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RESEARCH ARTICLE

‘Alternate-goal bias’ in antisaccades and the influence of expectation

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Abstract Saccadic performance depends on the requirements of the current trial, but also may be influenced by other trials in the same experiment. This effect of trial context has been investigated most for saccadic error rate and reaction time but seldom for the positional accuracy of saccadic landing points. We investigated whether the direction of saccades towards one goal is affected by the location of a second goal used in other trials in the same experimental block. In our first experiment, landing points (‘endpoints’) of antisaccades but not prosaccades were shifted towards the location of the alternate goal. This spatial bias decreased with increasing angular separation between the current and alternative goals. In a second experiment, we explored whether expectancy about the goal location was responsible for the biasing of the saccadic endpoint. For this, we used a condition where the saccadic goal randomly changed from one trial to the next between locations on, above or below the horizontal meridian. We modulated the prior probability of the alternate-goal location by showing cues prior to stimulus onset. The results showed that expectation about the possible positions of the saccadic goal is sufficient to bias saccadic endpoints and can account for at least part of this phenomenon of ‘alternate-goal bias’.

Keywords Antisaccade · Prosaccade · Direction · Global effect · History · Probability

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Introduction

Saccades are often tested in series of trials, with parameters averaged across all trials to index performance. Such analyses ignore influences from other trials in the same block. However, studies have shown that the context of these other trials can influence saccades, particularly their error rates and reaction times (Fecteau and Munoz 2003; Tatler and Hutton 2007). In ‘post-error slowing’ for example, saccadic latency is increased after an error is made (Polli et al. 2006). Latency increases have also been described after switching the direction of a saccade (Dorris et al. 2000; Fecteau et al. 2004; Barton et al. 2006; Reuter et al. 2006) or after switching of the type of saccade (Cherkasova et al. 2002; Fecteau et al. 2004; Barton et al. 2005), for example from a prosaccade, in which one shifts gaze to the stimulus, to an antisaccade, in which one looks away from the stimulus.

The physiological basis of some of these contextual effects has been demonstrated in altered pre-target baseline activity in monkey collicular neurons (Dorris et al. 2000) and changes in human frontal eye field activity on functional neuroimaging (Manoach et al. 2007). In a condition of high prior probability for example, activity levels in buildup neurons of the superior colliculus are elevated, and this in turn translates to faster saccadic reaction times (Dorris et al. 1997; Basso and Wurtz 1998). A similar

correlation of preparatory pre-target activity with saccadic latency was found in single neurons of the frontal eye field which project to the superior colliculus (Everling and Munoz 2000). Taken together, these results suggest that baseline neural activity can be influenced by the context of prior events and foreknowledge of upcoming events, both resulting in effects on response latency.

Less investigated is whether saccadic spatial coordinates are also influenced by other trials, which would suggest that not just the level and timing of neural activity but also its distribution in spatial maps could be affected by this context. The possibility that factors other than the current goal may influence saccadic spatial coordinates is not without precedent. Simultaneous distractors far from the goal increase prosaccade latency (Lévy-Schoen 1969; Walker et al. 1997), while prosaccades deviate towards a nearby distractor in the "global effect" (Findlay 1982; Ottes et al. 1984). Distractors more remote in time can also influence the latency of a saccade (Walker et al. 1995), but whether these can also affect saccadic spatial coordinates is not known. The potential for stimuli or saccades in other trials to influence saccadic spatial coordinates is suggested by the 'range effect' (Kapoula 1985): when many goal amplitudes are used, prosaccades directed to the further goal are hypometric, while those directed to nearer goal are hypermetric.

In this study, we examine whether saccadic direction is influenced by the location of the goals in other trials. We found this true and used our paradigm to address a number of questions. First, we asked whether spatial bias differed between prosaccades and antisaccades: we hypothesized that the weaker neural activity associated with antisaccades (Everling et al. 1999; Everling and Munoz 2000) may allow such effects on spatial programming to emerge more strongly with antisaccades than with prosaccades. Second, we asked whether spatial bias varied with the distance between the two saccadic goals. If saccadic spatial coordinates reflect a 'weighted average' of the locations of the goals in current and prior trials, then spatial bias should change with the distance between the current and alternate goal. Third, we asked whether expectation effects, reflecting increased prior probability of the requirement for a saccade to the alternate goal, might account for at least part of this spatial bias.

Experiment 1

Methods

Subjects

Eleven subjects with a mean age of 34 years (range 25–43) participated, five of whom were men. All were healthy, with no prior psychiatric or neurological illness, not on medication, and had normal or corrected-to-normal vision and viewed the stimuli with both eyes. We did not record caffeine intake, and of the eleven subjects only one was a smoker: nicotine can improve antisaccade performance and working memory (Rycroft et al. 2006), though how this substance might affect the phenomena we investigate in this report is unknown. The institutional review boards of Vancouver General Hospital and the University of British Columbia approved the protocol, and all subjects gave informed consent in accordance with the declaration of Helsinki.

Apparatus and protocol

Subjects sat in dim illumination 57 cm away from 22″ CRT screen, with their head position maintained by a chin-rest. Screen resolution was 1,024 by 768 pixels, which covered 39° and 30° of visual field, respectively. Eye movements were recorded by a video-based system using the pupil and the corneal infrared-light reflex to estimate gaze position (Eyelink 1000 from SR Research Ltd, Mississauga, Canada). Stimuli, trials and experimental blocks were created using SR Research Experiment Builder 1.1.2.

