaccade) by 2 (visual field: left, right) by 3 (weighting condition: control condition, proximal-weighting, distal-weighting) by 3 (target eccentricity: ‘proximal’ [10.5°], ‘middle’ [15.5°], ‘distal’ [20.5°]) repeated measures ANOVA. Results produced main effects for task, $F(1,19) = 57.04$, $p < 0.001$, weighting condition, $F(2,38) = 17.48$, $p < 0.001$, target eccentricity, $F(2,38) = 951.05$, $p < 0.001$, and interactions involving task by weighting condition, $F(2,38) = 20.36$, $p < 0.001$, and task by target eccentricity, $F(2,38) = 298.16$, $p < 0.001$. In terms of the task by weighting condition interaction, antisaccade, $F(2,38) = 24.46$, $p < 0.001$, but not prosaccade, $F(2,38) = 0.72$, $p = 0.50$, amplitudes were reliably influenced by the different weighting conditions. In particular, Figures 4 and 5 show that antisaccade amplitudes for the proximal-weighting condition were less than the control condition ($t(19) = -3.75$, $p < 0.001$), whereas amplitudes for distal-weighting condition were greater than the control condition ($t(19) = 6.24$, $p < 0.001$). In other words, antisaccade amplitudes scaled in relation to the most frequently presented target included in a block. In terms of the task by target eccentricity interaction, pro- and antisaccades amplitudes increased in relation to increasing target eccentricity (only linear effects significant: $Fs(1,19) = 3207.31$ and 140.57, respectively for pro- and antisaccades, $ps < 0.001$). To further decompose the interaction, I first contrasted pro- and antisaccade amplitudes separately for matched target eccentricities and subsequently computed participant-specific slopes relating pro- and antisaccade amplitudes to target eccentricity. Pro- and antisaccade amplitudes to the 'proximal' target did not reliably differ, $t(19) = -0.50$, $p = 0.62$; however, antisaccade amplitudes to the 'middle' and 'distal' targets were less than their prosaccade counterparts ($ts(19) > -7.65$, $ps < 0.001$). Additionally, antisaccades produced a shallower slope (0.35°, $CI_{95\%} = 0.06$) than prosaccades (0.89°, $CI_{95\%} = 0.06$), $t(19) = 19.14$, $p < 0.001$ (Figure 4)[5].

---

[5] Here and elsewhere confidence intervals were computed as a function of within-participant variability (Loftus and Masson, 1994).

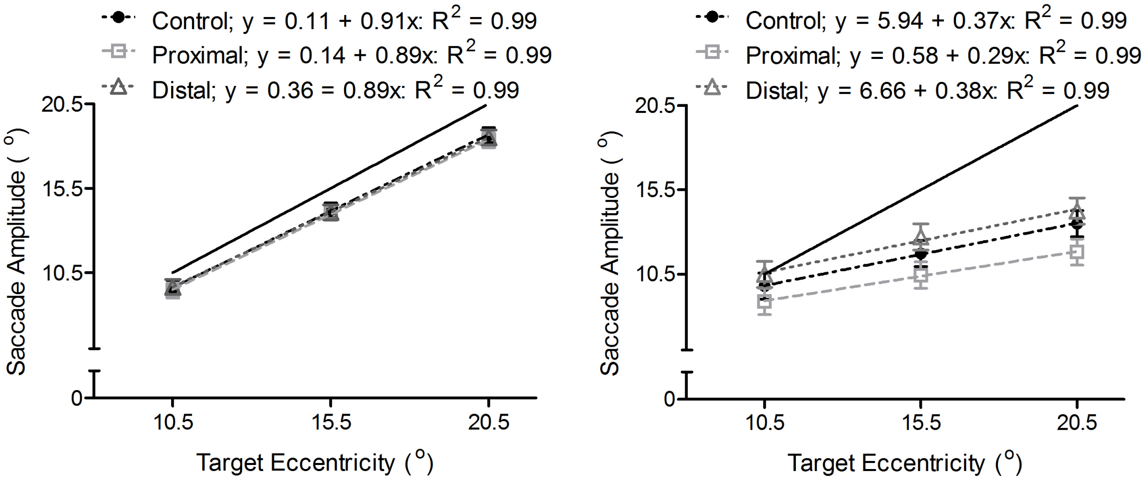


Figure 4. Mean pro- (left panel) and antisaccade (right panel) amplitudes (°) as a function of weighting condition and target eccentricity and their respective linear regression equations. Black closed circles, light grey open squares, and dark grey open triangles represent control, proximal- and distal-weighting conditions, respectively. The solid line in each panel represents veridical target location, whereas the hatched lines represent the linear regression for each weighting condition to target eccentricity. Error bars represent the 95% within-participants confidence intervals (Loftus and Masson, 1994).

