SACCADE TRIAL TYPE PROBABILITY AND ITS EFFECTS ON RESIDUAL INHIBITION AND TASK SWITCHING COSTS

by

JORDAN ELISABETH PIERCE

(Under the direction of Jennifer E. McDowell)

ABSTRACT

Eye movement circuitry involved in saccade production offers a model for studying cognitive control: visually-guided prosaccades are reflex-like, while goal-driven antisaccades rely upon complex control processes. By manipulating the relative proportion of these saccade types, this study sought to illuminate differences in cognitive load and corresponding behavioral responses. Results indicated that prosaccade percent correct decreased when there was a smaller ratio of prosaccades in the run, yet antisaccade percent correct was constant across runs. Increasing probability of antisaccades in a run led to slower reaction times for both saccade types, particularly after a previous antisaccade trial. The effects of saccade type probability were investigated further by modifying the stimulus timing. With a shorter cue, the proportion of antisaccades in the run modulated antisaccade response characteristics. These findings suggest that residual inhibition from antisaccades alters performance based on the cognitive load, task switching demands, and stimulus timing within a run.

INDEX WORDS: Cognitive Control, Antisaccade, Cognitive Load, Inhibition, Task Switching, Stimulus Design

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TABLE OF CONTENTS

Page

CHAPTER

LIST OF TABLES

Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The cognitive processes in which one engages everyday require allocation of neural resources and efficient responses based on the particular situation at hand. Cognitive control is a mechanism through which the brain regulates functioning to achieve goals. Top-down influences from prefrontal cortex modulate the activity in more basic sensory and motor areas so that certain stimuli in the environment are attended while others are ignored (Everling & Fischer, 1998; E. K. Miller & Cohen, 2001). These processes occur throughout the day and allow one to interact with the world without becoming overwhelmed by a cacophony of sensory stimulation. Cognitive control focuses attention on a professor’s lecture instead of counting ceiling tiles or listening to the construction sounds down the hall; it enables an individual to remember a phone number in the time between hearing it and dialing. Measuring the implementation of such a general process as cognitive control, however, remains a challenging proposition for researchers. One method of circumventing this difficulty is by utilizing a specific cognitive system as a model for broader cognitive control functioning.

Such a model may be found in studying the ocular motor system and saccadic eye movements (Hutton, 2008; Pierrot-Deseilligny, Muri, Ploner, Gaymard, & Rivaud-Pechoux, 2003). One of several types of eye movements, saccades are rapid glances to a visual location of interest. The neural system supporting saccades has been well-characterized in previous work and its basic organization and response patterns have been described by many researchers both in humans (Evdokimidis et al., 2002; Everling & Fischer, 1998; Hoffman & Subramaniam, 1995; Hutton, 2008; McDowell, Dyckman, Austin, & Clementz, 2008; Munoz & Everling, 2004) and non-human primates (Bell, Everling, & Munoz, 2000; Funahashi, Bruce, & Goldman-Rakic, 1991; Johnston & Everling, 2008; Munoz & Wurtz, 1995). What makes this system appealing as a model is the ease with which responses can be quantified and contrasted when different degrees of cognitive control are demanded (Hutton, 2008; Munoz & Everling, 2004). Lower-level, reflexive neural responses can be studied via the prosaccade: a visually-guided glance towards a stimulus. A prosaccade is a simple eye movement and something that humans do easily, instinctively, and frequently. On the other hand, higher-level goal-directed responses can be represented by the antisaccade: a glance to the mirror location of a stimulus (Hallett, 1978). This task requires inhibition of the reflexive glance towards the stimulus and volitional generation of a saccade in the opposite direction, often towards nothing in particular (Everling & Fischer, 1998). An antisaccade is more difficult to perform, calling upon more cognitive control processes for successful execution than a prosaccade (Unsworth, Schrock, & Engle, 2004).

When observing saccades in a laboratory setting, trials may begin with a fixation point in the center of the screen, followed by a cue indicating the trial type to be performed (prosaccade or antisaccade), and finally a peripheral target towards or away from which the participant must glance as quickly and accurately as possible (Everling & Fischer, 1998; Hutton, 2008). A number of saccadic response variables can be measured: whether the participant makes an initial glance in the appropriate direction, how long it takes to initiate this eye movement, how accurate the movement is in relation to the target's location, and how frequently errors are committed and corrected (Everling & Fischer, 1998). Generally, antisaccades have response latencies about 100 milliseconds (ms) longer than prosaccades and participants tend to make more errors (a glance towards the stimulus, around 20% of trials; (Hutton, 2008; Smyrnis et al., 2002)). This delay may reflect additional time required to inhibit the reflexive response, to transform the positional information about the stimulus into the mirror location, and to generate a volitional saccade (Munoz & Everling, 2004; Olk & Kingstone, 2003). The increase in error rate on antisaccade tasks has been explained by competitive processing of prosaccade and antisaccade responses in the brain (Anderson, Husain, & Sumner, 2008; Massen, 2004). Cognitive control mechanisms in prefrontal cortex (PFC; (Munoz & Everling, 2004; Pierrot-Deseilligny, Muri, Nyffeler, & Milea, 2005)) or local inhibitory connections in the superior colliculus (Cutsuridis, Smyrnis, Evdokimidis, & Perantonis, 2007) must suppress the reflexive glance towards a stimulus while the volitional saccade is programmed. Otherwise, this innate response can occur (as an error) before the slower endogenous antisaccade is generated (Massen, 2004).

The saccadic system is flexible in how efficiently and accurately eye movements of both types are performed; specific response latencies and error rates of saccades depend on a number of features of the stimulus design and presentation. For example, individuals respond differently if the saccade trials are presented in a blocked versus an interleaved design (Cherkasova, Manoach, Intriligator, & Barton, 2002; Dyckman, Camchong, Clementz, & McDowell, 2007; Ethridge, Brahmbhatt, Gao, McDowell, & Clementz, 2009), and if the cues for saccade type and saccade generation overlap, are separated by a brief gap, or occur simultaneously (Fischer & Weber, 1993; Reuter-Lorenz, Hughes, & Fendrich, 1991; Saslow, 1967; Weber & Fischer, 1995). Knowledge of the location of the saccadic cue or response also can drastically reduce reaction times (Abegg, Manoach, & Barton, 2011; Carpenter & Williams, 1995; Dorris & Munoz, 1998; Liu et al., 2010).

The studies mentioned above demonstrate that particular aspects of eye movements are affected by environmental variables and subject to manipulation by experimental design. To separate effects on the basic saccade processes common to both prosaccades and antisaccades from effects on the higher cognitive control processes primarily demanded by antisaccades, researchers can measure how response characteristics change with stimulus design. If a design alteration impacts performance on both saccade types similarly, then it likely affects simple saccade components, such as motor activity; if the manipulation affects antisaccades more strongly, then the design component likely alters cognitive control processes. For example, the use of a gap between the saccade cue and target reduces response latencies for both reflexive and voluntary saccades (though not necessarily to the same degree (Craig, Stelmach, & Tam, 1999; Fischer & Weber, 1992; Forbes & Klein, 1996)), whereas providing practice with saccades yields improvement for antisaccade performance, but not prosaccades (Dyckman & McDowell, 2005). Thus, a parsimonious interpretation could be that the gap effect is based on changes in fixation disengagement relevant to both types, while saccade practice affects one's ability to inhibit a reflexive glance or speed of generating a volitional saccade. Knowing how the saccadic system responds in these different circumstances allows one to disentangle component processes and specifically investigate cognitive control functioning when environmental demands change.

One approach to studying cognitive control adaptability focuses on the effects of the overall cognitive load of a task. This is studied often in working memory (WM), another type of executive function with long-recognized capacity limitations (Baddeley & Hitch, 1974; G. A. Miller, 1956). Recently, Engle and Kane described WM capacity as the ability of cognitive control to maintain task instructions and information in an active state, rather than a memory storage limit per se (Engle & Kane, 2003). Many WM studies use the n-back paradigm, where participants see a series of letters (for example), are required to maintain them in WM, and must make a response if the current letter matches the letter shown a certain number of trials ago (Gevins et al., 1996). By increasing the number of trials that must be held in WM (1-back, 2-back, etc.) the cognitive load of the task is increased accordingly, with the individual's performance dropping as their capacity limit is approached or surpassed (e.g.(Jansma, Ramsey, Coppola, & Kahn, 2000; McEvoy, Smith, & Gevins, 1998; Sala-Llonch et al., 2012). Studies suggest that PFC activity is responsible, at least in part, for this dose response curve and the practical limits of WM (Braver et al., 1997; Callicott et al., 1999).

Furthermore, tasks that place concurrent demands on several cognitive functions supported by PFC have been found to result in substantially worse performance than when the tasks are performed separately. For example, Roberts and colleagues (1994) had participants perform antisaccades while simultaneously solving mental arithmetic problems or repeating numbers. Antisaccade error rate and response time increased relative to the WM load of the secondary task, suggesting a depletion of mutual cognitive resources (Roberts, Hager, & Heron, 1994). In another study, researchers found that performing a concurrent controlled tapping sequence also slowed antisaccades, and in some cases prosaccades (Stuyven, Van der Goten, Vandierendonck, Claeys, & Crevits, 2000). Such findings support the notion that saccades require a working memory component, or at least are supported by similar cortical regions (e.g. PFC), and, thus, may have similar load constraints as other working memory tasks. Indeed, previous studies have found that WM span is correlated with antisaccade performance, where individuals with low WM span make more errors and are slower to respond correctly than those with high WM span (Kane, Bleckley, Conway, & Engle, 2001; Unsworth, et al., 2004). Therefore, manipulating task difficulty and cognitive load during a saccade task should lead to performance deficits if a cognitive control/ inhibition “capacity” exists and is approached or exceeded.

The present study probed the global limitations of the saccadic system by manipulating the putative cognitive load across several saccade runs via the relative proportion of prosaccades and antisaccades. Prosaccade trials require reflex-like responses, while antisaccade trials require additional cognitive control to inhibit the prepotent prosaccade response and transform stimulus location information to generate a volitional saccade. Therefore, the cognitive load for a series of antisaccades theoretically is higher than for prosaccades due to these differences in task demands. By changing the probability of prosaccades and antisaccades across several runs, the current experiment varied the cognitive load for each set of saccades to measure response patterns and possible limits of effective performance within the saccadic system.

Two previous studies have investigated the effects of saccade type probability on response characteristics. Massen (2004) presented runs of horizontal saccade trials with 25%, 50% or 75% of antisaccades in order to slow the endogenous component of saccadic generation through what was described as an attentional manipulation. The author found that prosaccades were statistically unaffected by the probability level, while antisaccade error rates and response latencies increased as the probability of an antisaccade decreased. In another study, researchers assigned runs of 20%, 50%, and 80% antisaccade trials to investigate performance differences between prosaccades and antisaccades (Chiau et al., 2011). Their results indicated that typical antisaccade costs (longer RTs and more errors) were eliminated when antisaccades were more frequent than prosaccades within a run (i.e. antisaccades were faster than prosaccades in the 80% run). Also, antisaccade error rates were higher than prosaccade error rates only for the 20% run. Their design, however, offered no pre-target trial type cue, and instead used the orientation of a colored rectangle within the target array to indicate the appropriate response type. This makes it difficult to compare with the work of Massen (2004) which used a 200 ms trial type cue, because the participants in Chiau et al. (2011) could not respond immediately and reflexively to the target for prosaccade trials, but first had to distinguish the singleton's orientation before performing a more controlled and slower prosaccade, necessarily making the responses more similar to antisaccade trials. The current study sought to clarify these findings and extend them by including additional conditions as described below.

Increasing overall cognitive load is not the sole method of influencing saccade response characteristics. For example, as mentioned earlier, performance differs based on whether trials are presented in a blocked versus an interleaved fashion. In a blocked task design, trials of the same type are performed consecutively and participants are thus capable of knowing the upcoming trial type and priming the appropriate response. On the other hand, an interleaved design involves the mixed presentation of multiple trial types, in whatever order the experimenter determines to be optimal for his or her research questions; thus, the participants may or may not be prepared for the upcoming trial type. As such, participants often have an increased percentage of correct responses and reduced response time for both saccade types in a blocked presentation compared to interleaved (Cherkasova, et al., 2002; Ethridge, et al., 2009; Li et al., 2012). The current study utilized both single-trial runs (all prosaccades or all antisaccades) and interleaved trial types (mixed proportions of prosaccades and antisaccades). This allowed for direct comparison of reflexive or volitional saccades performed alone or together, extending the range of measured probabilities and cognitive loads from previous work.