In the prosaccade task, subjects were instructed to make a saccade towards the stimulus as soon as it appeared. In the antisaccade task, subjects were instructed to make a saccade of the same amplitude in the direction opposite to the stimulus as soon as it appeared. Stimuli were white discs with a diameter of 1° superimposed upon a black background.

Each trial began with a fixation cross at screen centre, which was replaced after 750 ms of fixation by the stimulus at 9.5° (242 pixels) eccentricity.[1] At 850 ms after the subject performed a saccade greater than 3.0° in amplitude, the stimulus disappeared and was replaced by the fixation cross at screen centre to indicate the start of the next trial.

There were eight blocks for antisaccades and two blocks for prosaccades. These ten blocks were presented in random order (Fig. 1a). Each block contained two types of trials: one had a stimulus located on the horizontal meridian in the right hemifield, while the other had a stimulus in a different location in the same hemifield. In one set of blocks, this second location was above the horizontal meridian, while in another set of blocks, it was below the horizontal meridian. In the two prosaccade blocks and two of the eight antisaccade blocks, these stimuli differed between blocks in angular direction from the meridian by 20°. Because initial pilot

[1] To avoid confusion with the degrees of polar angle that denote angular direction, we report Cartesian (X–Y) coordinates in pixels rather than degrees of visual angle. The conversion of 25.5 pixels per degree of visual angle is provided in each figure.