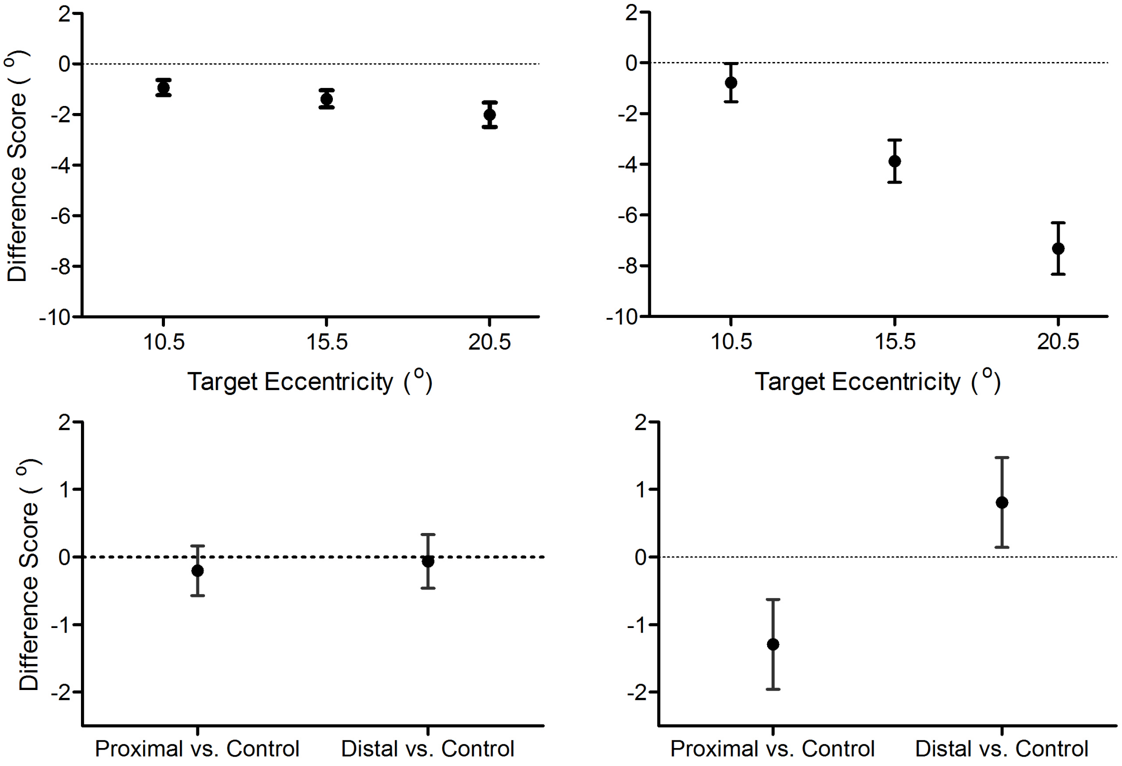


Figure 5. The top panels depict mean target eccentricity-specific differences scores (°: amplitude minus veridical target location) for pro- (left panel) and antisaccades (right panel). The bottom panels depict weighting-condition specific difference scores (°: proximal-weighting condition minus control condition; distal-weighting condition minus control condition) computed separately for pro- (left panel) and antisaccades (right panel). For all panels, errors bars represent 95% confidence intervals. The absence of overlap between error bars and zero (i.e., the horizontal dotted line) represents a reliable difference that can be interpreted inclusive to a test of the null hypothesis (Cumming, 2013).

Figure 4 provides qualitative evidence that pro- and antisaccades across each block and weighting condition undershot veridical target location. To directly address this issue, the top panel of Figure 5 presents difference scores relating pro- and antisaccade amplitudes to veridical target location (i.e., prosaccade [antisaccade] amplitude minus veridical target location) for each weighting condition and target eccentricity combination. Notably, Figure 5 demonstrates that pro- and antisaccades reliably undershot target location independent of weighting condition and target eccentricity (ts (19) > -6.60, ps < 0.001). As well, Figure 5 shows that the magnitude of the antisaccade undershooting bias increased with increasing target eccentricity.

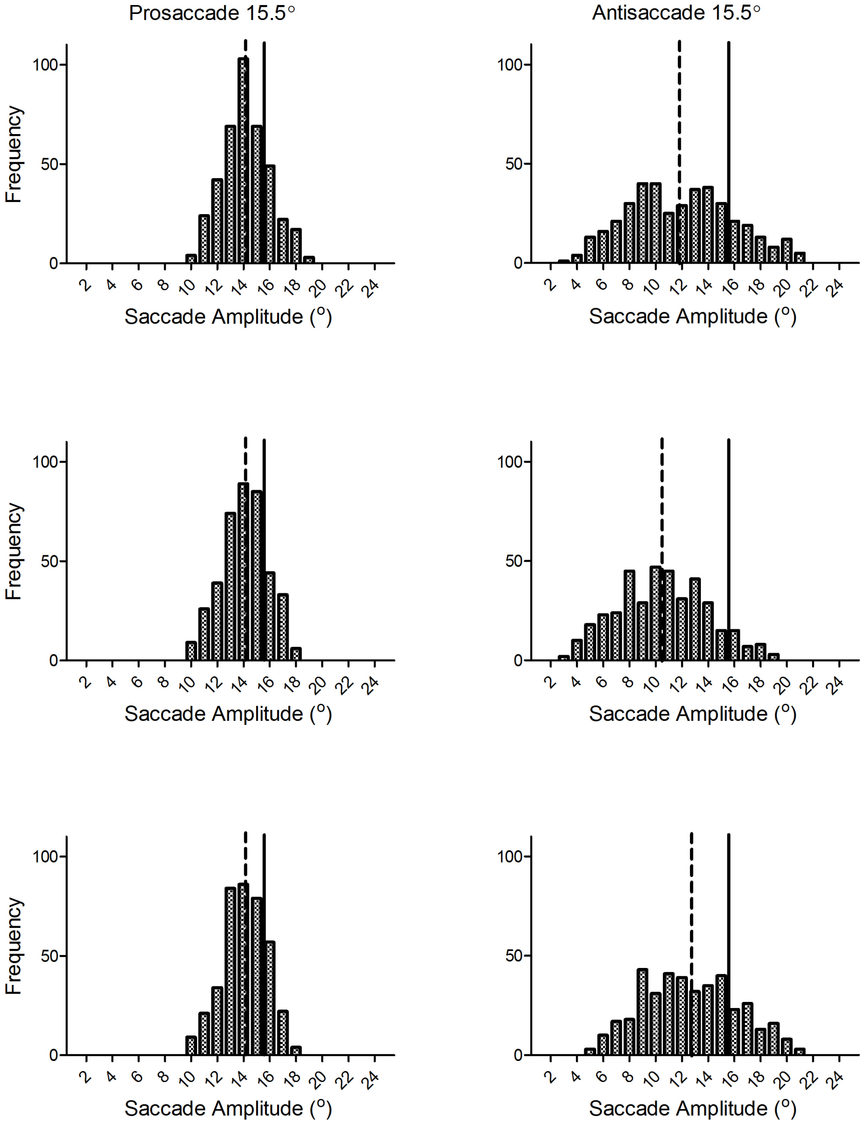


Figure 6. Frequency histograms for pro- (left) and antisaccade (right) amplitudes for the middle target eccentricity (i.e., 15.5°) for the control (top), proximal- (middle), and distal-weighting (bottom) condition. For each histogram, veridical target location and mean saccade amplitude are represented by *solid* and *hashed black* vertical lines, respectively, and the bin width for each histogram is 1.0°. Notably, the histograms demonstrate that the magnitude of saccade amplitude associated with the 'middle' target was influenced in the direction of the most frequently presented target.

Pro- and antisaccade RTs

RT data were subjected to the same ANOVA model as described above and elicited main effects for task, $F(1,19) = 122.42$, $p < 0.001$, and weighting condition, $F(2,38) = 7.32$, $p < 0.01$. RTs for antisaccades (302 ms, $CI_{95\%} = 29$) were longer than prosaccades (229 ms, $CI_{95\%} = 29$), and control condition RTs (269 ms, $CI_{95\%} = 19$) were longer than proximal- (255 ms, $CI_{95\%} = 19$) or distal-weighting (249 ms, $CI_{95\%} = CI_{95\%} = 19$) conditions ($ts(19) = 3.57$ and 2.64, $ps < 0.03$), which did not differ ($t(19) = -1.27$, $p = 0.22$)[6](Figure 7).

