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# THE INTER-TRIAL SPATIAL BIASES OF STIMULI AND GOALS IN SACCADIC PROGRAMMING

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Prior studies have shown an 'alternate antisaccade-goal bias', in that the saccadic landing points of antisaccades were displaced towards the location of antisaccade goals used in other trials in the same experimental block. Thus the motor response in one trial induced a spatial bias of a motor response in another trial. In this study we investigated whether sensory information, i.e. the location of a visual stimulus, might have a spatial effect on a motor response too. Such an effect might be attractive as for the alternate antisaccade-goal bias or repulsive. For this purpose we used block of trials with either antisaccades, prosaccades or mixed trials in order to study the alternate-trial biases generated by antisaccade goals, antisaccade stimuli, and prosaccade goals. in contrast to the effects of alternate antisaccade goals described in prior studies, alternate antisaccade stimuli generated a significant repulsive bias of about 1.8°: furthermore, if stimulus and motor goal coincide, as with an alternate prosaccade, the repulsive effect of a stimulus prevails, causing a bias of about 0.9°. Taken together with prior results, these findings may reflect averaging of current and alternate trial activity in a salience map, with excitatory activity from the motor response and inhibitory activity from the sensory input.

**Keywords: averaging, colliculus, antisaccade, deviation, saccade, prosaccade**

## Introduction

Saccades are affected by the context of the trial in which they are executed - that is, by the nature of the other trials being performed in the experiment. Most commonly reported are effects modulating latency and accuracy, such as post-error slowing (Polli et al., 2006), task-switching (Barton, Cherkasova, Lindgren, Goff, & Manoach, 2005; Cherkasova, Manoach, Intriligator, & Barton, 2002; Fecteau, Au, Armstrong, & Munoz, 2004), and inhibition of return (Klein, 2000). Less frequently investigated are effects on the spatial programming of the saccade trajectory. Recently we demonstrated such effects for antisaccades, which require a subject to look away from rather than towards a suddenly appearing stimulus (Hallett, 1978): When a subject performs antisaccades to one of two possible goal locations within an experimental block, the spatial endpoints of antisaccades directed to one goal location are deviated towards the location of the other goal, an effect we called "*alternate goal bias*" (Abegg, Rodriguez, Lee, & Barton, 2010). This effect was not found for prosaccades, which may reflect the fact that antisaccades have weaker neural activity in ocular motor structures than prosaccades (Everling, Dorris, Klein, & Munoz, 1999) and therefore may more easily reveal modulation by residual activity patterns originating in other trials. In follow-up experiments we showed that *alternate goal bias* derives from two sources, one being a historical effect based on the frequency of recently performed trials (Rastgardani, Lau, Barton, & Abegg, 2012), and the other being the immediate expectations (or prior probabilities) of the responses that might be required (Abegg, Rodriguez, Lee & Barton, 2010).



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The *alternate goal bias* in these experiments was generated in experimental blocks in which the goals of the two different antisaccade trials were adjacent to each other in the same hemifield. This bias may reflect averaging of two spatial loci of excitatory goal-related neural activity, one from the current trial and one from the alternate trial, in a 'salience' map of some structure involved in saccadic preparation like the superior colliculus or frontal eye field (Fecteau & Munoz, 2003; Krauzlis, Liston, & Carello, 2004). This would be a mechanistic explanation similar to that proposed for the global effect, in which a prosaccade is biased towards the location of a simultaneously presented distractor (Findlay, 1982).

A method that can measure the impact of other trials in the same block makes it possible to study the spatial effects associated with other trial features besides an antisaccade goal. If a form of averaging - such as weighted vector averaging (van Opstal & van Gisbergen, 1990) - in a spatial map is responsible for alternate trial effects, then the magnitude and direction of bias will reflect the nature of the activity that persists between trials at the adjacent alternate location. In particular, averaging would predict that excitatory spatial fields would generate "attractive biases", in which responses deviate towards the locus of activity, whereas inhibitory spatial fields would generate "repulsive biases", in which responses deviate away from the locus of activity. In this report, we extend the method to investigate two other alternate trial effects, as follows.