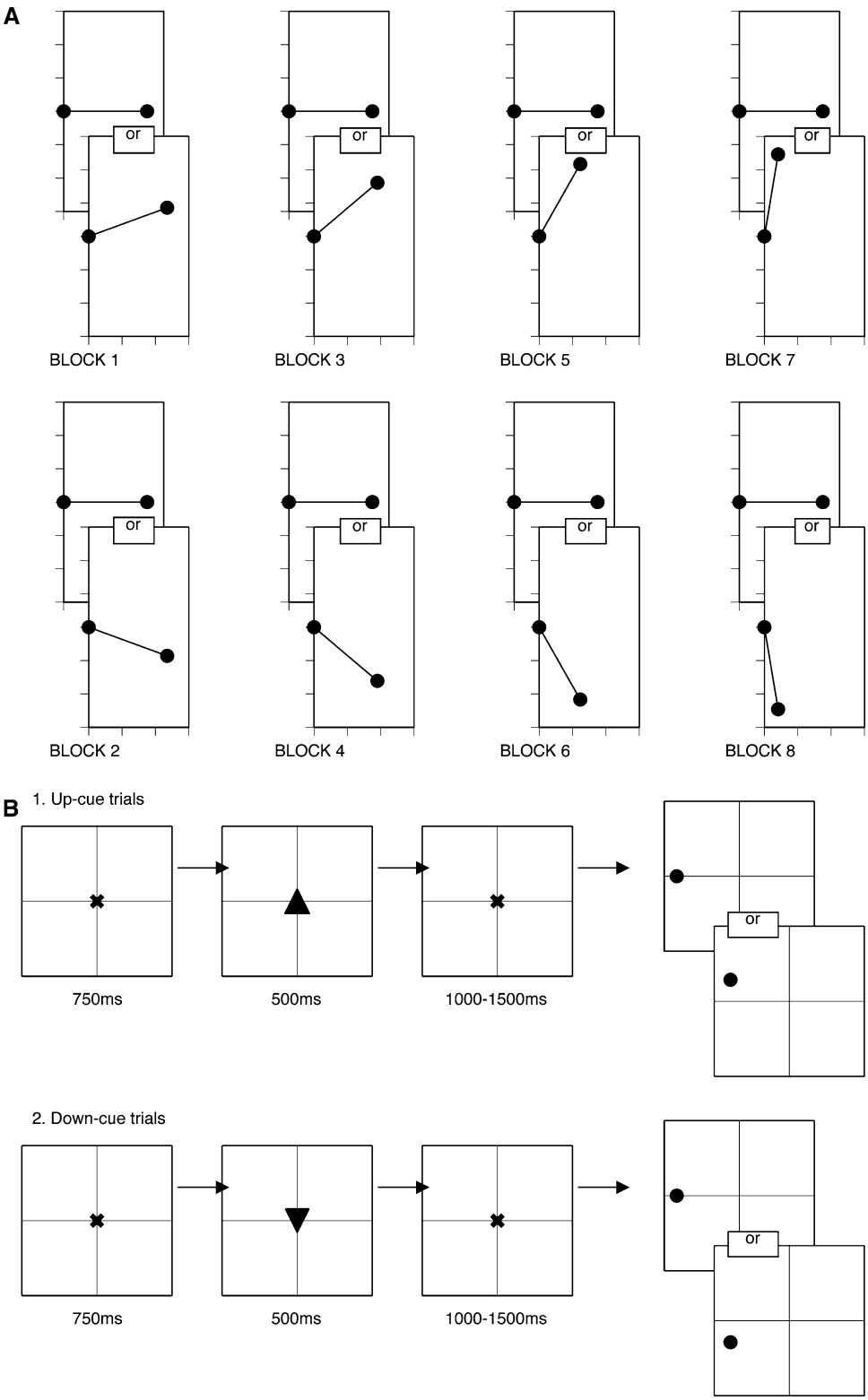

Fig. 1 Design of experiments 1 and 2. **a** *Examples of stimuli used in a right-hemifield set in experiment 1.* In each plot, the fixation point at screen center is shown as a black disc on the left margin, linked by a line showing the vector to the stimulus location, depicted as a black disc in the right hemifield. All stimuli are located at 9.5° eccentricity. Each block has two types of trials. The two possible goals are separated by 20° angular distance in blocks 1 and 2, by 40° in blocks 3 and 4, by 60° in blocks 5 and 6, and by 80° in blocks 7 and 8. The obliquely located stimulus is in the upper quadrant in odd-numbered blocks, and in the lower quadrant in even-numbered blocks. Subjects performed antisaccades in these blocks. In blocks 9 and 10, stimuli identical to those in blocks 1 and 2 were used, but subjects performed prosaccades in these blocks. **b** *Illustration of the four trial types in block 3 of experiment 2.* In the two 'up-cue' trial types, the fixation cross is followed by an upward arrowhead, which is replaced by the fixation cross, then the appearance of the stimulus, which may be either on the horizontal meridian or in the upper quadrant, resulting in goals on either the horizontal meridian or the lower quadrant. In the two 'down-cue' trial types, the cue is a downward arrowhead, indicating that the stimulus will appear either on the horizontal meridian or in the lower quadrant. Thus, up-cue trials have 50% prior probability of the lower quadrant goals and 0% probability of the upper quadrant goals, and down-cue trials have the reverse. However, because equal numbers of down-cue and up-cue trials occur in block 3, the block has equal number of lower and upper quadrant goals

data showed that there was an alternative goal bias in antisaccades but not prosaccades, additional blocks were included to explore the parametric variation of this bias in antisaccades with the degree of angular separation between the alternate goals. Hence, we also included blocks where the second stimulus differed in angular direction from the horizontal meridian by 40°, 60° or 80°.

Each block had 40 trials, 20 of each type and the experiment contained a total of 400 trials.

Analysis

Data was analysed using SR Research Data Viewer 1.7.5. Saccades were detected when eye velocity exceeded 31°/s, acceleration exceeded 9,100°/s^2 and position changed by more than 0.15°. Only the first saccade after stimulus onset was analysed in each trial. Reaction time was calculated as the time from stimulus onset to saccadic onset, and saccades with reaction time less than 80 ms or more than 800 ms were excluded from further analysis (Lee et al. 2010; Koehn et al. 2008), with the 80-ms cut-off chosen to exclude anticipatory responses (Kalesnykas and Hallett 1987). Saccades that started from a point greater than 2° (50 pixels) from the fixation cross were also discarded. We also excluded trials with directional errors of more than 45° difference from the goal vector. The analysis was confined to trials with stimuli on the horizontal meridian.

Our dependent variable was the vertical position of the landing point ("endpoint") of saccades from trials with goals located on the horizontal meridian. For statistical analysis, we used two general linear models. The first determined whether prosaccades and antisaccades differed. It assessed responses from trials with the alternative goal 20° away from the horizontal meridian, with main factors of saccade type (prosaccade versus antisaccade) and alternate-goal hemifield (upper versus lower), with subject as a random factor. The second focused on the effect of angular separation between current and alternate goals. It assessed only antisaccades, with main factors of angular separation (20, 40, 60, 80), and alternate-goal hemifield (upper versus lower), and subject as random factor. We used Tukey's honestly significant difference (HSD) test at a significance level of 0.05 to identify significant contrasts. Statistical analysis was performed using JMP version 5.1.2 (http://www.jmp.com).

To determine whether vertical change in antisaccade endpoint varied as a function of the angular separation between current and alternate goals, we calculated for each subject and at each angular separation the difference between the mean vertical position of antisaccades in trials with alternate goals in the upper field, and the mean vertical position of antisaccades in trials with alternate goals in the lower field. We then performed a linear regression of this change in antisaccade vertical position versus angular separation.

Results

Our first goal was to examine whether an alternate goal 20° away from the horizontal meridian influenced the vertical position of the saccade landing point for prosaccades and for antisaccades. The general linear model showed a main effect of saccade type ($F(1, 798) = 15.7$, $P < .0001$) and of alternate-goal hemifield ($F(1, 798) = 91.8$, $P < .0001$). There was a significant interaction between saccade type and the alternate-goal hemifield ($F(1, 798) = 90.0$, $P < .0001$). Tukey's HSD test showed that all conditions differed significantly from each other, except for the contrast between the two prosaccade conditions (Fig. 2a). Thus the vertical position of prosaccades is not affected by the location of the alternate goal, while antisaccades are significantly shifted towards the alternate goal.

Our second goal was to determine whether the alternate-goal bias for antisaccades varied as a function of the angular separation between the two goals. The general linear model showed a significant main effect of the alternate-goal hemifield ($F(3,1631) = 228$, $P < .0001$) and a significant interaction between hemifield and angular separation ($F(3,1631) = 7.55$, $P < .0001$). Tukey's HSD test showed that all contrasts between the upper and lower goals at each angular distance differed from each other (Fig. 2b). However, the only difference between goals in the same hemifield was between the 20 and 80° conditions for the top hemifield. Nevertheless, the linear regression of change in vertical position versus angular separation between current and alternate goals showed a significant negative slope (−0.63) and correlation ($r = -0.32$, $F(1,43) = 4.81$, $P < .034$). Thus, the vertical deviation of antisaccades towards the alternative location diminished as the angular distance between the two stimulus locations increased (Fig. 3).