---

[6] As indicated in Footnote 5, confidence intervals were computed as a function of within-participant variability. Thus, the confidence intervals reported for the RT main effects of task and weighting condition were based on the mean-squared error term for the individual effects.

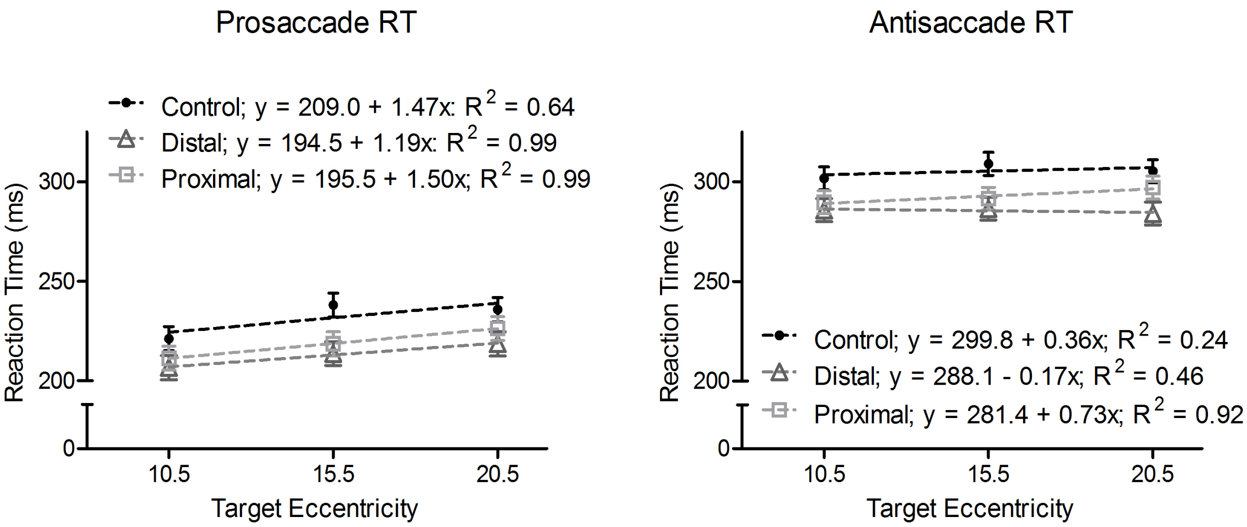


Figure 7. Mean pro- (left panel) and antisaccade (right panel) reaction times (ms) as a function of weighting-condition and target eccentricity. The lines in each panel represent linear regressions, and associated regression equations are reported in each panel. Error bars represent the 95% within-participants confidence intervals (Loftus and Masson, 1994).

To determine if saccade amplitudes were influenced by a planning-related speed-accuracy trade-off, I computed correlation coefficients separately for pro- and antisaccades based on mean participant performance for each target eccentricity and weighting condition combination. For prosaccades, Table 3 shows that the ‘proximal’ and ‘distal’ targets in the control condition, the ‘proximal’ target in the proximal- and distal-weighting conditions, and the ‘middle’ target in the distal weighting-condition produced a reliable – and negatively correlated – relationship between RT and amplitude; however, the remaining weighting condition and target eccentricity combinations did not (ps > 0.05). For antisaccades, RT and amplitude did not elicit a reliable relationship. Thus, planning times were not reliably or consistently related to pro- or antisaccade amplitudes.

Target Eccentricity (°)	Prosaccade		Antisaccade	
	R-Value	*P-Value*	*R-Value*	*P-Value*
Control				
10.5	-0.72	0.000	-0.25	0.287
15.5	-0.38	0.100	0.15	0.566
20.5	-0.55	0.011	0.07	0.803
Proximal Weighting				
10.5	-0.69	0.000	-0.13	0.587
15.5	-0.23	0.320	-0.18	0.438
20.5	-0.33	0.160	-0.18	0.478
Distal Weighting				
10.5	-0.50	0.025	-0.12	0.607
15.5	-0.50	0.025	-0.06	0.793
20.5	-0.32	0.166	0.12	0.616

Table 3. Correlation coefficients and p-values for the relationship between RT and saccade amplitude in the control, proximal and distal weighting conditions for both pro- and antisaccades (left and right, respectively). Values indicate RT and saccade amplitude are not reliably related.

Discussion

The goal of this study was to test the assertion that the visual percept supporting antisaccades is, in part, governed by a statistical summary of the target eccentricities *within* a stimulus-set (i.e., perceptual averaging hypothesis). To accomplish that goal, antisaccades performed in a block of trials involving an equal weighting (i.e., control condition) of target eccentricities (10.5°, 15.5°, and 20.5°) were contrasted to blocks wherein the ‘proximal’ (i.e., 10.5°: proximal-weighting block) and ‘distal’ (i.e., 20.5°: distal-weighting block) targets were presented five times as often. Additionally, I included complementary prosaccade blocks to demonstrate whether the visual information mediating responses with direct stimulus-response compatibility are refractory to the manipulation of target frequency. In the below, I describe pro- and antisaccades latencies and the general properties of prosaccade amplitudes prior to discussing the results related to my primary objective.

Pro- and antisaccades, and the manipulation of target frequency influences response latencies.

Antisaccades yielded longer RTs than prosaccades. This well-documented finding is taken to evince the additional time required to suppress a stimulus-driven prosaccade (i.e., response suppression) and invert a target’s spatial location to mirror-symmetrical space (i.e., vector inversion) (Hallett, 1978; for review see Munoz and Everling, 2004). Additionally, proximal- and distal-weighting conditions produced shorter RTs than the control condition independent of task (i.e., pro-, antisaccade) and target eccentricity. Recall that previous studies have shown that the frequent presentation of a target in a specific visual field (e.g., left or right and/or above or below a central fixation) results in shorter RTs for the most frequently presented visual field (Geng and Behrmann, 2005; Gmeindl et al., 2005; Liu et al., 2010; 2011) - a finding attributed to improved pre-saccade motor preparation (Dorris and Munoz, 1998), attentional processing (Kustov and Robinson, 1996), and target/movement selection (Glimcher and Sparks, 1992). In contrast to previous work however, I manipulated the frequency of *target eccentricity* independent of the visual field (i.e., left, right) in which the target was presented. Thus, my methods differ from previous work insomuch as they show that manipulating the frequency of a specific target eccentricity within a stimulus-set influences oculomotor planning. I suggest that implicit or explicit knowledge related to target frequency improved visuospatial attention (Posner, 1980; see also Fitts and Peterson, 1964; Krueger, 1970) and resulted in a movement-related response-set (Schluter et al., 1999) that decreased RTs for each target eccentricity within the proximal- and distal-weighting conditions.