First, because the stimulus and the goal are spatially dissociated in an antisaccade, we ask whether the *stimulus* on an antisaccade trial biases the direction of another antisaccade performed to a location near that stimulus. Since generating an antisaccade is thought to involve inhibition of erroneous prosaccades directed toward the stimulus (Munoz & Everling, 2004), one might hypothesize that an antisaccade stimulus possesses an inhibitory spatial field. If so, this should be revealed as a repulsive bias, an effect opposite to the "attractive bias" we observed from an alternate antisaccade goal.

Second, by examining blocks containing mixtures of prosaccades and antisaccades, we can determine whether alternate prosaccades also generate biases on current antisaccades. Unlike antisaccades, prosaccades have spatially congruent stimuli and goals. Whether they would generate biases more like those associated with antisaccade goals or those associated with antisaccade stimuli is not clear.

Finally, although we did not find biases on current prosaccades from alternate prosaccades in our prior study, this does not exclude the possibility that an alternate antisaccade goal could influence the spatial position of a current prosaccade. In this study we include a condition that addresses this issue. If antisaccades are able to exert bias on a prosaccade, despite the fact that antisaccades have weaker excitatory neural activity in the superior colliculus and frontal eye field, this would indicate some important differences in other aspects of spatial programming between these two types of saccades.

## METHODS

### *Subjects*

16 subjects of mean age 23.1 years (range 18 to 35) participated, 5 males and 11 females. All subjects had normal or corrected-to-normal vision. The protocol was approved by the institutional review boards of Vancouver General Hospital and the University of British Columbia, and all subjects gave informed consent in accordance with the declaration of Helsinki.

### *Protocol*

Subjects were seated 57 cm away from a monitor with dimensions of 1024 pixels by 768 pixels. Head position was stabilized by forehead and chin rests. Lighting conditions in the room were kept constant across all subjects. Stimuli were created and presented on the monitor using SR Research Experiment Builder 1.1.2. Eye movements were recorded using the Eyelink 1000 system (SR Research Ltd., Mississauga, Canada). All subjects were calibrated with a nine-point array for a horizontal visual range of 30° and a vertical visual range of 25°.

Each trial began with a black fixation cross at the screen center on a white background. After 750 ms the fixation cross disappeared and a stimulus appeared simultaneously. The stimulus was always a solid black disc 1° in diameter, located at an eccentricity of 9.5°of visual angle from the fixation point. All stimuli were located either 40° above the horizontal meridian, on the horizontal meridian, or 40° below the horizontal meridian. The stimulus remained on the screen for 850 ms after the subject performed a saccade greater than 1.5° in ampli-



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tude, and was then replaced by the fixation screen for the next trial.

The entire experiment consisted of four conditions (Figure 1), each with two blocks of 60 trials each, for a total of 480 trials. Common to all blocks was a trial type that required a saccade to a location on the horizontal meridian. These horizontal trials will be referred to as the "current saccade", and it will be these trials alone that will be subject to statistical analysis. To minimize errors, the response location for all horizontal trials was kept in the same lateral hemifield for each subject. Subjects were randomly assigned so that half of them performed the experiment with all horizontal trials requiring a response to the right hemifield, and the other half performed the experiment with all horizontal trials requiring a response to the left hemifield.

Condition A replicated the parameters in prior experiments demonstrating 'alternate goal bias' for antisaccades. In the first of the two blocks in condition A, one set of trials required antisaccades to a goal on the horizontal meridian – the 'current antisaccade', while the other set required antisaccades to a goal 40° above the horizontal meridian in the same hemifield – the 'alternate antisaccade'. The second block also contained trials requiring antisaccades along the horizontal meridian, but now the alternate trial type required antisaccades to a goal 40° below the horizontal meridian, again in the same hemifield. In both blocks the order of trials was random.