One last issue to consider is whether the appearance of alternate-goal bias resulted from selection error (making occasional saccades to the wrong goal) rather than a targeting bias of saccades that correctly selected the goal on the horizontal meridian. Both phenomena can occur in experiments with targets and simultaneous distractors, for example (Ottes et al. 1985; Findlay and Blythe 2009). A selection error would be revealed by a pattern in which the subject made two types of saccades on trials with goals on the horizontal meridian: one to the goal on the meridian and the other to the alternate goal (Arai et al. 2004), sometimes called a bistable pattern (Ottes et al. 1985). Since we excluded saccades with a direction more than 45° away from the horizontal meridian, this eliminates selection errors from the data for alternate goals at 60° or 80°. However, trials from blocks with alternate goals at 20° or 40° could have contained selection errors, which would not be evident in an analysis that looked only at mean vertical position. Such selection errors would be evident as a cluster of saccades with endpoints at the location of the alternate goal (e.g. Fig. 6 in Arai et al. 2004 and Fig. 3 in Ottes et al. 1985). To examine this, we plotted histograms of the distribution of vertical saccadic endpoint across these different conditions (Fig. 4). These do not show twin-peaked

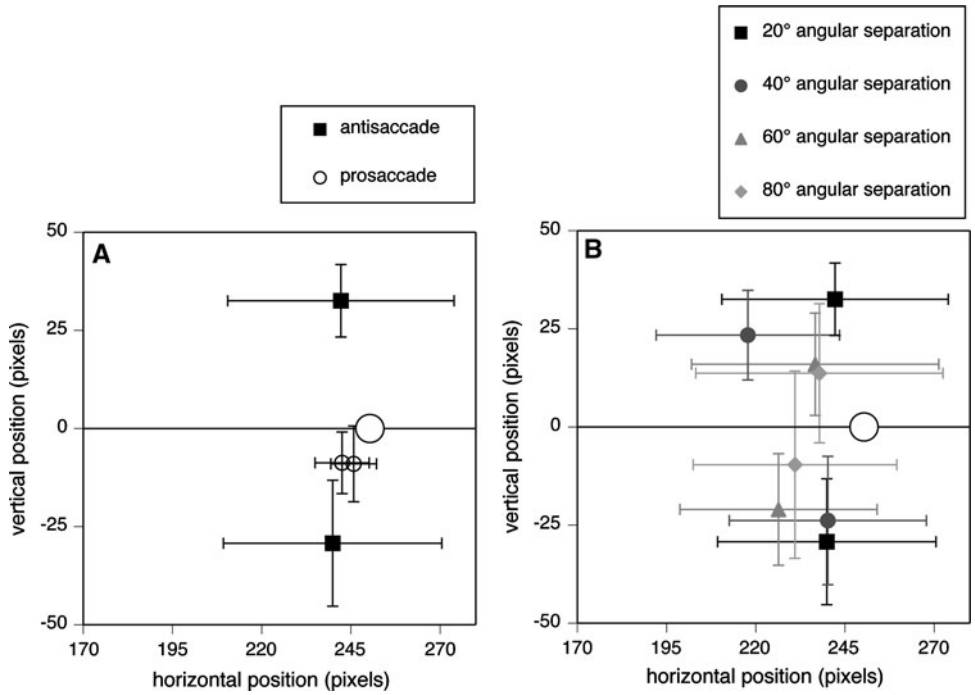

Fig. 2 Results, Experiment 1. **a** *Mean endpoint for prosaccades and antisaccades to goals on the horizontal meridian*. Data from trials where the alternate goal had a directional angle of 20° from the horizontal meridian. The large disc on the horizontal meridian shows the desired goal. Two mean endpoints are plotted for each type of saccade, one from trials in blocks where the alternate goal was in the upper quadrant and one from blocks where it was in the lower quadrant. Vertical position of prosaccades is not affected by the location of the alternate goal, while antisaccades deviate towards the alternate goal (the mean data point in the upper quadrant is from trials in which the alternate goal was in the upper quadrant, and the mean data point in the lower quadrant is from trials in which the alternate goal was in the lower quadrant). **b** *Mean endpoint for antisaccades to goals on the horizontal meridian, as a function of angular separation between current and alternate goals*. Conventions are similar to A. All mean data points in the upper quadrant are from trials in which the second goal was in the upper quadrant, and all mean data points in the lower quadrant are from trials in which the other goal was in the lower quadrant. The deviation of vertical position towards the location of the second goal decreases as angular distance to the second goal increases. Error bars show one standard error. 25.5 pixels equal 1 degree of visual angle

distributions to indicate a significant contribution from selection error; rather, the distribution in each case is consistent with a shift of the main saccadic distribution towards the alternate goal, a targeting bias.