Prosaccade amplitudes are refractory to the manipulation of target frequency.

Prosaccades undershot each target eccentricity and the magnitude of the bias was independent of the different weighting-conditions. The undershooting bias is in line with an extensive literature and is thought to reflect an invariant control strategy that minimizes energy expenditure (Becker, 1989) and/or saccade flight time (Harris, 1995). Moreover, correlation coefficients showed that prosaccade RTs were not consistently nor reliably related to amplitudes across each target eccentricity and weighting condition combination. Thus, the undershooting bias cannot be attributed to a speed/accuracy trade-off in movement planning (c.f. Abrams et al., 1989; Gillen et al., 2013; Gillen and Heath, 2014b; but see Kowler and Blaser, 1995). Additionally, that the undershooting bias was equivalent across the control, proximal- and distal-weighting conditions is consistent with the assertion that retinotopically organized motor maps in the superior colliculus mediate prosaccade sensorimotor transformations (Wurtz and Albano, 1980). In other words, the top-down and context-dependent properties related to target frequency did not influence the absolute visual information mediating prosaccades.

Antisaccade amplitudes are characterized by perceptual averaging.

Figures 4 and 5 show that antisaccades undershot veridical target location and that the bias increased to a greater degree with target eccentricity than prosaccades (see also Dafoe et al., 2007; Evdokimdis et al. 2006; Gillen and Heath, 2014b). This finding counters the range effect hypothesis' (Poulton, 1981; see also Kapoula, 1985) assertion that the 'proximal' and 'distal' targets within a stimulus-set respectively over- and undershoot *veridical target location.* Instead, the current findings, as well as previous work (Amador et al., 1998; Gillen and Heath, 2014b; Irving et al., 2009; Nyffeler et al., 2007), indicate that a general undershooting bias characterizes antisaccades[7]. Moreover, the results for antisaccades are consistent with reports from the perceptual literature indicating that obligatory judgments (i.e., verbal reports) are increasingly underestimated as a function of target distance. For example, Helmholtz's (1962) seminal report showed that the perceived length of a peripherally presented line was inversely related to its eccentricity from a central fixation. Moreover, contemporary research has shown that perceptual judgments (Bingham and Pagano, 1998; Foley, 1980) and memory-based motor tasks (Heath 2005; Knapp and Loomis 2004; Sheth and Shimojo 2001; Westwood et al. 2003) exhibit a monotonic rise in underestimation/undershooting with increasing target distance. The increased underestimation/undershooting is thought to reflect that the proportional increase in 'noise' with increasing stimulus magnitude (i.e., target eccentricity: for outline of Weber's law see: Marks and Algom, 1998) engenders a compression of visual space toward a common and stable frame of reference (e.g., a central fixation cross). Importantly, the present results provide convergent

---

[7] As indicated in the Introduction, target eccentricities less than ~6° have demonstrated an antisaccade overshooting bias. To my knowledge however, studies employing the range of eccentricities used here have consistently reported an antisaccade undershooting bias (Amador et al., 1998; Evdokimidis et al., 2006; Nyffler et al., 2007; Irving et al., 2009; Heath and Gillen, 2014).

evidence that the top-down nature of antisaccades results in response mediation via the same relative percept as that associated with visual perceptions.

The most salient finding from the present study was the modulation of the antisaccade undershooting bias across the different weighting conditions. Figure 5 shows that the proximal- and distal-weighting conditions produced a respective increase and decrease in undershooting compared to the control condition. I believe that such a result supports the contention that perceptual averaging, in part, influences that visual percept supporting antisaccades. Recall that the perceptual averaging hypothesis asserts that the visual system represents target properties (e.g., size, luminance, distance) via an abstract approximation (i.e., the mean) of the individual targets included within a stimulus-set (Albrecht et al., 2012; Ariely, 2001; Chong and Treisman, 2003; Corbett and Oriet, 2011; Davarpanah Jazi and Heath, 2014). As indicated by Ariely, perceptual averaging allows the visual system to efficiently and effectively deal with limited attentional resources without simply reducing the resolution of individual target properties. Further, Treisman and Gormican (1988) reported that pre-attentive visual processes provide an average representation that is determined by the frequency that an individual feature (e.g., eccentricity) is presented within a visual set. Thus, and as demonstrated here (see also Gillen and Heath, 2014b), the presentation of target eccentricities with equal frequency resulted in the central target (i.e. the statistical summary) within the stimulus-set determining the direction and magnitude of the endpoint bias for the other targets in the set. In turn, the proximal- and distal-weighting conditions resulted in a statistical summary that was weighted in the direction of the most frequently presented target eccentricity. More directly, the visual percept supporting the proximal-weighting condition was governed by a statistical summary biased by the frequently presented ‘proximal’ target (i.e., 10.5°) – a bias that resulted in all targets within the stimulus-set eliciting greater undershooting than the control condition. In turn, the increased frequency of the 'distal' target (20.5°) resulted in a percept producing a decreased undershooting bias compared to the control condition.

A final issue that I address relates to the neural mechanism, or mechanisms, supporting perceptual averaging. Although I am unaware of neuroimaging or electrophysiological work examining this issue, one possible explanation is that the neural populations associated with individual target eccentricities (Georgopolous et al., 1986) are preshaped by partial information related to motor choices (Bastian et al., 2003; Cisek 2007). The preshaping is thought to allow the neural populations to encode a distribution of potential – as opposed to a single - motor responses (Cisek and Kalaska, 2005). Thus, the top-down and cognitive nature of antisaccades may result in the distributed peaks of neural activity related to different motor outcomes (i.e., the different target eccentricities) becoming partially aggregated into a single peak that represents the statistical summary of a stimulus-set. A second – and not mutually exclusive - explanation can be drawn from the prosaccade distractor literature. Indeed, a distractor presented proximal to a target results in a prosaccade amplitude that falls between the target and distractor (i.e., the global effect: see Walker et al., 1997). Further, electrophysiological evidence from non-human primates has linked the global effect to a spatial combination of visual and preparatory target and distractor signals within the visuomotor neurons of the superior colliculus (Dorris et al., 2007). Thus, the top-down control of antisaccades may result in a low-level averaging of the relative target locations used in a stimulus-set.