In addition to these design considerations at the global level, changes to the local trial history of a saccade task can also elicit response differences when using an interleaved presentation. Two factors that have been studied for their influence on saccade responses are task switching and prior antisaccade costs, both of which describe an effect of the previous trial type on current trial performance. Task switching costs occur when a trial of one type follows a trial of a different type and performance decreases, perhaps due to the remapping of response instructions (Monsell, 2003; Vandierendonck, Liefooghe, & Verbruggen, 2010) or task-set inertia (Allport, Styles, & Hsieh, 1994). These costs may be asymmetric if one task is more dominant and reflexive (here a prosaccade) than the other, weaker task (an antisaccade), resulting in worse performance when switching from the weaker to the stronger task (Allport, et al., 1994; Cherkasova, et al., 2002). The length of time that the saccade type cue precedes the generation of the saccade also affects how well the brain is prepared to respond and the magnitude of task switching effects (Barton, Greenzang, Hefter, Edelman, & Manoach, 2006; Ethridge, et al., 2009; Vandierendonck, et al., 2010). Additionally, prior antisaccade costs are observed for responses to either saccade type when the previous trial was an antisaccade: reaction times are slower, perhaps as a result of inhibitory processes remaining active in the system (Barton, et al., 2006; Chiau, et al., 2011; Lee, Hamalainen, Dyckman, Barton, & Manoach, 2011). Such effects are not consistently reported in the literature, however, with some studies showing prior antisaccade costs only for current prosaccade trials and no differences for antisaccades (Weiler & Heath, 2012); or even improved antisaccade performance following an antisaccade (Barton, et al., 2006; Ethridge, et al., 2009). The current study may clarify these conflicting implications from theories of task switching and prior antisaccade costs in the case of repeated antisaccade trials (i.e. task switching suggests better performance due to response priming, while prior antisaccade costs necessitate worse performance from lingering inhibition).

Additionally, the present study explored the effects of task design through changes to trial presentation style and the timing of fixation and saccade cues. The previous studies that manipulated saccade probability differed in their stimulus design: Massen (2004) used brief saccade type cues (prosaccade or antisaccade) with an overlap condition, while Chiau et al. (2011) did not provide any preparation time, simply including the cue for trial type in the target array. The current study compared cue timing parameters, as well as “overlap” and “gap” presentation styles. Overlap designs include the presentation of a trial type cue that remains visible after the target is displayed. Gap designs, on the other hand, present the trial cue first, then the “gap” (a blank screen typically lasting ~200 ms), and finally the peripheral target by itself. Reaction times generally are reduced in gap conditions, while error rates are higher than other presentation styles (Fischer & Weber, 1997; Saslow, 1967). The current study investigated whether these response patterns held true when the proportion of prosaccades and antisaccades in a run was varied, as well as the amount of preparation allowed by fixation and cue times of different lengths. The relationship between prosaccade and antisaccade percent correct and reaction time also was explored across timing conditions to replicate previous reports of speed accuracy trade-offs, particularly in regard to prosaccade RT and antisaccade percent correct (Crawford, Parker, Solis-Trapala, & Mayes, 2011; Ethridge, et al., 2009; Li, et al., 2012).

Furthermore, the current design parameters were selected based on an event-related design for use in the functional magnetic resonance imaging (fMRI) environment, because a tertiary purpose of the study was to determine the most suitable design to carry forward into future fMRI research. Therefore, the design included sufficient fixation time to allow baseline comparisons of the fMRI blood oxygen level dependent (BOLD) signal, and prosaccades and antisaccades were distributed such that the neural signals arising from each task could be optimally distinguished (Amaro & Barker, 2006; Dale, 1999; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). This consideration necessarily differentiates the present work from the previous studies using behavioral designs where stimuli could appear in any order with any inter-trial interval.

For the present study, eye movement data were collected for prosaccade and antisaccade trials from the five runs with various proportions of each trial type: 1) 100% prosaccades/0% antisaccades; 2) 75% prosaccades/25% antisaccades; 3) 50% prosaccades/50% antisaccades; 4) 25% prosaccades/75% antisaccades; and 5) 0% prosaccades/100% antisaccades, which hereafter will be referred to by only the antisaccade proportion. Comparisons were made between prosaccades and antisaccades, and within each trial type for the various levels of the probability manipulation. It was hypothesized that response characteristics would show that 1) the 0% antisaccade run (all prosaccades) is the least demanding and participants would have the highest percent correct (fewest directional errors) and respond most quickly. 2) The 100% antisaccade run requires higher levels of cognitive control, and performance on this run would be worse than for prosaccade trials (more erroneous responses and slower). Compared to antisaccade responses in the mixed runs, however, more correct and faster responses were predicted in the 100% run because of repetition priming and the lack of maintaining multiple task sets in working memory. 3) The 50% antisaccade run involves the most frequent task switching; therefore, a low percentage of correct responses and long response latencies were expected specifically on trials that involve a switch from antisaccade to prosaccade or vice versa, relative to repeated trials. 4) Finally, it was hypothesized that the 25% and 75% antisaccade runs would show equal effects of task switching (both involve similar numbers of switches/repeats), but different effects of cognitive load. When considering prosaccades and antisaccades separately in these two runs, each would elicit worse performance in the run that contains the fewest of that trial type because the other, more frequent saccade response program would be primed and cause interference in preparation for the less frequent type.

In regards to the alterations in design timing, it was predicted that 1) shorter saccade type cues would lead to worse performance across runs by allowing less preparation time before trials. 2) The use of a gap condition as opposed to an overlap condition would cause a general reduction in response times and percentage of directionally correct responses as observed in previous studies (Fischer & Weber, 1997; Forbes & Klein, 1996; Saslow, 1967), due to attentional disengagement from fixation (Craig, et al., 1999; Jin & Reeves, 2009) and motor preparatory activity (Rolfs & Vitu, 2007) during the gap. 3) Visual orienting speed (as indexed by prosaccade reaction time) would exhibit a positive relationship with antisaccade percent correct, such that participants with slower response times would generate more correct responses (Crawford, et al., 2011; Ethridge, et al., 2009; Li, et al., 2012).

To summarize, the current study investigated the limitations of the saccadic system through manipulation of cognitive load with trial type probability. Participants performed several single- and mixed-trial runs of prosaccades and antisaccades, with percentage of correct responses and response latency recorded to index task difficulty and response characteristics. Volitional saccade generation, inhibition, task set maintenance, and task switching processes contribute singly and collectively to the cognitive load of a saccade run. If the saccadic system has a capacity limit similar to other executive functions, performance on the most demanding trials should be worse than for trials requiring minimal cognitive control as the neural network struggles to effectively process conflicting inputs and select the appropriate behavioral output. Understanding how the global and local context of a saccade trial influences performance builds upon previous work characterizing this neural system and its cognitive control processes, and models the functioning of the executive control system as a whole. Thus, researchers can form a more precise theory of how cognitive control processes supervise basic functioning and how the brain responds to increasing cognitive demands.

CHAPTER 2

METHODS

Participants

Participants were recruited from the University of Georgia Department of Psychology's online undergraduate research pool. Students enrolled in introductory psychology classes were required to participate in research activities or complete an alternate written assignment. One hundred and twenty-three students (18 to 28 years old) participated in this study all together. Of the four stimulus conditions (described below), fifty-nine participants completed Condition 1, twenty completed Condition 2, twenty-one completed Condition 3, and twenty-three completed Condition 4. All activities were approved by the Institutional Review Board of the University of Georgia.

Saccade Task Design

Participants were assigned to one of four stimulus conditions based on the date of their participation, as conditions were collected sequentially. Within a condition, all participants performed five runs of saccade trials. The runs differed in the relative proportion of prosaccades to antisaccades: one run was 100% prosaccades and 0% antisaccades, a second run was 75% prosaccades and 25% antisaccades, a third run was 50% prosaccades and 50% antisaccades, a fourth run was 25% prosaccades and 75% antisaccades, and a fifth run was 0% prosaccades and 100% antisaccades (see Table 2.1). The order in which participants performed these five runs was counterbalanced within a condition, such that across a set of 10 participants each run was equally likely to be presented in each of the five ordinal positions.

All conditions utilized event-related timing with interleaved saccade trial types (with the exception of the 0% and 100% antisaccade runs) and random inter-trial fixation periods. The timing was optimized for the functional magnetic resonance imaging (fMRI) environment (using scripts from AFNI neuroimaging software (Cox, 1996)) to maximally distinguish hemodynamic response functions (Miezin, et al., 2000) from brain activity in response to fixation, prosaccade, and antisaccade trials. Runs lasted five minutes and sixteen seconds each, began with at least five seconds of fixation and ended with at least ten seconds of fixation. Within a run, fixation periods were pseudorandomly dispersed among the saccade trials according to the most efficient design determined by the AFNI script (Birn, Cox, & Bandettini, 2002).

For all conditions, fixation trials consisted of a light gray cross in the center of a black background; participants were instructed to stare at the cross whenever it appeared on the screen. Prosaccade trial cues added a square around the cross, which indicated to the participant that they should look towards the peripheral stimulus that would soon appear. Antisaccade trial cues added a diamond around the fixation cross, which informed the participant not to look at the upcoming stimulus, but instead to glance to the mirror location (opposite side, same distance from the center). The peripheral cue to initiate the appropriate saccadic response was itself a filled circle (see Figures 2.1-2.2). All stimuli were two centimeters in height and width (participants were positioned such that this subtended approximately 1 degree of visual angle), and the peripheral stimulus appeared randomly either left or right of center at 5 or 10 degrees.

Each stimulus condition consisted of these same basic elements with particular changes made to the stimulus design at three points during data collection (yielding four distinct design conditions). In the initial stimulus design (Condition 1), fixation trials were jittered between 1500 and 7500 milliseconds (ms), with an average inter-trial interval (ITI) of 3000 ms of fixation. Trial type cues then appeared (square or diamond) and lasted for 1000 ms. Finally the circle appeared to the left or right of the central square or diamond and both remained on screen for another 1000 ms while the participant made their response (Figure 2.1). Conditions 2, 3, and 4 presented gap trials instead of overlap and differed from each other in the timing of the fixation and trial type cue. In Condition 2, the fixation lasted between 1000 and 7000 ms (average ITI of 2500 ms). The trial type cue then appeared for 1500 ms, followed by a 200 ms black screen (gap), and finally the peripheral circle was displayed alone for 800 ms. For Condition 3 the timing was altered slightly; however, the images and their order were identical to Condition 2. The trial type cue time was reduced to 500 ms and the fixation trials were reciprocally increased to between 2000 to 8000 ms, with an average ITI of 3500 ms. In Condition 4 the timing of the fixation and cue was changed again such that fixation varied from 1000 to 6000 ms (average ITI of 2200 ms) while the cue lasted for 500 ms (Figure 2.2).

Prior to beginning the task, participants completed a mixed saccade practice run: in the first three conditions, the practice was 20 trials long; for Condition 4 the participants performed a full 80-trial practice run of half prosaccades and half antisaccades. For the task proper in the first three conditions, each of the five runs consisted of 60 total saccade trials according to the assigned proportion (e.g. 25% run had 45 prosaccade and 15 antisaccade trials). Thus, for the overall experiment each participant completed 300 saccade trials (150 prosaccades and 150 antisaccades). In Condition 4, the simultaneous reduction of both fixation and cue time allowed for a greater number of trials per run. Therefore, each run in this condition consisted of 80 trials, yielding 400 total saccades; however, only the first 60 trials of each run were analyzed to allow for equivalent comparison with the other conditions.

Procedure

Each participant first provided written informed consent and completed a thirteen-item demographic survey, which included questions on age, gender, race, handedness, grade point average, native language, and corrective lenses. Participants were then shown still images of the stimulus presentation and instructed how to respond to each shape when they saw it. Participants were not explicitly informed about the different probabilities in each run, merely that they may see more or fewer of each shape throughout the experiment, but to keep responding per the instructions. They were then seated with their head in a chin rest that was 120 cm in front of the display monitor (Samsung 40-inch LCD). The eye-tracking apparatus (EyeLink II, SR Research, Ontario) was fitted on the participant’s head with an adjustable headband; two small infrared cameras were directed at the participant’s eyes and kept out of their line of sight for the stimuli. Participants were instructed to keep their heads still during the task and move only their eyes as quickly and accurately as possible to the correct location. Participants sat in a quiet, darkened room, while the researcher monitored performance from an adjacent room. Once the pupils were identified by the software and being tracked, the participant began the task. Prior to beginning each run, two calibrations were performed: the first was EyeLink’s built-in nine point calibration to configure the participant’s gaze position relative to four sensors attached to the display monitor; the second was a horizontal seven point calibration used by in-house scoring scripts.