Comment

These results show that antisaccades deviate towards the alternate goal used in the same experimental block. The direction of this deviation is reminiscent of the global effect, in which a prosaccade deviates towards a distractor or lands in between two simultaneously presented stimuli (Findlay 1982). Our "alternate-goal bias" differs from the global effect in a number of ways. First, it is not generated by a distractor on the same trial, but by the goal on other trials in the same block. Second, while the global effect has been demonstrated for prosaccades, we find alternate-goal bias for antisaccades but not prosaccades. While such results do not exclude that a smaller alternate-goal bias might be found for prosaccades with a larger sample size, they nevertheless show that the bias is larger for antisaccades. To our knowledge, the global effect has not yet been investigated in antisaccades, although studies have shown that other spatial effects of simultaneous distractors such as deviation of saccadic trajectory are, like alternate-goal bias, greater for antisaccades than prosaccades (van Zoest et al. 2008).

We had hypothesized that the inter-trial context effect would be greater for antisaccades than prosaccades. If this effect results from averaging of (a) activity generated by the parameters of the current trial and (b) activity related to the goal in other trials, then the effects of alternate-goal activity would be more evident in trials in which the current parameters generate lower levels of neural activity. Our hypothesis then follows from the fact that neural activity in structures like the superior colliculus and frontal eye field is lower for antisaccades than prosaccades (Everling et al. 1999; Everling and Munoz 2000), due at least in part to the lack of a visual stimulus at the antisaccade goal (Edelman and Goldberg 2003).

What is the origin of alternate-goal bias? There are at least two main possibilities (Gmeindl et al. 2005). One is that the subject's expectations regarding the future are

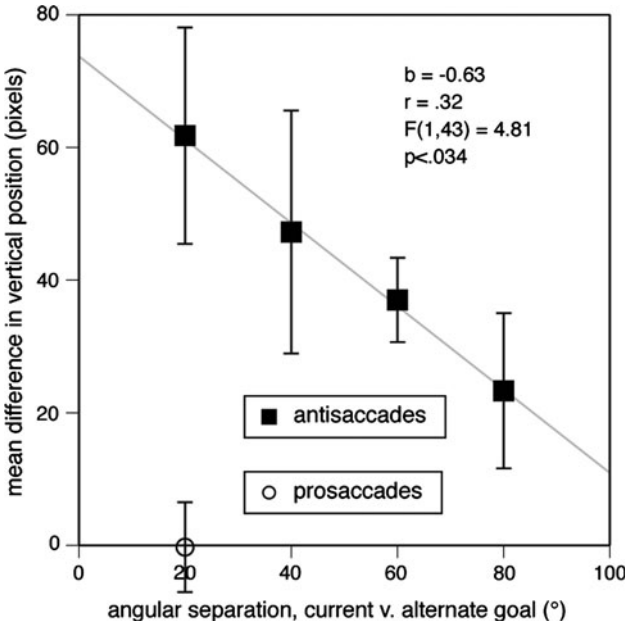

Fig. 3 Alternate-goal bias as a function of angular separation between current and alternate goals. For each subject at each value of angular separation, we calculate for responses to the goals on the horizontal meridian, the difference between the mean endpoint from blocks with alternate goals in the upper quadrant and the mean endpoint from blocks with alternate goals in the lower quadrant. The graph shows the group average of this difference score plotted as a function of angular separation. For antisaccades, there is a significant linear relation (*solid line*), and results of linear regression analysis are shown, including slope (*b*) and correlation coefficient (*r*)

responsible. For example, in a block where the only two goals are one on the horizontal meridian and one above it, each trial has a 50% prior probability of the goal to be in the upper quadrant, and a 0% prior probability of it being in the lower quadrant. Thus, the upper but not the lower goal may be partially selected or primed by expectation, even before the trial begins. Another possible explanation is that it may be generated by the increased recent frequency of saccades to the alternate goal. If so, then this would imply that neural activity related to the alternate goal persists from one trial to the next, a 'historical' effect in that properties of the current response are shaped by recent events.

To determine whether expectancy effects could account for alternate-goal bias, we performed a second experiment.

Experiment 2

Methods

Subjects

Sixteen subjects with a mean age of 35 (range 27–43) participated, five of whom were men, two of whom had participated in experiment 1. As in experiment 1, we included only healthy subjects with no neurological or psychiatric conditions, who were not on prescription medication, and with normal or corrected-to-normal visual acuity.

Apparatus and protocol

Recording conditions and apparatus were identical to experiment 1, with the exception that the monitor was viewed through a circular aperture in a black cardboard screen placed on the screen, which obscured the view of the screen edges to eliminate any visible reference points that might have influenced the results. In all trials, subjects made antisaccades in the direction opposite to the same white discs of 1° diameter as in experiment 1, seen against a black background. The stimuli were presented in the right hemifield for half of the subjects and in the left hemifield for the other half. Each of the three blocks of trials was preceded by a practice sequence of 10 trials.

Blocks 1 and 2 replicated the antisaccade design in experiment 1. Each trial began with a central fixation cross on a black background, which disappeared after 1,250 ms, when the stimulus appeared. At 850 ms after subjects initiated a saccade, the stimulus was replaced by the central fixation cross for the start of the next trial. Block 1 consisted of 40 trials with stimuli appearing randomly and with equal probability either on the horizontal meridian or 20° above, at eccentricities of 9.5°(242 pixels). Block 2 was similar, with 40 antisaccade trials but with stimuli either on the horizontal meridian or 20° below.