Condition B was similar, except that the positions of the stimuli and goals for the trials directed into the quadrants were reversed. This allowed us to examine the inter-trial effects of an antisaccade *stimulus* on antisaccades to a nearby goal. Thus the first block contained a random order of two trial types, one again requiring antisaccades to a goal on the horizontal meridian – the current antisaccade again, while the alternate set of trials required antisaccades to a goal 40° below the horizontal meridian in the *opposite* hemifield. In the second block, one set of trials required antisaccades to a goal on the horizontal meridian, while the other set of trials required antisaccades to a goal 40° above the horizontal meridian in the opposite hemifield.

Conditions C and D differed from conditions A and B in that half of the trials required prosaccades and half required antisaccades. In condition C, the two blocks both contained trials requiring antisaccades to goals on the horizontal meridian – a current antisaccade. In the first block, the alternate trial required a prosaccade to a goal 40° above the horizontal meridian in the same hemifield; in the second block, the alternate trial required a prosaccade to a goal 40° below the horizontal meridian in the same hemifield.

Condition D reversed the positions of the prosaccade and the antisaccade. Although prosaccades did not show an *alternate goal bias* from other prosaccades in the same block in our prior study (Abegg, Rodriguez, Lee & Barton, 2010), this does not exclude the possibility that antisaccades in the same block may generate an *alternate goal bias* in prosaccades. Thus the two blocks both contained trials requiring prosaccades to goals on the horizontal meridian – a 'current prosaccade'. In the first block, the alternate trial required an antisaccade to a goal 40° above the horizontal meridian in the same hemifield; in the second block, the alternate trial required a antisaccade to a goal 40° below the horizontal meridian in the same hemifield.

For block order, conditions A and B were linked as an 'antisaccades-only' section, and conditions C and D as a 'mixed prosaccade/antisaccade' section. These two sections were given in random order across subjects. Within each section, the order of the two conditions (A,B and C,D) of that section was also randomized. Within each condition, the order of the two blocks (upper field, lower field) was randomized.

Subjects were given both written and verbal instructions at the beginning of the experiment, outlining all stimulus locations and the appropriate goal locations. Before each of the four conditions (A-D), a practice block relevant to the upcoming condition was performed. Each practice block was at least ten trials long, but subjects were allowed to practice as much as they felt necessary to become comfortable with the task.

### *Analysis*

Data was obtained using SR Research Data Viewer 1.7.5. Saccades were detected when eye velocity exceeded 31°/sec, acceleration exceeded 9100°/sec$^2$, and position changed by more than 1.5°. The first saccade after stimulus onset was considered the saccadic response. Saccade latency was calculated as the time from target onset to saccadic onset. Those saccades with latencies less than 80 ms (considered anticipatory saccades or blinks) or more than 800 ms (considered delayed move-



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ments) were excluded from further analysis. Trials in which the first saccade started from a point greater than 2º in eccentricity from the fixation cross were also discarded. Finally, trials in which the first saccade vector was greater than 90° off the appropriate goal vector were considered errors and excluded from further analysis. Based on these criteria 16% of all the trials were excluded (range of excluded trials per subject 2% - 27%).

Analysis was limited to the 'current saccades': i.e., trials with goals on the horizontal meridian, since the object of the analysis was to contrast the effects of biasing from alternate trials on one side of the goal of the current saccade versus that from alternate trials on the other side. The dependent variable was the visual angle of the first saccade, in polar coordinates. Data were collapsed across the left and right hemifields across subjects and presented in graphs as though all trials were directed into the right hemifield only. Statistical analyses were performed with JMP 8.0.2 software (www.jmp.com).