Conclusions

The present results indicate that antisaccade sensorimotor transformations are supported via a relative visual percept. Moreover, my results show that the percept is governed, in part, via a statistical summary of the range of target eccentricities included in a stimulus-set (i.e., the perceptual averaging hypothesis).

General Discussion

Antisaccades require the specification of a movement endpoint via a perceived target location (i.e., visual percept). The primary objective of my thesis was to determine whether a range effect or a strategy of perceptual averaging governs the endpoint properties associated with the antisaccade visual percept. To accomplish my objective, Experiment One of my thesis employed a methodology originally developed by Kapoula (1985) wherein participants completed antisaccades in separate blocks (i.e., proximal and distal) that contained an equal number of target eccentricities but differed with regards to the magnitude of their eccentricities. Based on results from Experiment One, Experiment Two was designed to examine whether the statistical summary associated with antisaccades is influenced not only by the magnitude of target eccentricities presented within a stimulus-set, but also the frequency by which an individual target eccentricity is presented. As such, Experiment Two employed a methodology that manipulated the frequency of target presentation.

Experiment One provided tentative evidence for an oculomotor range effect. Figure 1 shows that the proximal block elicited an over- and undershooting bias to the ‘proximal’ (i.e., 3.0° and 5.5°) and ‘distal’ (i.e., 10.5° and 13.0°) targets, respectively. In turn, a null bias was associated with the block’s central target (i.e., 8.0°). Notably however, results for the distal block showed a reliable undershooting bias independent of target eccentricity. Moreover, the 10.5° and 13.0° target eccentricities (i.e., the eccentricities common to the proximal and distal blocks) elicited a reliable undershooting bias regardless of the block in which they were performed. This result is particularly important because it directly counters the oculomotor range effect hypothesis' (see Poulton, 1981; Kapoula, 1985) assertion that the 'proximal' and 'distal' targets included *within* a stimulus-set can be made to respectively over- and undershoot veridical target location.

Experiment One showed that the slopes relating antisaccade amplitudes to veridical target location were shallower than prosaccades and antisaccade slopes did not vary across proximal and distal blocks. This finding indicates that antisaccades did not scale as accurately to veridical target location as their prosaccade counterparts. Moreover, the shallow slopes associated with antisaccades indicate that amplitudes did not robustly vary with increasing target eccentricity. Thus, results show that antisaccade endpoint bias was independent of the target eccentricities included within the block of trials in which they were performed, and further indicates that the bias associated with the central target within a stimulus-set determined the magnitude and direction of endpoint bias for the other targets included in the stimulus-set. As such, Experiment One provides tentative evidence that antisaccades are mediated via a perceptual averaging strategy.

In terms of Experiment Two, Figure 4 shows that antisaccade amplitudes across control, proximal- and distal-weighting conditions reliably undershot veridical target location. Importantly, however, the magnitude of the undershooting bias was influenced by the different target-weighting conditions. In particular, the proximal-weighting condition resulted in an increased undershooting bias compared to the control weighting condition, whereas the distal-weighting condition resulted in a decreased undershooting bias compared to the control-condition. Thus, Experiment Two's results provide evidence that the statistical summary representing each stimulus-set was influenced in the direction of the most frequently presented target and therefore provides support for the perceptual averaging strategy.

In light of the results from Experiments One and Two, it is important to discuss why previous antisaccade studies have not proposed a strategy of perceptual averaging. Indeed, Dafoe et al. (2007) and Evdokimidis et al. (2006) used a single block of trials and found over- and undershooting bias for their 'proximal' and 'distal' targets, respectively. Of course, the results of Dafoe et al. and Evdokimidis et al. are consistent with the proximal block in Experiment One. However, Experiment One's inclusion of a second (i.e., distal) block and results showing a reliable undershooting bias across each target eccentricity in the distal block demonstrates that a range effect does not generalize to antisaccade endpoints across a range of target eccentricities. Indeed, such a result in combination with Experiment Two's results showing that endpoints are biased in the direction of the most frequently presented target provides parsimonious evidence supporting a strategy of perceptual averaging.

A final issue that I address is that of a possible neural mechanism associated with perceptual averaging. One possible explanation stems from the neural populations supporting individual target eccentricities within the retinotopic motor map and that the populations supporting a current motor choice may be preshaped by previous information (Cisek, 2007; Bastian et al., 2003). Specifically, a collection of motor responses may be combined into a single peak that represents a distribution of related motor outcomes. The single peak then, may act as the information preshaping the current motor response (Cisek and Kalaska, 2005). In other words, the single peak in the present account would represent the statistical summary, and act as the preshaping mechanism (neural information) influencing the current antisaccade response. Another possible framework can be drawn from the distractor literature. Specifically, Walker et al. (1997) demonstrated that prosaccade amplitudes land between the location of a target and distractor (i.e., the global effect), and Dorris et al. (2007) have linked the distractor-based spatial averaging to a collicular averaging of the visual and preparatory signals related to both target and distractor. As such, the visual percept supporting antisaccades may be influenced by an averaging of the visual and preparatory signals associated with the range of target eccentricities within a stimulus-set. To my knowledge, there is of yet no neuroimaging or electrophysiological work examining the putative mechanism supporting perceptual averaging. Thus, my studies provide a framework by which future electrophysiological (i.e., event-related brain potentials) and neuroimaging studies can understand the neural correlates associated with perceptual averaging for a goal-directed action.

General Conclusion

My results show that perceptual averaging influences the relative target percept mediating antisaccades. I believe that this represents an important contribution to the antisaccade literature as it demonstrates that the relative visual percept mediating antisaccades is governed by the same properties as that associated with perception-based visual judgments.

References

Abrams RA, Meyer DE, Kornblum S (1989) Speed and accuracy of saccadic eye movements: Characteristics of impulse variability in the oculomotor system. J Exp Psychol Hum Percep Perf 15:529-543.

Albrecht AR, Scholl BJ, Chun MM (2012) Perceptual averaging by eye and ear: Computing summary statistics from multimodal stimuli. Atten Percept Psychophys 74:810-815.