Block 3 consisted of 80 trials. Each trial was initiated with a central fixation cross that was replaced after 750 ms by a triangle pointing upwards (up-cue) or downwards (down-cue) lasting for 500 ms, followed by the reappearance of the central fixation cross (Fig. 1b). After an interval varying randomly between 1,000 and 1,500 ms, the central fixation cross disappeared. In up-cue trials, the stimulus then appeared randomly on either the horizontal meridian or 20° above, at an eccentricity of 9.5° (242 pixels), both being equally likely. In down-cue trials, the stimulus was either on the horizontal meridian or 20° below. Thus, in up-cue trials there was a 50% probability of the goal to be at the location below the horizontal meridian, a 50% probability of it appearing on the horizontal meridian and a 0% probability that it would be located above the meridian, the same probabilities as present in all the trials of block 1. Likewise, down-cue trials had the same probabilities as the trials of block 2.

In this manner, the cued trials of block 3 replicated the prior probabilities operating in blocks 1 and 2. However, because block 3 had equal number of up-cue and down-cue trials, the entire block had equal numbers of trials with stimuli above and below the horizontal meridian. Hence, unlike blocks 1 and 2, there was no imbalance in the

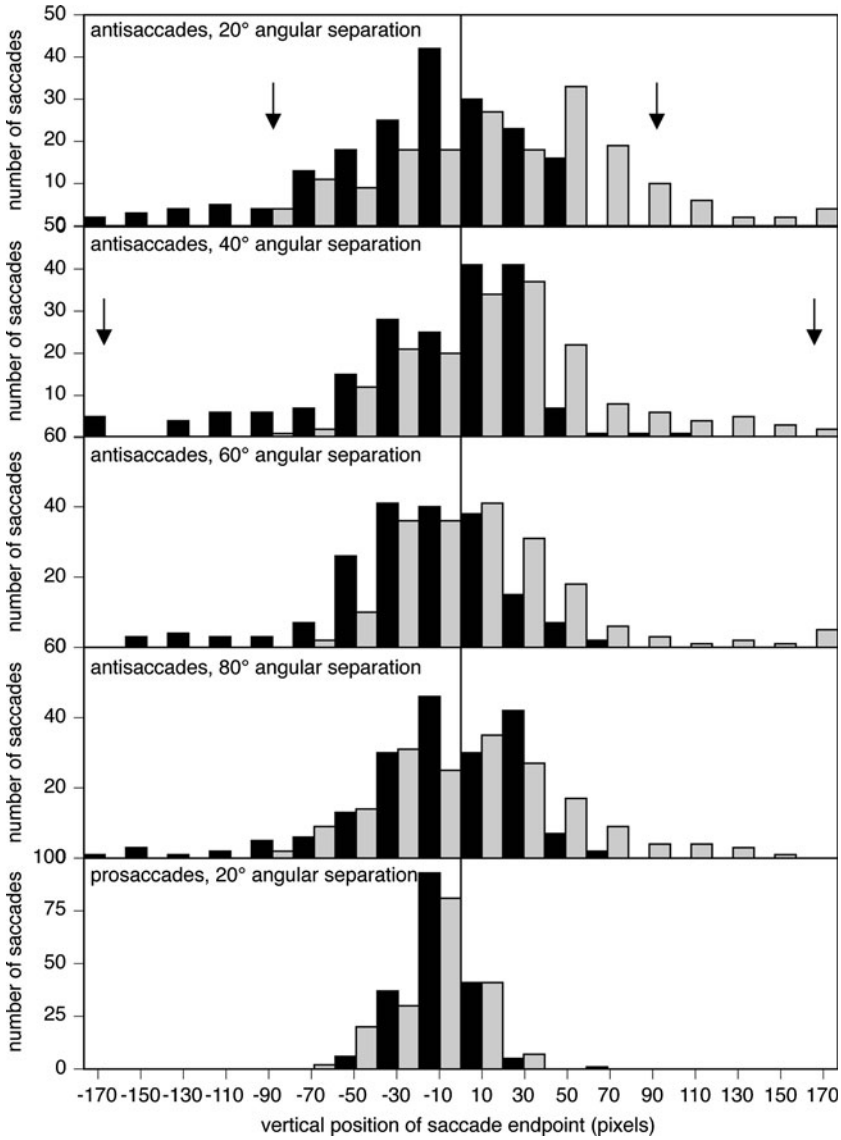

Fig. 4 Distribution of vertical position of saccade endpoints. Each graph shows the number of saccades in each 20-pixel bin, where 25.5 pixels equals 1° of visual angle, for both the block with the alternate goal in the upper hemifield (*light bars*) and the block with the alternate goal in the lower hemifield (*dark bars*). Vertical arrows in the top two graphs show the approximate location of the goals at 20° and 40°. There is no evidence of secondary peaks at the location of the alternate goals to suggest that selection errors rather than targeting biases are responsible for alternate-goal bias in these two conditions

frequency of stimuli appearing above or below the meridian. Thus, blocks 1 and 2 contained both recent-frequency and prior-probability effects favouring the alternate goal in one vertical hemifield. However, block 3 allowed us to analyse isolated prior-probability effects, since trials in block 3 had a balanced recent frequency, i.e., they had equal probabilities to be preceded by a trial with a goal in the upper hemifield as by a trial with a goal in the lower hemifield. For simplicity, we refer to blocks 1 and 2 as the '*recent-frequency* condition' (note, though, that it actually contains both recent-frequency and prior-probability effects) and block 3 as the '*prior probability* condition'.