Each participant completed the mixed practice run, followed by the five counterbalanced task runs (*0% Anti*, *25% Anti*, *50% Anti*, *75% Anti*, and *100% Anti*). Participants were allowed a short break between runs to rest as desired. Stimuli were presented using Presentation Software (Neurobehavioral Systems, Inc., Albany, CA) in a darkened room while the relative pupil position of both eyes was sampled and digitized every 2 ms (500 Hz).

Analysis

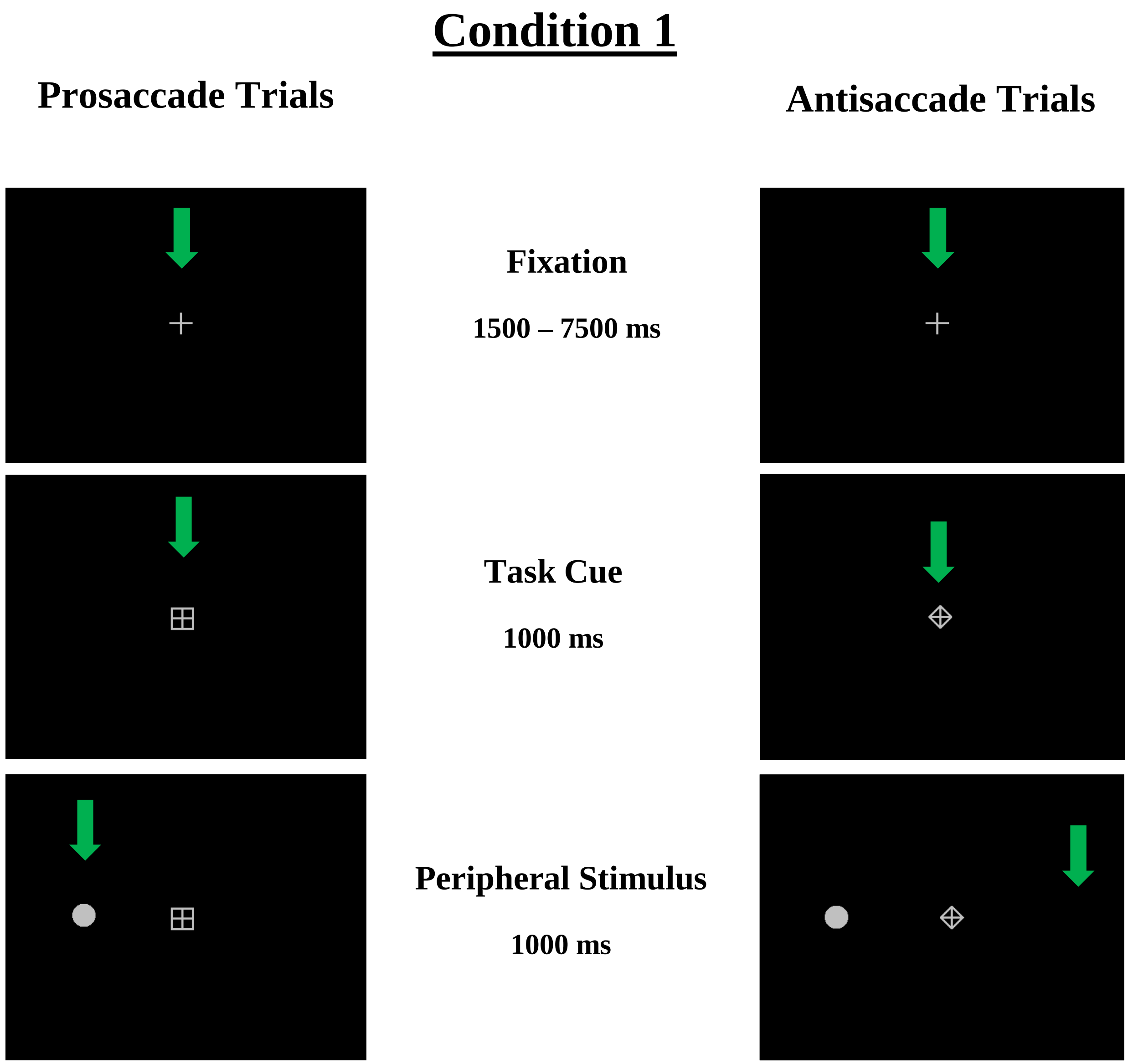
Eye position data were scored using in-house scripts written in Matlab (MathWorks, Natick, MA). The seven-point calibration from each run was first plotted to determine the relative position of certain reference points on the screen and the corresponding amplitude of eye movements. Data from one eye (with the cleanest recording) was selected for use in the subsequent scoring analysis. The scripts epoched the continuous data for a run into individual trials based on triggers sent from Presentation to EyeLink at the end of each saccade trial. The horizontal position of the participant's gaze was plotted alongside its velocity. Trials were manually scored for initial direction of response and response latency. Saccade onsets were defined by an initial minimum velocity of 20°/sec and ended when the velocity fell below this threshold again. Any trials with blinks at stimulus onset, no response, anticipatory saccades (less than 90 ms response latency or during the gap period), or insufficient data quality were excluded from further analyses. For all conditions, only responses within 800 ms of peripheral target onset were scored.

Data from Condition 1 were analyzed across runs for percent correct, response latency for correct and error trials, gender differences, task switching interactions, and prior antisaccade costs. A subset of participants (N=20) from Condition 1 were then compared to Conditions 2, 3, and 4 to examine effects of the stimulus design and timing on performance measures. Analyses were performed using SAS Version 5.1 (SAS Institute Inc., Cary, NC) and SPSS Version 20 (IBM Corp., Armonk, NY) statistical software packages.

Table 2.1 Study Design. All participants completed five runs of varying saccade load, but were assigned to only one stimulus design condition.

Between Subjects

	Condition 1	**Condition 2**	**Condition 3**	**Condition 4**
Within Subjects	100% Prosaccades/ 0% Antisaccades			
	75% Prosaccades/ 25% Antisaccades			
	50% Prosaccades/ 50% Antisaccades			
	25% Prosaccades/ 75% Antisaccades			
	0% Prosaccades/ 100% Antisaccades			



<u>Figure 2.1</u> Stimuli Presented During Saccade Trials for Condition 1. Prosaccade and antisaccade trials were presented in an interleaved manner with the task cue indicating the trial type to participants. Fixation times were randomly dispersed between trials within a minimum of 1500 milliseconds, but timing was constant across participants. The green arrows show the correct gaze position and did not appear during the task.

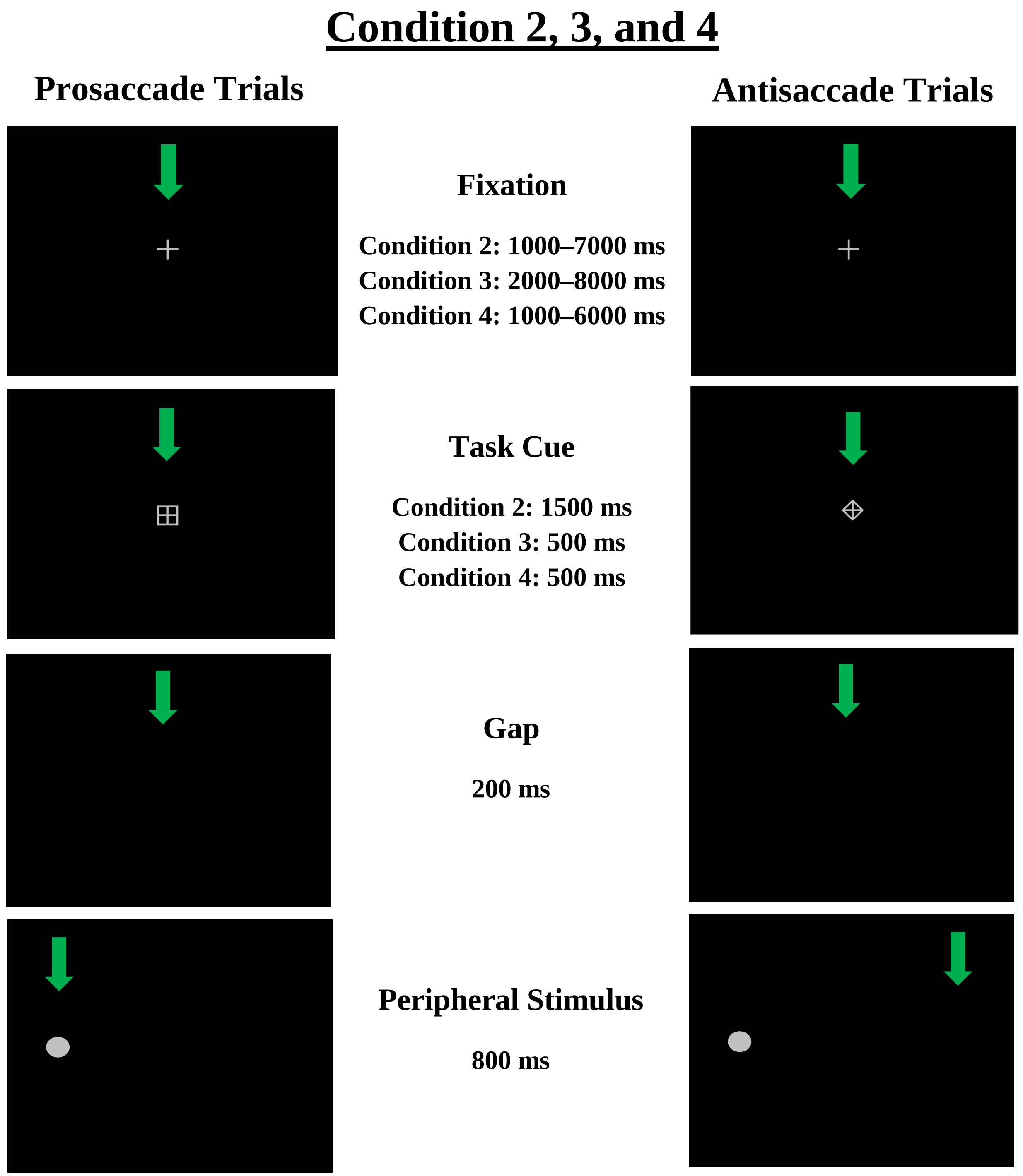


Figure 2.2 Stimuli Presented During Saccade Trials for Conditions 2, 3, and 4. Prosaccade and antisaccade trials were presented in an interleaved manner with the task cue indicating the trial type to participants. Conditions 2, 3, and 4 differed in the fixation and task cue timing, with Condition 2 having shorter fixation corresponding to longer cue time; Condition 3 having longer fixation with a short cue, and Condition 4 having short fixation and short cue. Fixation times were randomly dispersed between trials, but timing was constant across participants within a condition. The green arrows show the correct gaze position and did not appear during the task.

CHAPTER 3

RESULTS

Condition 1Probability Manipulation

Demographics

59 participants completed the task with the first stimulus design condition. Five subjects' data were excluded due to poor quality or missing runs. Demographic information for the first condition is summarized in Table 3.1. The majority of participants were female, right-handed, white, and native English speakers.

Table 3.1 Condition 1 Demographics. Summary of demographic information for participants in the first condition. Where applicable, data is reported as mean (standard deviation).

N	Age (years)	Gender (% Female)	Handedness (% Right)	Race (%)	Native Language (% English)	Grade Point Average (4-point scale)
54	19.3 (1.3)	76	94	70 White 15 Black 15 Other	89	3.4 (0.4)

Percentage of Correct Responses

Overall, correct responses were made for prosaccades more frequently than for antisaccades, as expected, with an average difference of 12.5% ($t(430)=13.8$, $p<.001$). A repeated-measures analysis of variance (ANOVA) was performed for prosaccades and antisaccades separately to compare across runs. A Mauchly's test of sphericity indicated unequal variances of the different cells, so Huynh-Feldt adjusted degrees of freedom were used for calculating significance levels. For prosaccades, there was a significant effect of run ($F(2,107)=10.04$, $p<.001$, $\varepsilon=.67$). Pairwise comparison tests (Figure 3.1) showed that percentage correct on the 0% antisaccade run (99.59% (standard deviation (SD) =1.2)) was greater than the 25% run (98.34% (3.8)), the 50% antisaccade run (97.33% (3.6)), and the 75% antisaccade run (95.55% (6.2)). Also, the 25% run was significantly better than the 75% run, though the 50% run did not differ from these two. For antisaccades, percentage correct did not differ across runs ($F(2,131)=.02$, $p>.05$, $\varepsilon=.83$), with an average of 85.2% (12.5).