Amador N, Schlag-Rey M, Schlag J (1998) Primate antisaccades. I. Behavioral characteristics. J Neurophysiol 80:1775-1786.

Ariely D (2001) Seeing sets: Representation by statistical properties. Psychol Sci 12:157-162.

Baird JC, Noma EJ (1978) Fundamentals of scaling and psychophysics. John Wiley & Sons, New York.

Bastian A, Schöner G, Riehle A (2003) Preshaping and continuous evolution of motor cortical representations during movement preparation. Eur J Neurosci 18:2047-2058.

Becker W (1989) The neurobiology of saccadic eye movements. Metrics. Rev Oculomot Res 3:13-67.

Becker W, Fuchs AF (1969) Further properties of the human saccadic system: eye movements and correction saccades with and without visual fixation points. Vis Res 9:1247-1258.

Bell AH, Everling S, Munoz DP (2000) Influence of stimulus eccentricity and direction on characteristics of pro- and antisaccades in non-human primates. J Neurophysiol 84:2595-2604.

Bingham GP, Pagano CC (1998) The necessity of a perception--action approach to definite distance perception: Monocular distance perception to guide reaching. J of Exp Psychol: Hum Percept and Perform 24:145.

Brainard DH (1997) The Psychophysics Toolbox. Spat Vis 10:433-436.

Chong SC, Treisman A (2003) Representation of statistical properties. Vision Res 43:393-404.

Cisek P (2007) Cortical mechanisms of action selection: the affordance competition hypothesis. Philos Trans R Soc Lond B Biol Sci 362:1585-1599.

Cisek P, Kalaska JF (2005) Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. Neuron 45:801-814.

Corbett JE, Oriet C (2011) The whole is indeed more than the sum of its parts: perceptual averaging in the absence of individual item representation. Acta Psychol (Amst) 138:289-301.

Cumming G (2013) Understanding the new statistics: Effect sizes, confidence intervals, and meta-analysis. Routledge, New York.

Dafoe JM, Armstrong IT, Munoz DP (2007) The influence of stimulus direction and eccentricity on pro- and anti-saccades in humans. Exp Brain Res 179:563-570.

Davarpanah Jazi S, Heath M (2014) Weber's law in tactile grasping and manual estimation: Feedback-dependent evidence for functionally distinct processing streams. Brain Cogn 86:32-41.

Deubel H, Wolf W, Hauske G (1986) Adaptive gain control of saccadic eye movements. Hum Neurobiol 5:245-253.

Dorris MC, Munoz DP (1998) Saccadic probability influences motor preparation signals and time to saccadic initiation. J Neurosci 18:7015-7026.

Dorris MC, Olivier E, Munoz DP (2007) Competitive integration of visual and preparatory signals in the superior colliculus during saccadic programming. J Neurosci 27:5053-5062.

Elliott D, Hansen S, Mendoza J, Tremblay L (2004) Learning to optimize speed, accuracy, and energy expenditure: a framework for understanding speed-accuracy relations in goal-directed aiming. J Mot Behav 36:339-351.

Evdokimidis I, Tsekou H, Smyrnis N (2006) The mirror antisaccade task: direction-amplitude interaction and spatial accuracy characteristics. Exp Brain Res 174:304-311.

Fitts PM, Peterson JR (1964) Information capacity of discrete motor responses. J Exp Psychol 67:103-112.

Fischer B, Weber H (1992) Characteristics of "anti" saccades in man. Exp Brain Res 89:415-424.

Foley JM (1980) Binocular distance perception. Psychol Rev 87:411.

Gaveau V, Martin O, Prablanc C, Pélisson D, Urquizar C, Desmurget M (2003) On-line modification of saccadic eye movements by retinal signals. Neuroreport 14:875-878.

Geng JJ, Behrmann M (2005) Spatial probability as an attentional cue in visual search. Percept Psychophys 67:1252-1268.

Georgopoulos AP, Schwartz AB, Kettner RE (1986) Neuronal population coding of movement direction. Sci 233:1416-1419

Gerardin P, Gaveau V, Pélisson D, Prablanc C (2011) Integration of visual information for saccade production. Hum Mov Sci 30:1009-1021.

Gillen C, Heath M (2014a) Asymmetrical weighting of target eccentricities within a trial block influence antisaccade endpoint bias. Poster presented at the meeting of the Vision Sciences Society, St. Pete’s Beach, FL.

Gillen C, Heath M (2014b) Perceptual averaging governs antisaccade endpoint bias. Manuscript In Press for publication in Experimental Brain Research.

Gillen C, Weiler J, Heath M (2013) Stimulus-driven saccades are characterized by an invariant undershooting bias: no evidence for a range effect. Exp Brain Res 230:165-174.

Glimcher PW, Sparks DL (1992) Movement selection in advance of action in the superior colliculus. Nat 355:542-545.

Gmeindl L, Rontal A, Reuter-Lorenz PA (2005) Strategic modulation of the fixation-offset effect: dissociable effects of target probability on prosaccades and antisaccades. Exp Brain Res 164:194-204.

Hallett PE (1978) Primary and secondary saccades to goals defined by instructions. Vision Res 18:1279-1296.

Harris CM (1995) Does saccadic undershoot minimize saccadic flight-time? A Monte-Carlo study. Vision Res 35:691-701.

Harris CM, Wolpert DM (1998) Signal-dependent noise determines motor planning. Nature 394:780-784.

He PY, Kowler E (1989) The role of location probability in the programming of saccades: implications for "center-of-gravity" tendencies. Vision Res 29:1165-1181.

Heath M (2005) Role of limb and target vision in the online control of memory-guided reaches. Motor Control 9:281-311.

Heath M, Dunham K, Binsted G, Godbolt B (2010) Antisaccades exhibit diminished online control relative to prosaccades. Exp Brain Res 203:743-752.

Heath M, Weiler J, Marriott K, Welsh TN (2011) Vector inversion diminishes the online control of antisaccades. Exp Brain Res 209:117-127.

Irving EL, Tajik-Parvinchi DJ, Lillakas L, González EG, Steinbach MJ (2009) Mixed pro and antisaccade performance in children and adults. Brain Res 1255:67-74.

Irwin DE, Carlson-Radvansky LA (1996) Cognitive suppression during saccadic eye movements. Psychol Sci 7:83-88.

Kalesnykas RP, Hallett PE (1994) Retinal eccentricity and the latency of eye saccades. Vision Res 34:517-531.

Kapoula Z (1985) Evidence for a range effect in the saccadic system. Vision Res 25:1155-1157.