Analysis

Saccades were detected as in experiment 1, using the same exclusion criteria regarding latency, fixation and gross directional error. Our dependent variable remained the vertical endpoint of the initial saccade on the trials with stimuli located on the horizontal meridian. We performed a general linear model with main factors of experimental condition (*recent frequency*, *prior probability*) and hemifield of the alternate goal (upper, lower). Contrasts were performed using the Tukey's HSD test with alpha level of significance set at 0.05.

Results

The analysis of the vertical position of saccadic endpoints with a general linear model showed a main effect of the alternate-goal hemifield ($F(1,1091) = 66.74$, $P < .0001$) and a significant interaction between alternate-goal hemifield and experimental condition ($F(1,1091) = 11.84$, $P < .0006$). Tukey's HSD test showed that all contrasts were significant, with the exception of the contrast between the

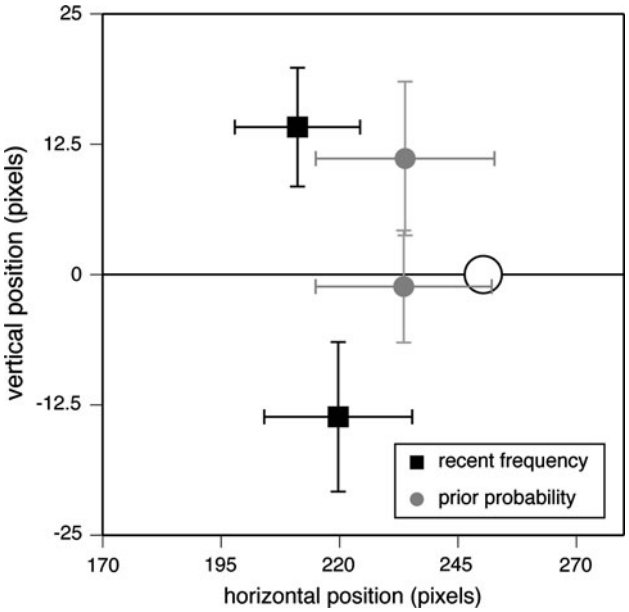

Fig. 5 Recent-frequency versus prior-probability conditions in Experiment 2. Conventions are similar to Figs. 2 and 3. The 'recent-frequency' condition is a replication of experiment 1, in that subjects performed blocks with only two goal locations, one on the horizontal meridian and the other either in the upper or in the lower quadrant. The 'prior-probability' condition is from a block containing the trials illustrated in Fig. 1b. A trial with an up-cue had goals either on the horizontal meridian or in the lower quadrant, while a trial with a down-cue had goals either on the horizontal meridian or in the upper quadrant. However, both trials were mixed in a single block, so that up and down alternate goals were equally frequent in the block. Mean data points in the upper quadrant are from trials where the alternate goal was also in the upper quadrant, and mean data points in the lower quadrant are from trials where the alternate goal was in the lower quadrant. 25.5 pixels equal 1 degree of visual angle

recent-frequency and *prior-probability* conditions for trials with an alternate goal in the upper hemifield (Fig. 5).

In the *recent-frequency* condition, linear contrasts confirmed a difference between blocks with upper- versus lower-hemifield alternate goals ($F(1,1091) = 11.06$, $P < .001$), with antisaccades deviating towards the alternate goal. This replicates the results for antisaccades in experiment 1.

In the *prior-probability* condition, linear contrasts showed a difference between trials with upper- versus lower-hemifield alternate goals ($F(1,1091) = 67.97$, $P < .0001$), again with antisaccades deviating towards the alternate goal. This indicates that, even when the recent frequencies of upper- and lower-hemifield goal locations are balanced within an experimental block, expectancy (*prior probability*) alone can generate an alternate-goal bias in antisaccades.

However, the significant interaction between alternate-goal hemifield and experimental condition indicates that the effects with prior probability alone are not the same as when both historical and prior-probability effects are present. Linear contrasts showed that, when the alternate goal is in the lower hemifield, the deviation is greater in the *recent-frequency* condition than in the *prior-probability* condition ($F(1,1091) = 11.14$, $P < .0009$), though there is no difference when the alternate goal is in the upper hemifield. We calculated the mean difference between trials with upper- versus lower-hemifield alternate goals for each subject as an index of the deviation induced by the alternate goal. A paired t-test comparing this index (I) for the *recent frequency* ($I = 1.09 \pm 0.31°$ (27.79 ± 7.98 pixels); mean $\pm$ s.e.m.) and *prior probability* ($I = 0.48 \pm 0.27°$ (12.28 ± 6.85 pixels); mean $\pm$ s.e.m.) conditions showed a trend towards a significant difference ($t(15) = 2.06$, $P = .057$). Thus, while the results of experiment 2 show that prior probability contributes to alternate-goal bias, it is possible that other factors such as recent frequency or history also make a contribution.