Reaction Times

Overall, reaction times on correct prosaccade trials were faster than correct antisaccade trials by 66 ms ($t(430)=17$, $p<.001$). A repeated-measures ANOVA was performed for prosaccade and antisaccade reaction times separately to compare across runs (again with Huynh-Feldt adjusted degrees of freedom). For prosaccades, there was a main effect of run ($F(2, 124)=3.02$, $p<.05$, $\varepsilon=.78$). Pairwise contrasts (Figure 3.2) showed that in the 0% antisaccade run (i.e. all prosaccades; 226 ms (SD=27)) participants had faster reaction times than the 75% run (243 ms (51)), with the 25% and 50% run RTs falling in between these two. For antisaccades, there was a significant effect of run ($F(2, 131)=3.32$, $p<.05$, $\varepsilon=.63$). Pairwise comparisons indicated that responses in the 25% antisaccade run (291 ms (43)) were faster than the 75% run (306 ms (41)) and the 100% run (310 ms (39)); the 50% run followed the same pattern but was not significantly different from the other runs.

For error trials (initial glance in the incorrect direction), prosaccade reaction times are not reported due to the small number of errors (< 5% of total trials per run). For antisaccades across runs, 14.8% of trials were errors, with at least 44 out of 54 participants committing an error in each run. Error trial reaction times were significantly shorter than correct trials for all runs ($t(43)>3$, $p<.005$). A one-way ANOVA was performed for RTs of antisaccades error trials to compare across runs and revealed no differences in reaction time (Figure 3.3).

Gender Differences

To examine any possible effects of gender on response characteristics, percentage of correct responses and correct reaction times were compared between males and females. Females outnumbered males 41 to 13 due to the composition of students in the research pool, but only minimal differences were evident in performance. There were no significant differences in percent correct for prosaccades or antisaccades. T-tests on reaction times revealed no differences for prosaccades, but for antisaccades in the 100% run, males were significantly faster than females ($t(52)=2.5$, $p<.05$). No other comparisons reached significance (Tables 3.2 and 3.3).

Task Switching

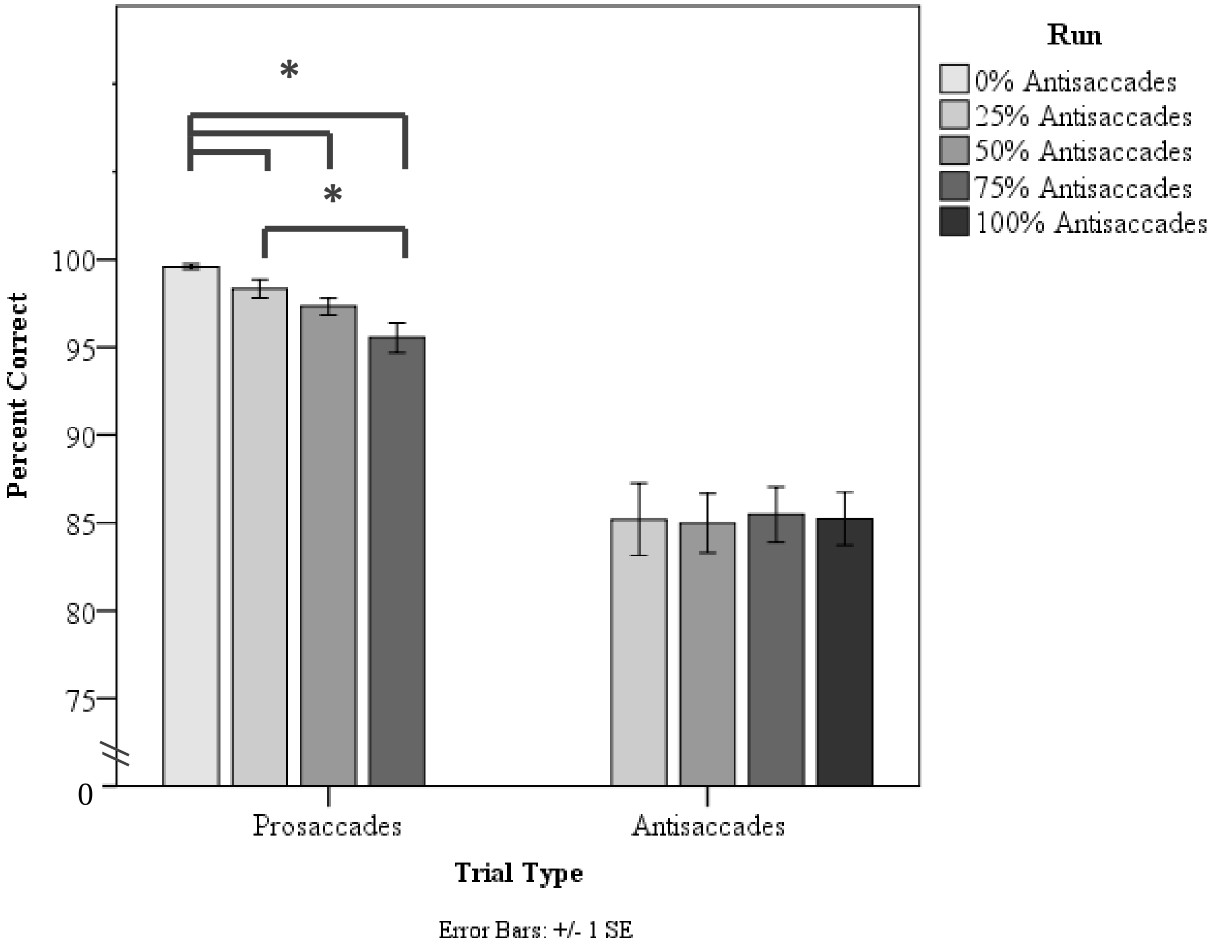
To examine the local effects of trial history, trials were sorted based on current and previous trial type (Cherkasova, et al., 2002; Manoach et al., 2007): prosaccades following a prosaccade (repeated prosaccade), prosaccades following an antisaccade (switched prosaccade), antisaccades following an antisaccade (repeated antisaccade), and antisaccades following a prosaccade (switched antisaccade). A 3x2 (Run (25, 50, 75) by Task Switch (repeated/ switched)) within-subjects ANOVA was performed on percent correct and correct reaction times for prosaccades and antisaccades separately. For percent correct on prosaccade trials, there was a main effect of task switching ($F(1,53)=33.5$, $p<.001$) such that participants were more accurate on repeated trials than switched; there was also an interaction between task switching and run (with Huynh-Feldt adjusted degrees of freedom), ($F(1,85)=3.8$, $p<.05$, $\varepsilon=.80$), with percentage correct on switched trials in the 75% run being much lower than the other conditions (Figure 3.4A). For antisaccade percent correct, there was an interaction between switching and run ($F(2,106)=4.7$, $p<.05$), with repeated trials showing more correct responses on the 50% run than switched trials, while performance on the other runs was equivalent (Figure 3.4B).

For reaction time, prosaccades again showed a main effect of task switching ($F(1,53)=27.1$, $p<.001$) with repeated trials being faster than switched trials, and an interaction between switching and run ($F(2,106)=4.3$, $p<.05$) with repeated trial RTs in the 25% run being essentially as long as the switched RTs (Figure 3.5A). Antisaccade trials showed only a main effect of task switching ($F(1,53)=6.7$, $p<.05$), with the repeated trials being slower than the switched (Figure 3.5B).

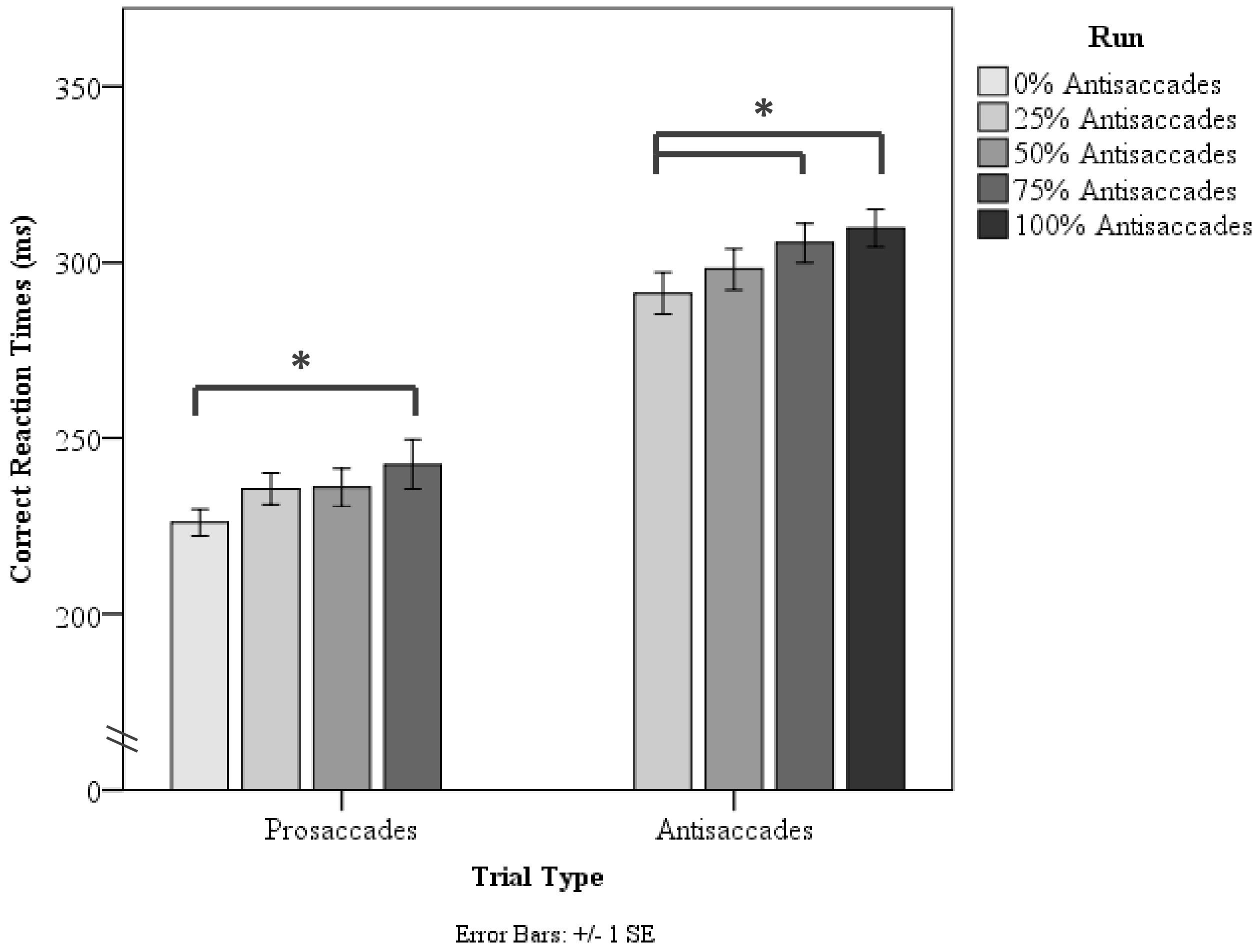
Prior Antisaccade Costs

Since task switching reaction time analyses showed a cost for prosaccades and a switch benefit for antisaccades, trial differences were instead examined within the framework that a prior antisaccade may affect current trial performance more than a switch (Barton, et al., 2006; Lee, et al., 2011). Within the two current trial types (antisaccades or prosaccades), differences in percent correct and reaction time were computed for prior antisaccade trials minus prior prosaccade trials. These differences represent the cost of following an antisaccade trial, with positive values indicating higher percent correct or longer reaction times for trials following an antisaccade. For prior antisaccade costs in percentage of correct trials on prosaccades, all runs showed a significant decrease following an antisaccade (25: -3.1% (SD=6.7); 50: -2.8% (6.2);