Kapoula Z, Robinson DA (1986) Saccadic undershoot is not inevitable: saccades can be accurate. Vision Res 26:735-743.

Kimmig H, Greenlee MW, Gondan M, Schira M, Kassubek J, Mergner T (2001) Relationship between saccadic eye movements and cortical activity as measured by fMRI: quantitative and qualitative aspects. Exp Brain Res 141:184-194.

Knapp JM, Loomis JM (2004) Limited field of view of head-mounted displays is not the cause of distance underestimation in virtual environments. Presence: Teleoperators and Virtual Environments 13:572-577.

Kowler E, Blaser E (1995) The accuracy and precision of saccades to small and large targets. Vision Res 35:1741-1754.

Krappmann P, Everling S, Flohr H (1998) Accuracy of visually and memory-guided antisaccades in man. Vision Res 38:2979-2985.

Krueger LE (1970) Effect of stimulus probability on two-choice reaction time. J Exp Psychol 84:377.

Kustov AA, Robinson DL (1996) Shared neural control of attentional shifts and eye movements. Nat 384:74-77.

Liu CL, Chiau HY, Tseng P, Hung DL, Tzeng OJ, Muggleton NG, Juan CH (2010) Antisaccade cost is modulated by contextual experience of location probability. J Neurophysiol 103:1438-1447.

Liu CL, Tseng P, Chiau HY, Liang WK, Hung DL, Tzeng OJ, Muggleton NG, Juan CH (2011) The location probability effects of saccade reaction times are modulated in the frontal eye fields but not in the supplementary eye field. Cereb Cortex 21:1416-1425.

Lemay M, Proteau L (2001) A distance effect in a manual aiming task to remembered targets: a test of three hypotheses. Exp Brain Res 140:357-368.

Loftus GR, Masson ME (1994) Using confidence intervals in within-subject designs. Psychon Bull Rev 1:476-490.

Marks LE, Algom D (1998) Psychophysical scaling. In: Measurement, judgment, and decision making (Birnbaum MH, eds), pp81-178. San Diego: Academic Press.

Moon SY, Barton JJ, Mikulski S, Polli FE, Cain MS, Vangel M, Hämäläinen MS, Manoach DS (2007) Where left becomes right: a magnetoencephalographic study of sensorimotor transformation for antisaccades. Neuroimage 36:1313-1323.

Munoz DP, Everling S (2004) Look away: the anti-saccade task and the voluntary control of eye movement. Nat Rev Neurosci 5:218-228.

Munoz DP, Wurtz, RH (1993) Fixation cells in monkey superior colliculus II. reversible activation and deactivation. J Neurophysiol 70:576-589.

Munoz DP, Wurtz, RH (1995) Saccade-related activity in monkey superior colliculus II. spread of activity during saccades. J Neurophysiol 73:2334-2348..

Nyffeler T, Hartmann M, Hess CW, Müri RM (2008) Visual vector inversion during memory antisaccades--a TMS study. Prog Brain Res 171:429-432.

Nyffeler T, Rivaud-Pechoux S, Pierrot-Deseilligny C, Diallo R, Gaymard B (2007) Visual vector inversion in the posterior parietal cortex. Neuroreport 18:917-920.

Oliveira FTP, Elliott D, Goodman D (2005) Energy-minimization bias: compensating for intrinsic energy influence of energy-minimization mechanisms. Motor Control 9:101-114.

Olk B, Kingstone A (2003) Why are antisaccades slower than prosaccades? A novel finding using a new paradigm. Neuroreport 14:151-155.

Pedhazur EJ (1997) Multiple regression in behavioral research: Explanation and prediction. Harcourt Brace College Publishers, Orlando.

Posner MI (1980) Orienting of attention. Q J Exp Psych 32:3-25.

Poulton EC (1981) Human manual control. Comprehensive Physiology. John Wiley & Sons, Inc.

Prablanc C, Jeannerod M (1975) Corrective saccades: dependence on retinal reafferent signals. Vision Res 15:465-469.

Robinson DA (1964) The mechanics of human saccadic eye movement. J Physiol 174:245-264.

Robinson DA (1971) Models of oculomotor neural organization. In: Bach-y-Rita P, Collins, C, Hyde JE (eds) The control of eye movements. Academic Press, New York, pp 515-538

Robinson DA (1973) Models of the saccadic eye movement control system. Kybernetik 14:71-83.

Schluter ND, Rushworth MF, Mills KR, Passingham RE (1999) Signal-, set-, and movement-related activity in the human premotor cortex. Neuropsychologia 37:233-243.

Sheth BR, Shimojo S (2001) Compression of space in visual memory. Vision Res 41:329-341.

Treisman A, Gormican S (1988) Feature analysis in early vision: evidence from search asymmetries. Psychol Rev 95:15-48.

Viguier A, Clément G, Trotter Y (2001) Distance perception within near visual space. Perception 30:115-124.

von Helmholtz H (1962) *Helmholtz's treatise on physiological optics*. Dover Publications.

Walker R, Deubel H, Schneider WX, Findlay JM (1997) Effect of remote distractors on saccade programming: evidence for an extended fixation zone. J Neurophysiol 78:1108-1119.

Weber RB, Daroff RB (1971) The metrics of horizontal saccadic eye movements in normal humans. Vision Res 11:921-928.

Weiler J, Heath M (2012) The prior-antisaccade effect influences the planning and online control of prosaccades. Exp Brain Res 216:545-552.

Weiler J, Heath M (2014) Repetitive antisaccade execution does not increase the unidirectional prosaccade switch-cost. Acta Psychol (Amst) 146:67-72.

Weiler J, Holmes SA, Mulla A, Heath M (2011) Pro- and antisaccades: dissociating stimulus and response influences the online control of saccade trajectories. J Mot Behav.