We categorized blocks by the alternate trial location (upper or lower field) and the condition (A to D). For conditions A, C and D, the classification of 'alternate trial location' corresponded to alternate goal location, in that a block designated as 'upper field' indicated that the alternate goal of the saccadic response was in the upper or lower hemifield. For condition B, it is the stimulus and not the goal of the alternate trial that is closest to the current antisaccade goal on the horizontal meridian: therefore for this block upper hemifield means that the alternate trial had a stimulus in the upper hemifield and a goal in the lower hemifield. We entered subject means into a general linear model with the two main factors of condition (A, B, C, D) and alternate trial location (upper or lower field), with subject as a random factor. *A priori* linear contrasts were also performed to quantify the difference between upper and lower field blocks for each condition.

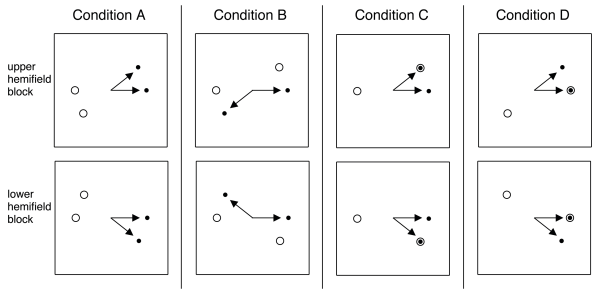


*Figure 1. Illustration of conditions and alternate-trial locations, for a subject in whom the key horizontal saccade is located in the right hemifield. Upper row shows blocks with alternate locations in the upper hemifield, bottom row shows blocks with alternate locations in the lower hemifield. Clear rings indicate stimulus locations, small black discs indicate saccade goals located at the tip of the arrows depicting the desired saccade. In condition A (leftmost column), horizontal antisaccades are paired with alternate trials with nearby antisaccade goals. In condition B (left middle column), horizontal antisaccades are paired with alternate trials with nearby antisaccade stimuli. In condition C (right middle column), horizontal antisaccades are paired with nearby prosaccades. In condition D (rightmost column), horizontal prosaccades are paired with alternate trials with nearby antisaccade goals.*

## RESULTS

The general linear model showed no main effect of condition or alternate trial location, but a significant interaction between condition and alternate trial location ($F(3,105) = 3.45$, $p = 0.019$, $\eta_p^2 = 0.28$). The *a priori* linear contrasts showed that this was due to differences in not only the magnitude but also the direction of the spatial biases (Figure 2). For condition A, the difference between upper and lower alternate trial locations was not significant, though the direction was consistent with prior reports of *alternate goal bias*, in that antisaccade endpoints were "attracted" towards the alternate goal location (that is, an attractive bias is one in which antisaccades from blocks with the alternate goal located in the lower field are displaced downwards more than those from blocks where the alternate goal was located in the upper field).

For condition B, the effect was in the reverse direction. When the alternate stimulus rather than the alternate goal was close to the current antisaccade goal on the horizontal meridian, the current antisaccade deviated into the opposite vertical field by a mean of 1.78°, a "repul-



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sive" effect (t(15) = 4.02, p = 0.0011, Cohen's d = 1.00). Thus, when the alternate stimulus was in the upper field, antisaccades to the horizontal location deviated into the lower field, and vice versa.

In condition C, the alternate trial type was a prosaccade directed to a point near the goal of the antisaccade. The result was a repulsive bias similar to condition B, in that antisaccades were deviated towards the vertical field opposite to that containing the stimulus and goal of the prosaccade, by a mean of 0.89° (linear contrast: t(15) = 2.24, p = 0.041, Cohen's d = 0.56).

Condition D switched the roles of the antisaccade and the prosaccade in condition C. Thus the alternate trial was an antisaccade directed to a goal near the goal (and stimulus) of a current prosaccade, to determine if antisaccade goals biased prosaccade programming in the same way they bias antisaccade programming. There was a suggestion of an attractive effect, but this failed to reach the level of a trend (t(15) = 1.68, p = 0.11).