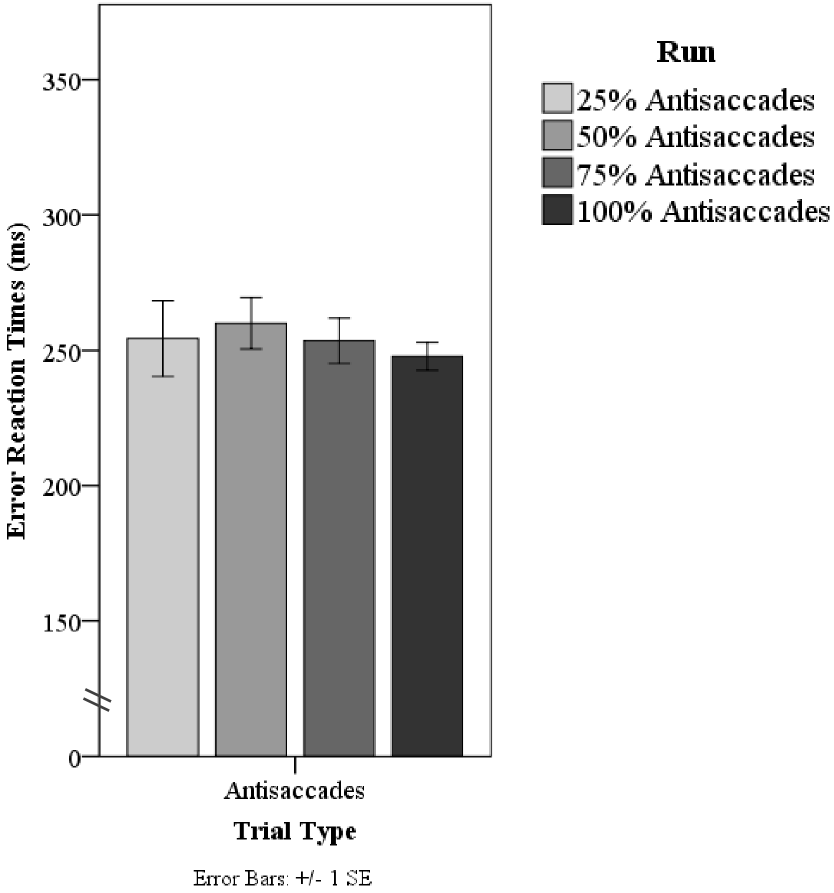
75: -7.1% (12.4)). Also, the 50% run differed significantly from the 75% run (*t*(53)=2.5, *p*<.05). For antisaccades, on the other hand, only the 50% antisaccade run differed from zero (6.6% (1.8)), indicating better performance following an antisaccade trial (Figure 3.6A). Percent of correct responses on this run was also significantly greater than in the other two runs (*t*(53)>2.5, *p*<.05). For the reaction time costs on both prosaccades and antisaccades, the 50% antisaccade (pro: 19 ms (25); anti: 8 ms (28)) and 75% antisaccade runs (pro: 20 ms (38); anti: 15 ms (35) showed significantly slower RTs following an antisaccade trial (Figure 3.6B). For prosaccades the 50% and 75% runs were greater than the 25% run (*t*(53)>2.5, *p*<.05), while for antisaccades these differences were not different across runs.



<u>Figure 3.1</u> Condition 1 Percent Correct. Data from 54 participants showing percentage of correct responses (initial glance in the expected direction) for prosaccades and antisaccades in each of the five runs. For prosaccades, the 0% antisaccade run had significantly higher percent correct than the other three runs, and the 25% antisaccade run was better than the 75% run. There were no significant differences between the runs for antisaccade trials. Significance levels were $p<.05$; error bars represent 1 standard error.



<u>Figure 3.2</u> Condition 1 Correct Reaction Times. Data from 54 participants showing average reaction times for only correct trials for prosaccades and antisaccades in each of the five runs. For prosaccades, RTs in the 0% antisaccade run were faster than the 75% antisaccade run. For antisaccades, RTs in the 25% antisaccade run were faster than the 75% and 100% antisaccade runs. Significance levels were $p<.05$; error bars represent 1 standard error.



<u>Figure 3.3</u> Condition 1 Error Reaction Times. Average response latencies for error trials (initial glance in incorrect direction) for antisaccades in four runs, showing no differences between the runs. Error times for each run were significantly shorter than the correct reaction times (compare to Figure 3.2). Data are shown from 44 participants with errors for the 25% run, 49 from the 50% run, 52 from the 75% run, and 53 from the 100% run. Significance levels were p<.05; error bars represent 1 standard error.

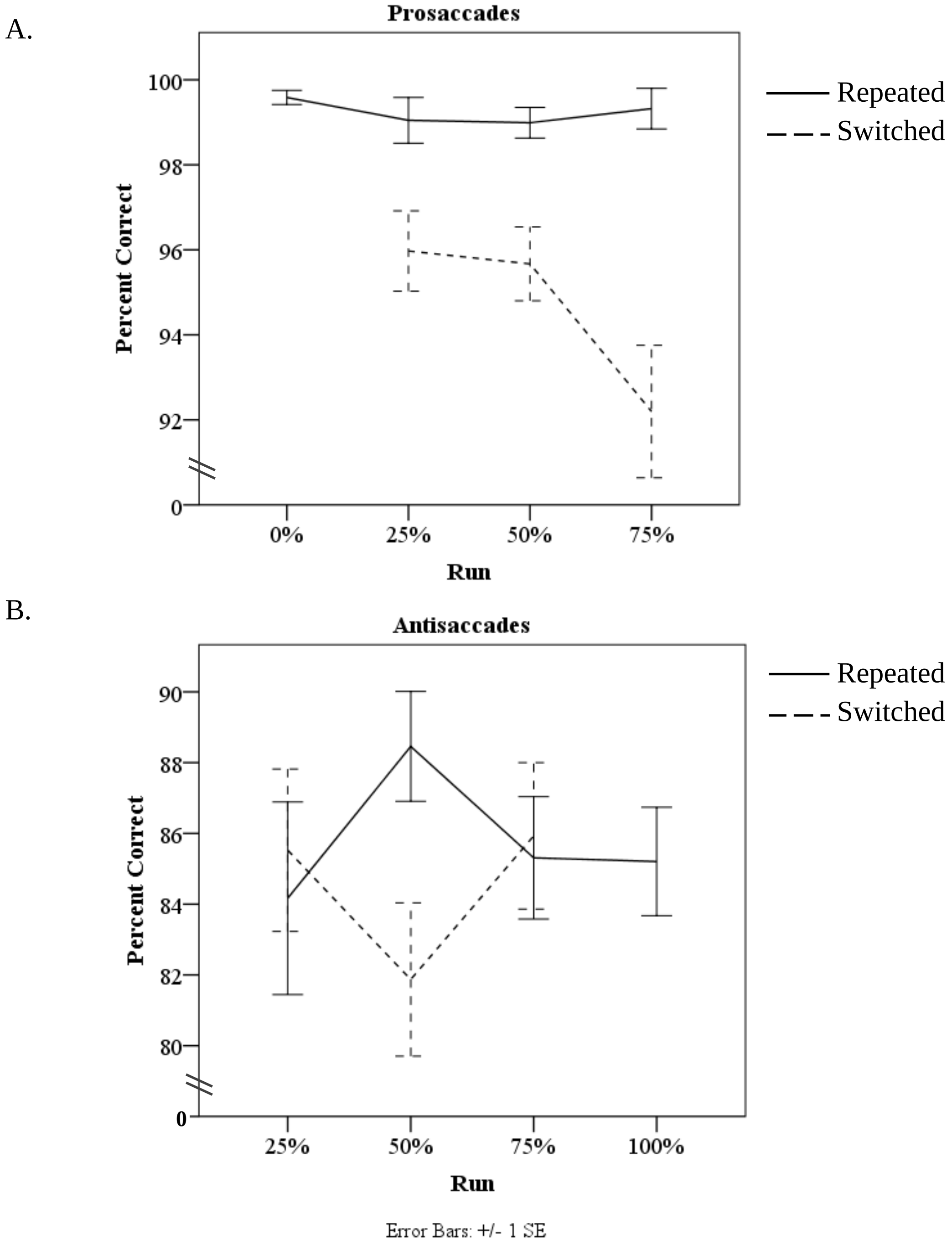
<u>Table 3.2</u> Gender Differences, Percent Correct. Percent correct for prosaccades and antisaccades for males (N=13) and females (N=41). Data are reported as mean (standard deviation). There were no significant differences between genders. Labels refer to the proportion of antisaccades in each run.

	Run:	0%	25%	50%	75%	100%
Prosaccades	Males	99.4(1.1)	98.9(1.9)	97.6(4.1)	96(5.1)	-
	Females	99.6(1.2)	98.2(4.2)	97.3(3.4)	95.4(6.6)	-
Antisaccades	Males	-	83.1(18)	89.0(8.9)	87.9(12.7)	85.2(12.2)
	Females	-	85.9(14.3)	83.7(13)	84.7(11.3)	85.3(10.8)

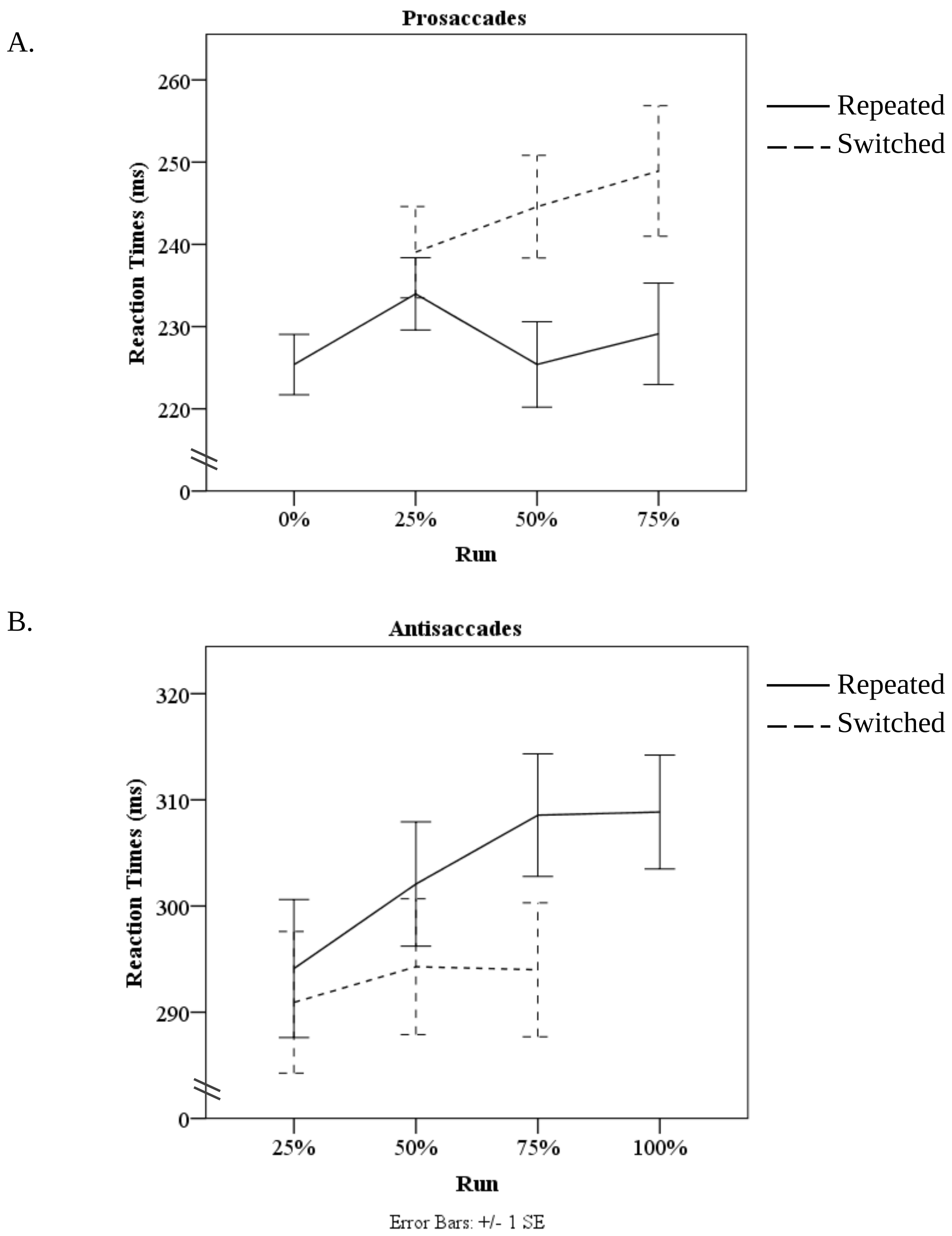
<u>Table 3.3</u> Gender Differences, Correct Reaction Times. Correct reaction times in milliseconds for prosaccades and antisaccades for males (N=13) and females (N=41). Data are reported as mean (standard deviation). Only the 100% antisaccade run showed a gender effect, with faster reaction times for males. Labels refer to the proportion of antisaccades in each run.