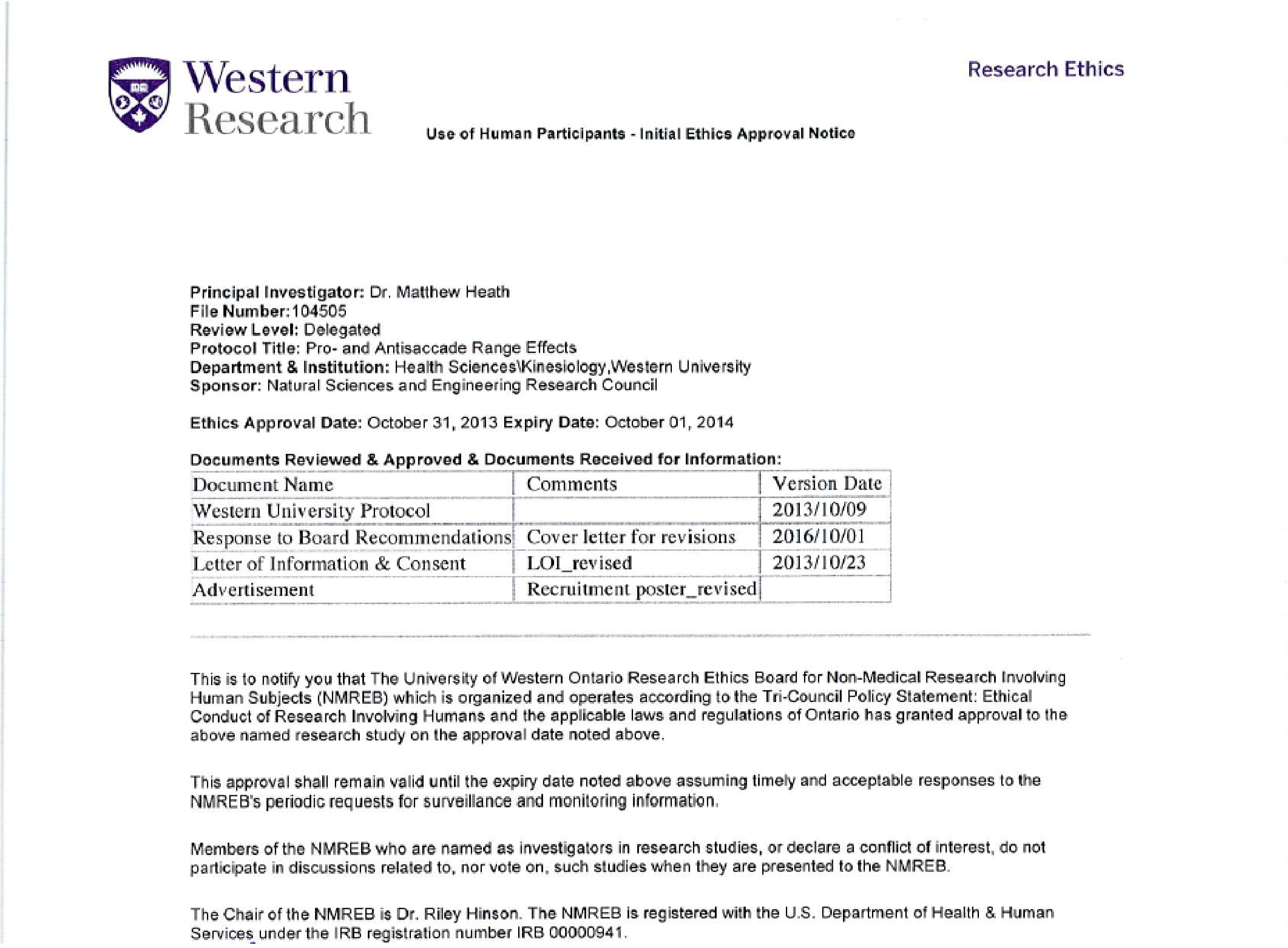
Westwood DA, Heath M, Roy EA (2003) No evidence for accurate visuomotor memory: systematic and variable error in memory-guided reaching. J Mot Behav 35:127-133.

Wurtz RH, Albano JE (1980) Visual-motor function of the primate superior colliculus. Annu Rev Neurosci 3:189-226.

Zhang M, Barash S (2000) Neuronal switching of sensorimotor transformations for antisaccades. Nature 408:971-975.

Appendix A

The University of Western Ontario Research Ethics Board of Approval notice.



Western Research

Research Ethics

Use of Human Participants - Initial Ethics Approval Notice

Principal Investigator: Dr. Matthew Heath
File Number: 104505
Review Level: Delegated
Protocol Title: Pro- and Antisaccade Range Effects
Department & Institution: Health Sciences\Kinesiology,Western University
Sponsor: Natural Sciences and Engineering Research Council

Ethics Approval Date: October 31, 2013 **Expiry Date:** October 01, 2014

Documents Reviewed & Approved & Documents Received for Information:

Document Name	Comments	Version Date
Western University Protocol		2013/10/09
Response to Board Recommendations	Cover letter for revisions	2016/10/01
Letter of Information & Consent	LOI_revised	2013/10/23
Advertisement	Recruitment poster_revised	

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 named research study 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 00000941.

Curriculum Vitae

Name: Caitlin Gillen

Post-secondary Education and Degrees:
The University of Western Ontario
London, Ontario, Canada
Masters of Science Candidate, Kinesiology
2014

The University of Western Ontario
London, Ontario, Canada
Kinesiology
2008-2012 B.Sc

Honours and Awards:
Province of Ontario Graduate Scholarship
2013-2014. $15,000.

Western Graduate Research Scholarship (WGRS)
Faculty of Health Science, The University of Western Ontario
2012-2014. $9,500.

Related Work Experience:
Graduate Teaching Assistant
School of Kinesiology, The University of Western Ontario
September 2012 - April 2013
Musculoskeletal Rehabilitation - 4th year
Practical Aspects of Athletic Injuries - 3rd year

Publications:
Gillen, C., Weiler, J., and Heath M. (2013). Stimulus-driven saccades are characterized by an invariant undershooting bias: no evidence for a range effect. Experimental Brain Research, 230: 165-174.

Gillen, C. and Heath, M. (2014). Perceptual averaging governs antisaccade endpoint bias. Experimental Brain Research, (In press).

Gillen, C. and Heath, M. (Submitted). Target frequency influences antisaccade endpoint bias: Evidence for perceptual averaging.

Research Presentations:

Gillen, C., and Heath, M. The asymmetrical weighting of target eccentricities within a trial block influences antisaccade endpoint bias. Poster. Vision Sciences Society.

Gillen, C., Bechamp, T., and Heath, M. (2013). Relational properties within a target set influence antisaccade amplitudes. Poster. Canadian Society for Psychomotor Learning and Sports Psychology.

Gillen, C., Weiler, J., and Heath, M. (2013). Target range properties do not influence oculomotor undershooting bias. Poster. Vision Sciences Society.

Professional Affiliations:

Vision Sciences Society
Canadian Society of Psychomotor Learning and Sport Psychology