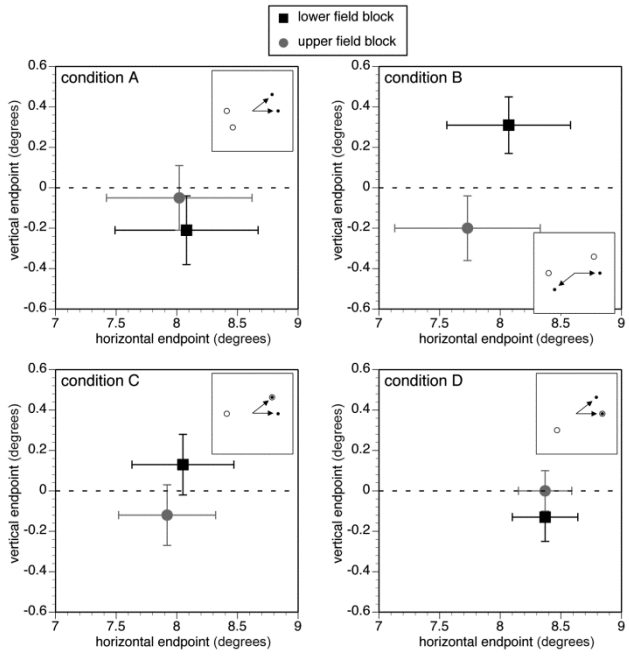


***Figure 2. Results.*** *Each graph plots the Cartesian (x,y) coordinates of the mean endpoint of horizontal saccades in each of the four conditions, from blocks in which the alternate trial was in the upper field and from blocks in which it was in the lower field. Error bars indicate one standard error. Note that conditions A and D have attractive biases (saccades in the lower field block are lower than those from the upper field block) while conditions B and C generate repulsive biases (saccades in the lower field block are higher than those from the upper field block). Insets illustrate the two trial types for the upper field block (corresponding to grey data symbols) for each condition.*

## DISCUSSION

We found that the parameters of an alternate saccade trial determine the type of spatial bias in a current trial. Our prior study showed that when this parameter is the goal of an alternate antisaccade, an attractive bias emerges, in which the current antisaccade deviates slightly towards that alternate goal (Abegg, Rodriguez, Lee & Barton, 2010). In the current study this effect did not quite reach significance, but a strong novel effect we found was that the stimulus location in an alternate trial has a repulsive effect on saccadic landing points of the current trial. Moreover we found that prosaccades, which are characterized by spatially congruent motor and sensory activity (condition C), also exert a similar repulsive effect on antisaccadic landing points. This suggests that the repulsive effect from stimulus location dominates over the attractive spatial effect of motor goal location.

We have suggested that an attractive bias between two antisaccade goals may reflect averaging in a spatial map between neural activity related to the current antisaccade and that from the alternate antisaccade, due to persistent excitatory activity from prior trials and/or priming by immediate expectations about the response set in the current trial (Abegg, Rodriguez, Lee & Barton , 2010; Rastgardani, Lau, Barton & Abegg, 2012). We hypothesized that, in contrast to the effects of an alternate antisaccade goal, the effect of having an alternate antisaccade stimulus in the vicinity of a current antisaccade might create a repulsive bias, given proposals that inhibition at this location is required to suppress reflexive errors of making a prosaccade to the stimulus (Levy, Mendell, LaVancher, & al, 1998; Munoz & Everling, 2004). The results of condition B are consistent with this prediction. Evidence for the presence of inhibition during antisaccade programming comes from neurophysiological studies showing reduced preparatory activity in the superior colliculus and frontal eye field after the cue for an antisaccade, but before the appearance of the stimulus (Everling, et al., 1999; Everling & Munoz, 2000). In addition, we have shown that there is a directionally specific inhibition at the site of the antisaccade stimulus that persists between trials and prolongs the latency of upcoming saccades (Abegg, Sharma, & Barton, 2012). The



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findings from condition B may indicate that inhibition at the location of the antisaccade stimulus not only affects the latencies but also the spatial properties of other trials, causing other antisaccades to deviate away from the inhibited stimulus location.