	Run:	0%	25%	50%	75%	100%
Prosaccades	Males	223(30)	230(25)	234(26)	231(37)	-
	Females	227(27)	237(34)	237(43.4)	246(55)	-
Antisaccades	Males	-	281(32)	285(37)	296(32)	287(37)*
	Females	-	294(46)	302(44)	308(43)	317(38)*

* significant gender difference, $p<.05$

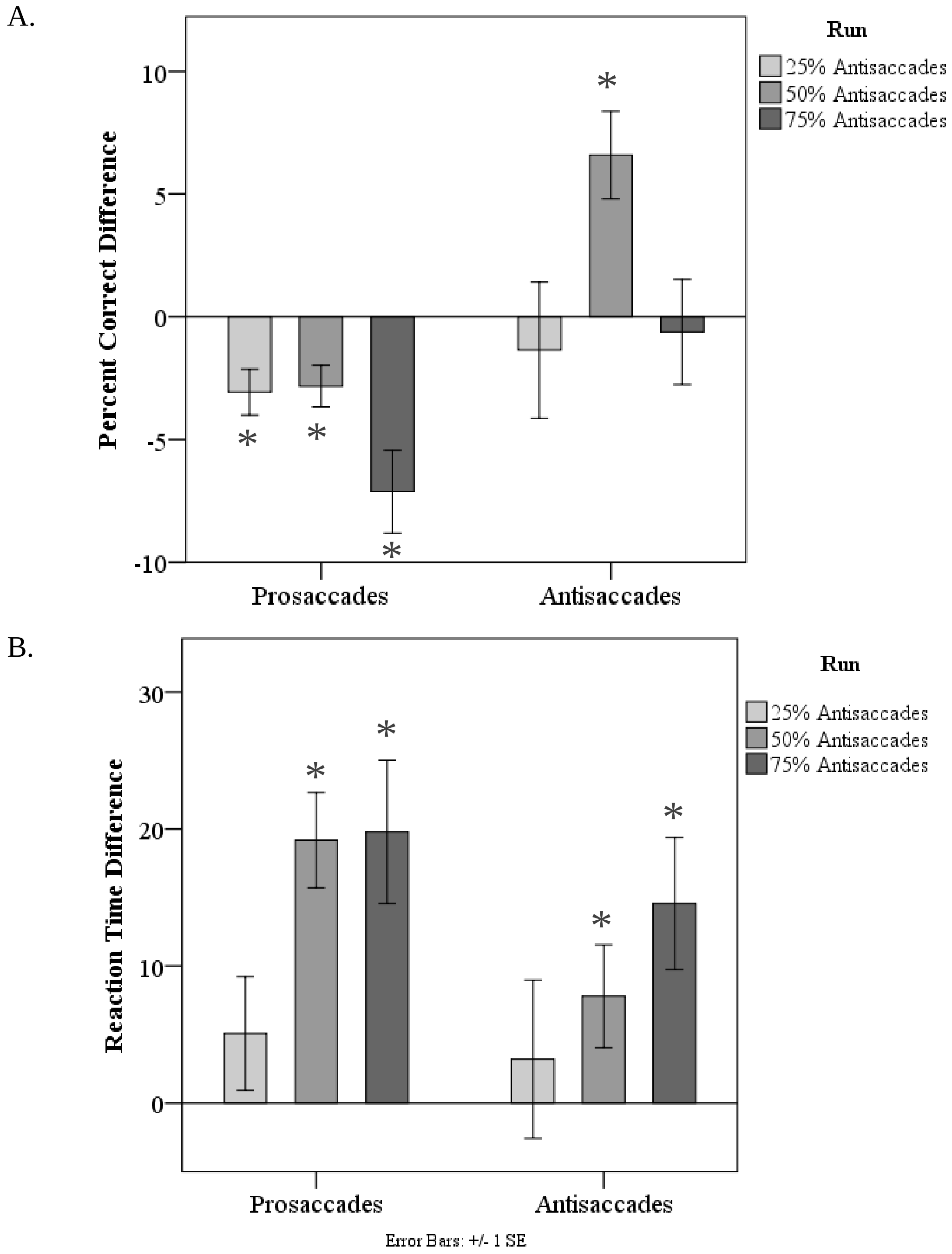


<u>Figure 3.4</u> Condition 1 Task Switching Percent Correct. Percent correct for prosaccades (A) and antisaccades (B) for each run based on the previous trial type. Prosaccades showed a main effect of task switching and an interaction between switching and run; antisaccades showed only an interaction between switching and run. The 0% and 100% runs were not included in the ANOVA and are shown here only for reference. Significance levels were $p<.05$; error bars represent 1 standard error.



Error Bars: +/- 1 SE

Figure 3.5 Condition 1 Task Switching Reaction Times. Reaction times for prosaccades (A) and antisaccades (B) for each run based on the previous trial type. Prosaccades had a significant main effect of task switching and an interaction between switching and run; antisaccades showed a main effect of task switching. The 0% and 100% runs were not included in the ANOVA and are shown here only for reference. Significance levels were p<.05; error bars represent 1 standard error.



<u>Figure 3.6</u> Condition 1 Prior Antisaccade Costs. Percent correct (A) and reaction time (B) costs following antisaccade trials for current prosaccades and antisaccades across the mixed runs. Positive values indicate higher percent correct or longer reaction times following an antisaccade trial. A) In percent correct for prosaccades, all runs were significantly less than zero, indicating worse performance following an antisaccade trial. For antisaccades, the 50% run was significantly greater than zero, indicating better performance following an antisaccade trial. B) In reaction times for both prosaccades and antisaccades the 50% and 75% antisaccade runs showed differences significantly greater than zero, indicating slower responses after antisaccades. Significance levels were $p<.05$; error bars represent 1 standard error.

Comparison across Conditions

Demographics

The effects of the stimulus design manipulations were investigated through the comparison of the four different timing conditions. The last 20 participants from Condition 1 were compared with all participants from the other three conditions except for four participants who were excluded from analysis due to poor data quality (one participant from the second condition, one from the third, and two from the fourth). Thus 20 participants remained from Conditions 1 and 3, 19 participants in Condition 2, and 21 participants in Condition 4. Condition 1 still had a large proportion of females, though Conditions 2, 3, and 4 were approximately balanced. Neither the average age ($F(3,76)=0.8$, $p>.05$), gender ($X^2(3, N=80) = 5.11$, $p>.05$), race ($X^2(15, N=80) = 12.05$, $p>.05$), nor grade point average ($F(3,70)=1.2$, $p>.05$) of participants differed significantly between conditions. Most participants were right-handed, white, and native English speakers. Demographic information for all conditions is summarized in Table 3.4.

Percentage of Correct Responses

A 4x4 (Condition (between subjects) by Run (within subjects)) ANOVA was performed separately for prosaccades and antisaccades to compare the percentage of correct responses across conditions. There were no significant main effects of condition for either trial type. For prosaccades, a Mauchly’s test of sphericity indicated unequal variances of the different cells, so Huynh-Feldt adjusted degrees of freedom were used for calculating significance levels. There was a main effect of run ($F(2,161)=7.2$, $p<.01$, $\varepsilon=.66$), showing a general trend of poorer performance on prosaccades on runs with larger proportions of antisaccades (Figure 3.7A). For antisaccades, there was also a main effect of run ($F(3,228)=3.3$, $p<.05$), where performance on runs with larger proportions of antisaccades tended to be more accurate. Antisaccades also showed an interaction between run and condition (*F*(9,228)=2.1, *p*<.05), with Conditions 1 and 2 showing less difference in percent correct across runs than Conditions 3 and 4 (Figure 3.7B).

Reaction Times

An ANOVA was performed for reaction times, with prosaccades showing main effects of condition (*F*(3,76)=25.7, *p*<.001) and run (*F*(2,186)=8.7, *p*<.001, ε=.71), again using Huynh-Feldt adjusted degrees of freedom. Condition 1 (overlap) RTs were much slower than Conditions 2, 3, and 4 (gap), and RTs increased with an increasing probability of antisaccades in the run (Figure 3.8A). For antisaccades, there were similar main effects of condition (*F*(3,76)=7.5, *p*<.001) and run (*F*(3,228)=8.1, *p*<.001), with Condition 1 having the longest and Condition 4 the shortest RTs. For the run effect, the antisaccade RTs also increased with larger proportions of antisaccade trials in the run (25% run was faster and 100% run was slowest, Figure 3.8B).

Regressions

In order to investigate the relationships between percent correct and correct reaction times for both prosaccades and antisaccades, data were combined across all four conditions (80 participants). Regression models were tested with linear and quadratic effects for each run between prosaccade percent correct, prosaccade reaction time, antisaccade percent correct, and antisaccade reaction time. The majority of these linear relationships were significant (*p*<.05), except the prosaccade percent correct versus prosaccade reaction time in the mixed runs, and prosaccade percent correct versus antisaccade percent correct in the 50% run. Quadratic effects explained significantly more variance than the linear model for five of the relationships (Table

3.5). Due to previous reports (Crawford, et al., 2011; Ethridge, et al., 2009; Li, et al., 2012; Massen, 2004) of the relationship between visual orienting speed (prosaccade reaction time) and failures of inhibition (antisaccade directional errors), this relationship was of particular interest and is displayed in Figure 3.9. All three mixed runs exhibited an inverted-U shaped relationship where shorter prosaccade latencies were associated with lower antisaccade percent correct, moderate latencies yielded high antisaccade percent correct, and long prosaccade latencies again were associated with lower percentage of correct responses.

Table 3.4 Comparison Demographics. Summary of demographic information for each of the four conditions. Where applicable, data is reported as mean (standard deviation).

Condition	N	Age (years)	Gender (% Female)	Handedness (% Right)	Race (%)	Native Language (% English)	GPA (4-point scale)
1	20	19.5 (1.4)	75	90	60 White 25 Black 15 Other	100	3.4 (0.4)
2	19	19.6 (2.1)	42	95	89 White 5 Black 5 Other	100	3.5 (0.4)
3	20	19.1 (0.8)	60	90	85 White 10 Black 5 Other	100	3.5 (0.4)
4	21	19.8 (1.9)	43	86	62 White 14 Black 24 Other	90	3.3 (0.3)

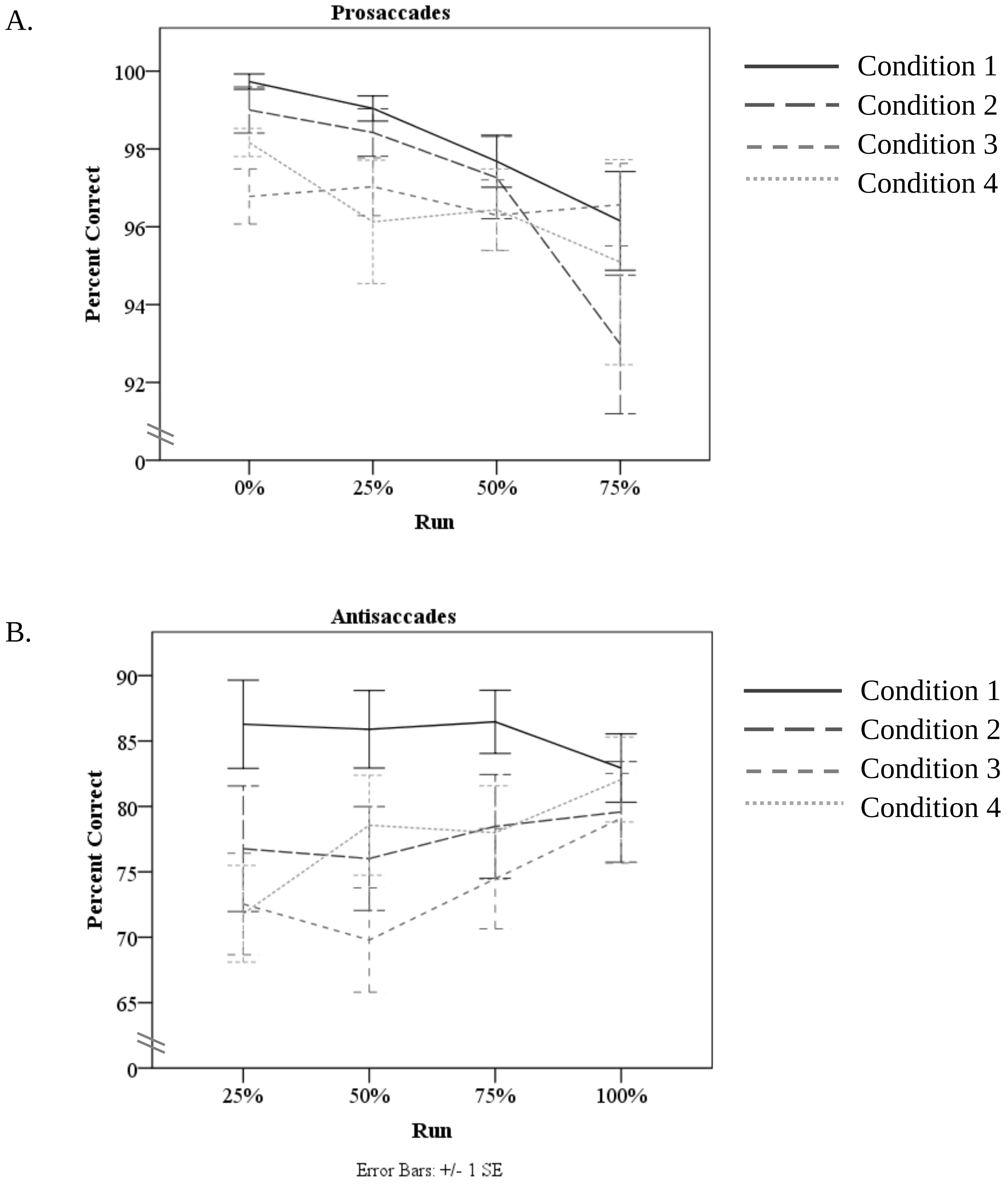


Figure 3.7 Percent Correct Comparison across Conditions. Average percentage of correct responses (initial glance in the instructed direction) for the four stimulus design conditions across the various runs for prosaccades (A) and antisaccades (B). Prosaccades showed only a significant main effect of run. Antisaccades showed a main effect of run as well as an interaction between run and condition. Significance levels were $p<.05$; error bars represent 1 standard error.