Discussion

Our results show that the direction of antisaccades but not prosaccades is biased towards the alternate goal in a block of trials. Experiment 1 showed that this effect declined with increasing angular separation between the current and alternate goals. Experiment 2 replicated the effect and showed that alternate-goal bias can be generated by the prior probability of a saccade to the alternate goal, indicating that targeting of antisaccades shows contextual modulation by expectation. However, the fact that the alternate-goal bias was greater in blocks where both recent frequency and expectancy were imbalanced in favour of a second goal suggests that additional contextual effects such as trial history may also play a role.

Alternate-goal bias is reminiscent of the global effect, which is produced by simultaneous stimuli and distractors (Coren and Hoenig 1972; Findlay 1982) and, to some degree, the averaging response to double stimuli presented sequentially within the same trial (Becker and Jürgens 1979). In both of these phenomena, investigated primarily (if not exclusively) with prosaccades, saccade endpoints deviate to a position between the two stimuli. This has been taken as evidence of both temporal (for sequential stimuli) and spatial averaging (for the global effect) in the saccadic system.

The range effect also demonstrates that spatial biasing can extend beyond the parameters of the current trial. In the clearest demonstration, prosaccades to stimuli of around 7–11° eccentricity were hypometric if the trials were embedded in a block containing other trials with less eccentric goals, and hypermetric if the block included trials with more eccentric stimuli (Kapoula 1985). This established that the range

effect is dynamic, dependent upon the other trials being performed, rather than a static fixed property of the ocular motor system. Although the range effect was demonstrated for prosaccades with multiple goal locations, whereas our alternate-goal bias is seen chiefly with antisaccades in a design with two goal locations, it is possible that both effects have a similar neurophysiological basis in persistent patterns of activity that influence motor preparation.

While there has been little modelling of the range effect, there has been much consideration given to the effects of double stimuli (Van Opstal and Van Gisbergen 1989; Arai et al. 1994; Trappenberg et al. 2001; Arai and Keller 2004). Findlay (1982) interpreted the global effect as due to "integrating information over a large spatial window…by an ensemble of cells with large and overlapping receptive fields". Even though alternate-goal bias differs in that it is generated by expectations or events during other trials, it may be that it too represents an averaging of activity in a 'salience' map containing signals related to stimuli, goals and expectations for motor preparation of the saccade (Fecteau and Munoz 2003; Krauzlis et al. 2004). Since previous work shows a role of the frontal cortex in the preparation of antisaccades (Munoz and Everling 2004), it is possible that alternate goal bias reflects averaging of activity signals in the frontal cortex; our results, however, cannot establish the anatomic basis of alternate-goal bias.

Early experiments on the global effect with two stimuli differing in amplitude showed increasing deviation of the saccadic endpoint with increasing distance between the two stimuli, over small separations of 2–8° (Coren and Hoenig 1972; Findlay 1982). Less data has been obtained on averaging between stimuli differing in directional angle. One study found global averaging of amplitude between stimuli and distractors at 4° and 8° eccentricity, and noted that the effect on amplitude declined with increasing angular separation to about 45°, beyond which the distractor had no effect on amplitude, but rather increased latency (Walker et al. 1997). Curiously, there was no analysis of effects on directional angle. However, another study did examine a directional global effect, with separations of 30-90°, and noted a gradual decline in global effect (measured as frequency of averaging saccades) up to 90° (Ottes et al. 1985). Thus, the effects of angular separation may be similar for the global effect and alternate-goal bias.

Our finding of spatial bias induced by prior probability in the second experiment is consistent with several studies that suggest effects of prior probability in the saccadic system, mainly for prosaccades. However, we add a new 'spatial' dimension to this literature, which until now has focused mainly on rates of directional error and latency (Fecteau and Munoz 2003; Tatler and Hutton 2007). Neurophysiological experiments have shown that increased prior probability of a prosaccade to a goal in a neuron's receptive field is associated with greater baseline preparatory activity of buildup neurons in the frontal eye fields, the superior colliculus and possibly other regions involved in saccade generation. The elevated activity in turn is correlated with reduced reaction times (Basso and Wurtz 1997; Basso and Wurtz 1998; Dorris and Munoz 1998). Faster latencies with increased probability have also been demonstrated in other studies for prosaccades (Carpenter 2004; Gmeindl et al. 2005) and antisaccades (Koval et al. 2004).

These studies do not directly address our issue, the influence of prior probability of saccades at one location on responses directed at another location. Neither does another study of recent frequency/prior probability on the global effect for prosaccades (He and Kowler 1989). This used two goal–distractor combinations, one with the goal 15° right of the vertical meridian and the distractor 15° left of the meridian, the second with the goal and distractor positions reversed. The bias of mean prosaccade endpoint towards the goal was increased when it was the more frequent goal location. While differing significantly from our study, this nevertheless suggests that recent frequency and/or prior probability can influence motor preparation and averaging effects, which is consistent with the conclusion we reach on the basis of our first experiment. Another study of distractor effects has more clearly shown that the trajectories of prosaccades deviate away not only from the location of a simultaneous distractor, but also from the expected location of a distractor that does not actually appear (Van der Stigchel and Theeuwes 2006). Our results join this latter report in demonstrating that expectancy is sufficient to alter the spatial programming of saccadic eye movements.

To conclude, we show that alternate goals can bias saccadic accuracy towards their locations, that this effect is greater for antisaccades than prosaccades, that it has an inverse relationship with the distance between the current and the alternate goal, and that it is generated at least in part by current expectations, though other contextual factors may also contribute to its generation.

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