Of course, inhibition of reflexive prosaccades cannot be the explanation of the repulsive bias in condition C, where the alternate trial is a prosaccade. Another possible effect that could generate a repulsive bias in this scenario is inhibition of return, in which saccades to a stimulus to which a prior saccade had been made are delayed. This phenomenon that is thought to increase the efficiency of visual search by reducing the likelihood of inspecting a recently visited location (Klein & MacInnes, 1999; Smith & Henderson, 2011). Because inhibition of return also occurs at the location of a previously attended stimulus, without a need for a saccade to this stimulus, it is linked more to prior stimuli than to prior responses (R. Klein, 2000). Furthermore, inhibition of return is not limited to a narrow region around this stimulus, but extends over a relatively large neighbouring zone within the same hemifield (Bennett & Pratt, 2001), easily encompassing the spatial distances used in our experiments. Thus, while inhibition of return is usually assessed as an effect on latency, it may impact spatial saccadic programming also. Such a spatial effect has also been suggested by other types of studies. In a cueing paradigm, saccades were biased away from a cued and toward an uncued location, an effect that was attributed to inhibition of return at the cued location (Watanabe, 2001). While saccadic trajectories curve towards a distractor, this effect is reduced by inhibition of return at the distractor location (Theeuwes & Godijn, 2004). A bias of saccadic landing points away from an inhibited location was recently described by Wang and Theeuwes (Wang & Theeuwes, 2012), an effect that lasts up to 1200ms or more. Our minimum inter-trial interval was 1600ms: hence it may be that the repulsive effect of stimulus location in our experiment reflects a similar spatial effect of inhibition of return.

A proposal that saccadic goals generate attractive spatial biases while saccadic stimuli generate repulsive biases, also provide a plausible explanation for the difference in effects seen between prosaccades and antisaccades in conditions C and D. In condition C we examined the effect of a nearby prosaccade stimulus and goal upon the endpoint of an antisaccade. One might have initially expected that, since prosaccades have greater neural activity in ocular motor structures like the superior colliculus, the effect of a nearby prosaccade goal in condition C would be an even greater attractive bias than that seen from a nearby antisaccade goal in condition. Instead we found a repulsive bias. Our proposal would suggest that a nearby prosaccade would have both a saccadic goal that creates an attractive bias and a saccadic stimulus that creates a repulsive bias. If the latter was stronger the net effect would be a repulsive bias. Inhibitory stimulus effects that are stronger than excitatory goal effects would also be consistent with the finding in studies of alternation advantage (Barton, Manoach, & Goff, 2006; Fecteau, et al., 2004) and inhibition of return (Klein, 2000), that the persistent effect of a prosaccade is inhibitory.

In summary, the *alternate goal bias* paradigm in this and other studies reveals, by the use of various combinations of prosaccades and antisaccades, a complex mixture of attractive and repulsive spatial biases that cannot be explained simply by the different in magnitude of neural activity generated by prosaccades versus antisaccades. Rather, they may be explained by a form of averaging of current and alternate saccadic activity within a spatial salience map, in which saccade goals are associated with attractive biases reflecting excitatory effects at their location, and saccadic stimuli generate repulsive biases, consistent with well-known effects of inhibition-of-return at the location of previously attended stimuli, and possibly augmented in the case of antisaccades by inhibition required to suppress reflexive prosaccades towards the stimulus. Our prior studies have shown that both historical effects of recent frequency and also effects of immediate expectancy contribute to the attractive bias linked to an alternate antisaccade goal (Abegg, Rodriguez, Lee & Barton, 2010; Rastgardani, Lau, Barton & Abegg, 2012). Whether both historical effects and expectancy also operate to generate the repulsive alternate-trial biases generated by prosaccade or antisaccade stimuli requires future study.



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