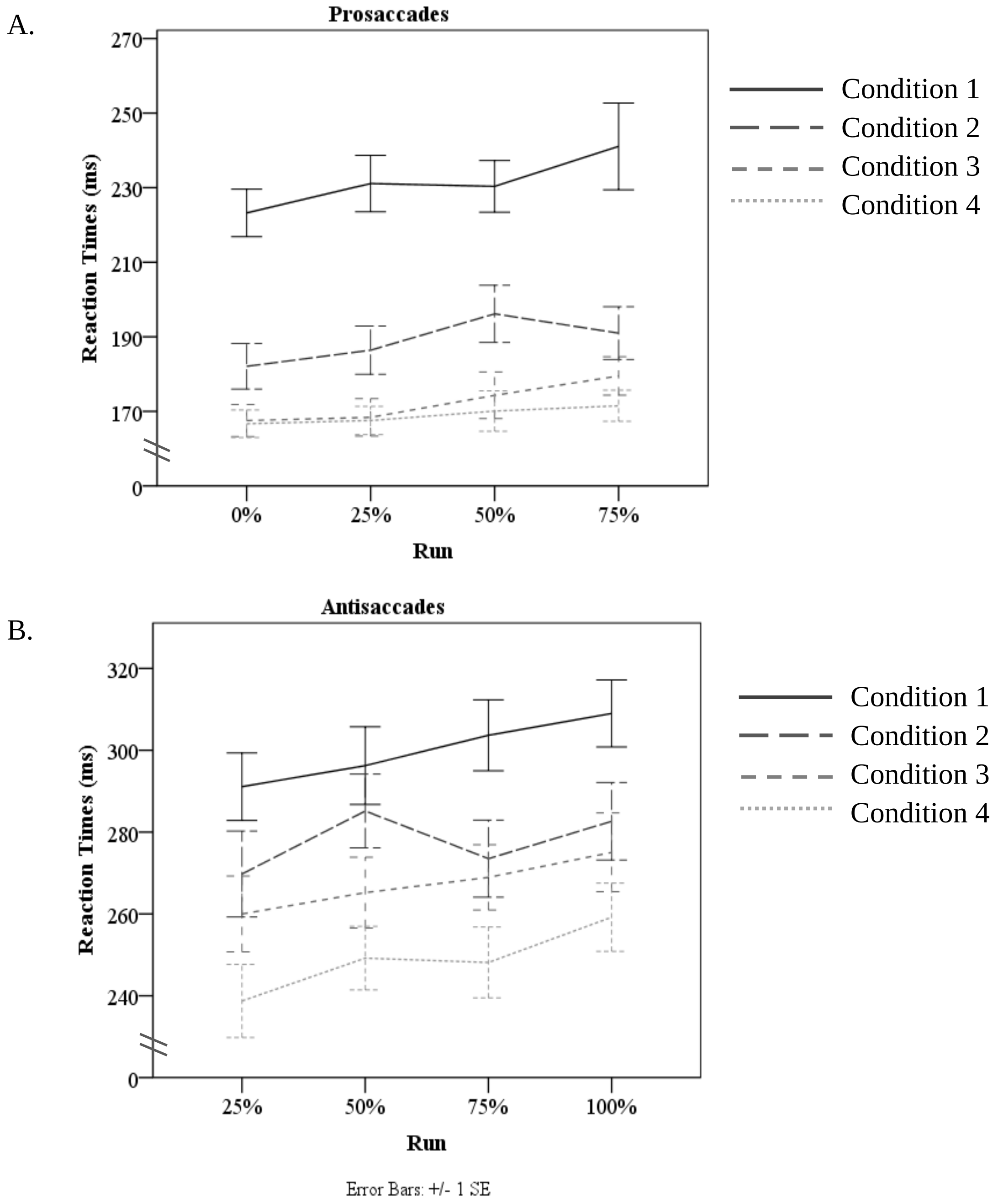
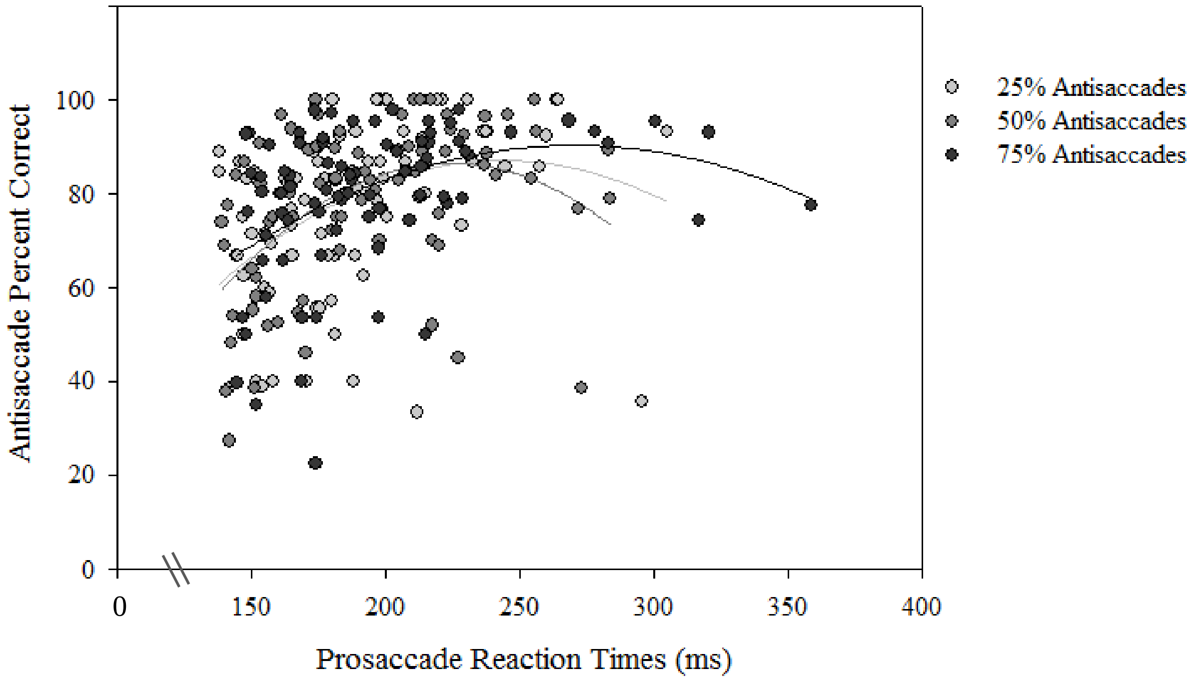


Figure 3.8 Reaction Time Comparison across Conditions. Average reaction times for the four stimulus design conditions across the various runs for prosaccades (A) and antisaccades (B). Both prosaccades and antisaccades showed main effects of run and condition, but no interactions. Significance levels were $p<.05$; error bars represent 1 standard error.

<u>Table 3.5</u> Prosaccade/Antisaccade Regressions, All Conditions. Proportion of variance accounted for (R^2) from linear or quadratic regressions for prosaccade and antisaccade percent correct and correct reaction times combined from all four conditions (N=80). Labels refer to the percent of antisaccades in the run.

Run	**Pro Percent Correct vs. Pro RT**	**Pro Percent Correct vs. Anti Percent Correct**	**Pro Percent Correct vs. Anti RT**	**Pro RT vs. Anti Percent Correct**	**Pro RT vs. Anti RT**	**Anti Percent Correct vs. Anti RT**
0%	.140**	-	-	-	-	-
25%	.018	.058*	.082**	.172 † **	.297**	.168 † **
50%	.000	.026	.055*	.238 † **	.271**	.085**
75%	.002	.058*	.259 † *	.175 † **	.341**	.172**
100%	-	-	-	-	-	.072 *

†quadratic, *p<.05, **p<.01



<u>Figure 3.9</u> Prosaccade RT vs. Antisaccade Percent Correct. Quadratic regressions with prosaccade correct reaction times in milliseconds and antisaccade percent correct in the mixed runs for all four conditions (N=80, see Table 3.5). Shades indicate the proportion of antisaccades in the run. All correlations are significant at the *p*<.01 level.

CHAPTER 4

DISCUSSION

The current study investigated the impact of varying putative cognitive load on saccade response characteristics through a manipulation of the relative proportion of prosaccade and antisaccade trials within a run, as well as the effect of timing parameters on these responses. Antisaccades require a greater degree of cognitive control than prosaccades, because one must inhibit the reflexive tendency to glance towards a newly appearing peripheral stimulus and volitionally generate a saccade in the opposite direction (Hutton, 2008; Munoz & Everling, 2004). Thus, a set of trials with many antisaccades was expected to be more challenging to participants than one with many prosaccades. Yet within each trial type, better performance was predicted when that saccade type was more probable (Chiau, et al., 2011; Massen, 2004), as its task set may be activated to a greater extent and more readily accessible. Additionally, trial history was expected to impact performance within a run, particularly when switching from an antisaccade to a prosaccade (Barton, et al., 2006; Cherkasova, et al., 2002; Lee, et al., 2011; Vermeiren, Liefooghe, & Vandierendonck, 2010; Weiler & Heath, 2012). Finally, by altering the timing of trial type cues and inter-trial fixation, this study examined the effects of preparation time on effective saccadic performance. Together these global and local cognitive demands reveal the nature of the saccadic response system when performing trials in runs with varying proportions of prosaccades and antisaccades.

Condition 1 Probability Manipulation

Results from the analyses of Condition 1 indicated that the percentage of correct responses on prosaccade trials gradually decreased as the proportion of prosaccades in the run decreased, while antisaccade responses did not differ across runs. The error rates for both saccade types reflect the difficulty and putative cognitive load of each run, yet they offer conflicting implications. For prosaccades, participants made more errors in runs where prosaccades were less frequent, perhaps as a result of the antisaccade task set being primed and thus interfering with normal prosaccade behavior (Rogers & Monsell, 1995). Accuracy was near 100% for the all prosaccade run, but in the mixed runs the task demands were higher (included complex antisaccades, had an increased working memory load due to the need to maintain multiple task sets (Unsworth, et al., 2004), required task switching reconfigurations), and participants' percent of correct responses decreased accordingly. Due to the increased cognitive demand, participants may have performed prosaccades in a more controlled manner in the mixed runs, making them susceptible to the effects of cognitive load (Stuyven, et al., 2000).

Conversely, antisaccade performance on the all antisaccade run was around 85% and more variable across individuals than prosaccade performance. Antisaccade trials already are cognitively demanding, and the probability manipulation in the mixed runs may not have increased the cognitive load enough on these trials to consistently affect the percentage of correct responses in the same way the easier prosaccades were affected. This result stands in contrast to a previous study using similar probability conditions: Massen (2004, Experiment 1) reported increased antisaccade error rate in runs with a lower proportion of antisaccades. She concluded that the lower probability of antisaccades served to slow the endogenous component of saccade generation and allow the prosaccade being programmed in parallel to reach the necessary threshold for completion first (as an error). The results from the current study, however, suggest that participants did not employ a strategy that utilized the higher frequency of antisaccade trials to improve performance. Antisaccade error rates in the current study were approximately 15% for all runs, yet in Massen (2004) they ranged from around 25 to 40%. Therefore, the current participants may not have been challenged enough to rely on prior probability information in Condition 1 (but see discussion on the comparison across conditions) as participants in Massen (2004) evidently did. Nonetheless, it was contrary to the hypotheses of the current study that antisaccade percent correct was not affected by the probability manipulation, while prosaccade trials did show an impact of cognitive load.

Reaction times yielded a different pattern of results from percentage of correct responses, increasing gradually for both prosaccade and antisaccade trials in parallel with the probability of antisaccades, again contrary to what was expected and what was observed in previous studies (Chiau, et al., 2011; Massen, 2004). One explanation for the increasing reaction times is that an overall inhibitory state is created by frequent antisaccades which slows down all responses of the saccadic system (Barton, et al., 2006; Manoach, et al., 2007; Vermeiren, et al., 2010). Following work in animal physiology on neural activity changes in motor preparation (Dorris, Pare, & Munoz, 2000), Barton and colleagues (2006) call this effect “response-system plasticity,” and suggest it may be related to suppression of saccade neurons in the frontal eye fields (Everling & Munoz, 2000) and superior colliculus (Everling, Dorris, Klein, & Munoz, 1999; Everling, Dorris, & Munoz, 1998) by prefrontal cortex or the supplementary eye field (Munoz & Everling, 2004; Schlag-Rey, Amador, Sanchez, & Schlag, 1997). The antisaccade trials require inhibition of the instinctive motor response towards the stimulus and, over time, repeated suppression of saccade-generating neurons may make it more difficult and time-consuming to reach the critical threshold for execution (Carpenter & Williams, 1995; Hanes & Schall, 1996).

The nature of the saccade performance in the mixed runs was investigated further in the context of trial history effects by sorting trial performance based on the preceding trial type. Previous work has shown that prior tasks can influence performance on the current trial and may be obscured when only considering overall differences in task behavior (Barton, et al., 2006; Ethridge, et al., 2009; Lee, et al., 2011; Manoach, et al., 2007; Monsell, 2003). In the current task, the same target (peripheral filled circle) cued the generation of both prosaccades and antisaccades; only the saccade type cue (square or diamond) indicated which task set to implement and necessitated a stimulus-response remapping in preparation for the target. If differences existed in responses for repeated trials (*pro*-pro or *anti*-anti) as well as switched trials (*anti*-pro or *pro*-anti), then the latent inhibitory effects could be said to equally influence trials in the mixed runs, regardless of local trial history and stimulus-response reconfigurations. The prosaccade results, however, indicated that differences in percentage of correct responses and reaction times predominated for only the switched trials. Switched trials yielded worse performance following an antisaccade, while repeated trials were comparatively faster and more accurate, revealing a behavioral cost for changing task sets. The switch costs also were greater with a decreasing probability of a prosaccade, with the 75% run (25% prosaccades) having the lowest percent of correct responses and longest RTs for switched prosaccades, while repeated trials remained constant across all runs (Figure 3.4A). Taken together, this pattern of results suggests that task switching demands were responsible for most differences in the prosaccade responses, perhaps due to diminished salience of the appearance of the stimulus (Fecteau &

Munoz, 2003) or task-set inertia (Allport, et al., 1994), though the degree of these effects was affected further by the probability manipulation and cognitive load of the run.

Antisaccade trials exhibited a distinct pattern from prosaccade trials: reaction times were slower for repeated trials (and increased with the probability level of antisaccades), while percentage of correct trials showed no differences between repeated and switched trials except for in the 50% run. Here, repeated trials were better than average and switched trials were worse, a similar pattern to prosaccade trials. The 50% run involved the most task switching and, perhaps, this increased demand was enough to make participants rely upon local trial history, whereas in the 25% and 75% runs either repeated or switched trials were infrequent enough to undercut such a strategy. All of the task switching effects can be attributed to prior antisaccade costs, with the exception of this increase in percentage of correct responses on repeated antisaccades in the 50% run. As suggested by previous work, the antisaccade task generates inhibition in the saccadic system that remains for at least the following trial, and cannot be eradicated by long inter-trial intervals or cues (Barton, et al., 2006; Manoach, et al., 2007). Several studies also have reported the unexpected benefit for switching to antisaccades (Barton, et al., 2006; Cherkasova, et al., 2002; Manoach, et al., 2007), as observed here in reaction times, possibly because lingering inhibition from a previous antisaccade slows down all saccadic responses, but a previous prosaccade may disinhibit the system and lead to relatively speeded responses (Manoach, et al., 2007).

While task switching costs and reaction times for correct trials inform theory for effective task reconfiguration and inhibition, reaction times for error trials speak to the characteristics of the saccadic system when it fails to activate the proper task set or inhibit prepotent responses. On prosaccade trials, there were too few errors committed to perform a meaningful analysis, but prosaccade error RTs (data not shown) tended to be longer than for correct responses, possibly suggesting a failure to maintain task instructions and inappropriate performance of a regular antisaccade (Unsworth, et al., 2004). In contrast, the antisaccade error reaction times analysis indicated that erroneous responses were faster than correct responses for all runs. These quick responses were similar to correct prosaccade RTs and may reflect failures of inhibition or task reconfiguration (Hutton, 2008; Munoz & Everling, 2004). The antisaccade error RTs did not differ across runs, corresponding to the equivalent error rates across all antisaccade probabilities.

Overall, the probability manipulation and task switch effects (the necessity for task-set reconfiguration/ stimulus-response remapping) may contribute to prosaccade differences more so than antisaccades because switching from the non-dominant/weaker response (antisaccade) to the dominant/stronger response (prosaccade) can impact performance to a greater degree than going from a dominant to non-dominant response due to the presence of task-set inhibition (Allport, et al., 1994). The stronger prosaccade stimulus-response set is more reflexive (look at a stimulus that appears) and must be inhibited more strongly during an antisaccade trial to allow the weaker response set to be performed (look away). This inhibition is thus more difficult to overcome when the participant must switch back to a prosaccade trial. When a prosaccade trial occurs first, however, only minor inhibition of the non-dominant antisaccade task set is necessary. Therefore, switching to the antisaccade task may be affected minimally by the previous prosaccade task set. Furthermore, the relatively long cue time (1000 ms) used in this condition may allow much of the reconfiguration process to be completed before the target appears, leaving only residual task-switch costs that depend upon the appearance of the peripheral target (Cherkasova, et al., 2002; Monsell, Yeung, & Azuma, 2000; Rogers & Monsell, 1995; Vandierendonck, et al., 2010). Thus, the stronger residual inhibition from frequent antisaccades on both the prosaccade task set and motor response may remain in the system even after a long inter-trial interval and cause more slowing of a current prosaccade response than a previous prosaccade could cause to a current antisaccade response.

Comparison across Conditions

In addition to the original design condition, the probability manipulation also was extended to conditions with different timing parameters. As expected, the latencies of responses were decreased for Conditions 2, 3, and 4 compared to Condition 1, due to the use of a “gap” rather than “overlap” paradigm (Fischer & Weber, 1997; Saslow, 1967). Prosaccade reaction times exhibited a main effect of run (probability) across all conditions combined, though this effect was most evident in Conditions 1 and 2. Antisaccade RT results show similar patterns (with different mean RTs) across conditions, indicating that the inhibitory state created by a large proportion of antisaccades slows responses regardless of inter-trial fixation or cue time.

Additionally, the percentage of correct prosaccades responses was affected by the probability of an antisaccade for Conditions 1 and 2, more so than for Conditions 3 and 4, whereas antisaccade percentage of correct responses differed across runs in Conditions 3 and 4, but not Conditions 1 and 2. Conditions 3 and 4 use a shorter saccade cue of 500 ms (compared to 1000 ms in Condition 1 and 1500 ms in Condition 2), which is closer to the cue time used in previous studies (Chiau, et al., 2011; Massen, 2004), of 0 or 200 ms, respectively, where antisaccade error rate was found to differ with probability. This suggests that, given enough time to prepare, one can modulate cognitive control (Fernandez-Duque & Knight, 2008) and perform antisaccades equally well, regardless of their overall probability; however, when preparation time is limited, the cognitive load is greater and one is more likely to make antisaccade errors when such trials are less frequent. In this case participants may rely more strongly on the probability context and use this prior information to improve performance (Abegg, et al., 2011). The gap effect may also partially account for differences in percentage of correct responses in Conditions 3 and 4, as the brief duration and subsequent disappearance of the central cue may disengage fixation processes (Fischer & Weber, 1997) and force participants to respond more reflexively to the peripheral target than in the overlap (Condition 1) or long cue (Condition 2) versions.

To investigate whether the speed of saccade responses was related to percent of correct responses (Crawford, et al., 2011; Ethridge, et al., 2009; Li, et al., 2012) and whether inhibition remaining from frequent antisaccade trials created a global slowing of reaction times (Barton, et al., 2006), regression models were fit for correct prosaccade and antisaccade trials within the mixed runs across all four conditions combined. Prosaccade reaction time (visual orienting speed) displayed an inverted-U shaped relationship with percentage of correct antisaccade responses across runs (Figure 3.9). In line with predictions of the competition model of antisaccade generation (Cutsuridis, et al., 2007; Massen, 2004), more correct responses were made by participants with moderately long prosaccade reaction time, perhaps because the endogenous component had more time to suppress the reflexive glance and reach the saccade execution threshold itself than at short latencies. Additionally, very long prosaccade latencies were associated with a drop in performance and may reflect a form of goal neglect or reduced attention to the task. This relationship was evident over all timing conditions and regardless of saccade trial type proportion.

Furthermore, in all runs, prosaccade and antisaccade reaction times were strongly positively correlated. This suggests the presence of an overall cognitive influence that constrains the responses of the saccadic system based on individual differences in circuitry. Reaction times generally increased in runs with larger proportions of antisaccades, so inhibitory processes may shift the feasible range of response times for the various runs by decreasing the baseline activity in movement-generating neurons (Dorris, et al., 2000) or slowing the rate of saccade build-up activity (Hanes & Schall, 1996). Nonetheless, the relationship between prosaccade and antisaccade reaction times remains relatively stable across the mixed runs, as many of the same processes are required for both tasks (Hutton, 2008; McDowell, et al., 2008).

One caveat of these comparisons is that the data in the various conditions were collected sequentially rather than simultaneously. Thus it is possible, though unlikely, that confounding factors associated with the order of data collection (such as the researcher's manner of explaining the study or the participants' motivation level) biased the pattern of results. The design of the later conditions, however, was informed by the results from earlier versions and therefore collected afterwards.

The observed behavioral response patterns from the cross-condition comparisons imply that cognitive resources are functioning uniquely in the various conditions and runs. Differences emerged for prosaccades versus antisaccades, overlap versus gap presentation, and low versus high antisaccade probability. Timing parameters affected prosaccades and antisaccades in both similar (gap effect) and distinct (error rates) ways. The saccade system is composed of basic sensory and motor regions and higher cognitive control regions that likely are differentially engaged by the changing task demands (McDowell, et al., 2008). Future research utilizing functional MRI should distinguish this activity for each run of varying probability and further illuminate the neural networks and cognitive control processes responsible for effective performance of saccade tasks. Specifically, the stimulus design in Condition 3 should offer the best opportunity for measuring these processes, as antisaccades showed larger differences in percentage of correct responses relative to cognitive load in this condition, while prosaccades showed the fewest differences between runs, more like what would be expected of primarily reflexive saccades.

Conclusions

This study demonstrated that the probability of occurrence of prosaccades versus antisaccades in a run can influence the response patterns of individuals based on demands on two major cognitive control processes: inhibition and task switching. The way in which responses differed depended on the overall ratio of each saccade type, the current and previous saccade trial type, and the preparation time provided by the stimulus design. Performance of an antisaccade created inhibition in the saccadic response system that slowed subsequent responses; this effect was compounded when antisaccades occurred more frequently. This lead to more directional errors on prosaccade trials or fewer on antisaccade trials, depending on the time provided to switch tasks and prepare for the next trial. Broadly, these findings show that increased cognitive load (here modeled as a greater need for cognitive control with frequent antisaccades and task switching) can slow behavioral responses with or without affecting accuracy (observed here across different timing conditions). Flexibility of cognitive control processes can allow for reasonably accurate performance on a difficult task when preparation time is sufficiently long or lead to benefits from repeating tasks with brief preparation time. In both cases, the brain strives to provide the optimal behavioral response, monitoring shifting demands and efficiently utilizing limited cognitive resources. A precise understanding of the way in which the brain adapts to changing cognitive demands can inform theories of controlled behavior and ultimately suggest avenues for improving function in cognitively challenging circumstances.

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