The spatial and temporal shape of oculomotor inhibition

Eugene McSorley [a,*], Patrick Haggard [b], Robin Walker [c]

[a] School of Psychology and Clinical Language Sciences, University of Reading, Harry Pitt Building, Earley Gate, Reading RG6 6AL, UK
[b] Institute of Cognitive Neuroscience, Department of Psychology, University College London, 17 Queen Square, London WC1N 3AR, UK
[c] Department of Psychology, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK

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ABSTRACT

Selecting a stimulus as the target for a goal-directed movement involves inhibiting other competing possible responses. Inhibition has generally proved hard to study behaviorally, because it results in no measurable output. The effect of distractors on the shape of oculomotor and manual trajectories provide evidence of such inhibition. Individual saccades may deviate initially either towards, or away from, a competing distractor – the direction and extent of this deviation depends upon saccade latency, target predictability and the target to distractor separation. The experiment reported here used these effects to show how inhibition of distractor locations develops over time. Distractors could be presented at various distances from unpredictable and predictable targets in two separate experiments. The deviation of saccade trajectories was compared between trials with and without distractors. Inhibition was measured by saccade trajectory deviation. Inhibition was found to increase as the distractor distance from target decreased but was found to increase with saccade latency at all distractor distances (albeit to different peaks). Surprisingly, no differences were found between unpredictable and predictable targets perhaps because our saccade latencies were generally long (~260–280 ms.). We conclude that oculomotor inhibition of saccades to possible target objects involves the same mechanisms for all distractor distances and target types.

1. Introduction

Selecting an appropriate behavioral goal typically involves successful inhibition of a vast range of other possible responses that are less appropriate in the current situation. This process of inhibiting inappropriate actions is a major function of the cerebral cortex. In general, goal-directed actions are performed serially (Koechlin, Ody, & Kouneiher, 2003). Therefore, at any particular time, the neural activity associated with irrelevant stimuli must be inhibited, and the selection of a single stimulus as the target for a goal-directed response must be enabled (Allport, 1993; Desimone & Duncan, 1995; McPeek, 2006; McPeek, Han, & Keller, 2003; Munoz & Istvan, 1998; Port & Wurtz, 2003). Inhibition has generally proved difficult to study behaviorally, because it results in no measurable output. However, recent oculomotor and reaching studies have provided novel, indirect evidence for inhibition, by studying how goal-directed movement trajectories are modulated by a competing stimulus that is inhibited (Godijn & Theeuwes, 2002, 2004; McPeek et al., 2003; Ludwig & Gilchrist, 2003; McSorley, Haggard, & Walker, 2004; Theeuwes & Godijn, 2004; Tipper, Howard, & Paul, 2001; Walker, McSorley, & Haggard, 2006; see: van der Stigchel, Meeter, & Theeuwes, 2006 and Walker & McSor-

ley, 2008, for recent reviews). In the basic paradigm, subjects make a goal-directed movement, such as an eye-movement (saccade), towards a target, in the presence of a distractor object. The distractor is considered a potential alternative target whose neural representation must be inhibited in order to saccade to the true target. In early studies, saccades were found, on average, to deviate away from the distractor. This deviation was interpreted as the consequence of active inhibition of a saccadic motor programme evoked by the appearance of the distractor (Sheliga, Riggio, Craighero, & Rizzolatti, 1995; Tipper et al., 2001).

More recent studies showed that saccade trajectories may initially deviate away from distracting stimuli or towards distracting stimuli, in apparently similar experimental conditions. The direction of trajectory deviation is fundamentally linked to development of distractor inhibition, as reflected in saccade latency. Saccades which have a short latency (less than 200 ms) deviate towards a distractor while those with longer saccades deviate away. The relation between trajectory deviation and saccade latency shows an increasing linear trend (McSorley, Haggard, & Walker, 2006). The progressive change in deviation direction from towards to away, is attributable to the relatively long latency of inhibitory interactions acting upon the activation of the distractor location.

The predictability of the target location has also been found to be important in modulating the direction of distractor-related trajectory deviations. If a target location is predictable, for example if

* Corresponding author.
E-mail address: e.mcsorley@reading.ac.uk (E. McSorley).

the target location is cued in advance, then saccades reliably deviate away from the distractor. If however, the location is unpredictable then trajectory deviation follows the pattern dictated by the latency of the saccade (Walker et al., 2006). The former result suggests a general preparatory application of inhibition to a region of space can occur prior to the onset of stimuli, while the latter result suggests an inhibitory process triggered by distractor or target onset, and increasing over time.

Recent studies have examined the spatial coding of inhibition by varying the target or fixation to distractor distance, or by manipulating the relative distance of two distractors to create an imbalance (McSorley, Haggard, & Walker, 2005; McSorley et al., 2004; Van der Stigchel, Meeter, & Theeuwes, 2007; Van der Stigchel & Theeuwes, 2006). They provided evidence showing that spatial coding is quite coarse. Although increasing the target to distractor distance reduces the extent of trajectory deviation, quite large separations still evoke a sizable trajectory deviation (McSorley et al., 2004).

These distractor-induced effects on saccade trajectories have been attributed to the state of activation at the distractor location at the onset of the saccade. Interactions occur on the underlying neural map that specifies potential saccade goals (evidence for this has been found in the superior colliculus and frontal eye fields: Aizawa & Wurtz, 1998; McPeek, 2006; McPeek & Keller, 2001; McPeek et al., 2003; Port & Wurtz, 2003; Quaia, Aizawa, Optican, & Wurtz, 1998). A local averaging process ensures that adjacent peaks of activation in the map are merged together and the initial saccade direction is assumed to be specified by the location of peak activation in the map. When the distractor-related activity is above surrounding baseline at the time of saccade initiation, it may merge with target-related activity resulting in a deviation of initial saccade direction *towards* the distractor location. In addition, an external inhibitory process may be applied to non-target regions of the map. The projection from the frontal eye fields (FEFs) to the superior colliculus, perhaps via the basal ganglia (Schlag-Rey, Schlag, & Dassonville, 1992; see: Tehovnik, Sommer, Chou, Slocum, & Schiller, 2000) may perform this function. This top–down inhibition suppresses the distractor-related activity below baseline, so that the averaging process now includes a negative contribution (Tipper et al., 2001). As a result, the saccade will deviate away from the distractor location. The inhibition applied by the FEFs to the collicular motor map is known to be broad (Schlag-Rey et al., 1992), which is consistent with the coarse tuning of deviation described above. The observed curvature of trajectories back towards the saccade goal has been attributed to a separate process that could involve the cerebellum (McSorley et al., 2004; Port & Wurtz, 2003; Quaia, Lefévre, & Optican, 1999).

Previous studies (McSorley et al., 2004; McSorley et al., 2006; Walker et al., 2006) have shown that inhibition of a distractor location increases over time, decreases as its location increases from the target, and can take place prior to the onset of stimuli if the target location predictable. We reasoned that it should be possible to: (1) reveal the temporal development of inhibition over time across a number of non-target spatial locations to determine whether its time course is spatially dependent and (2) examine differences in the spatial dependency of the temporal development of inhibition when inhibition can or cannot occur prior to the onset of imperative stimuli (i.e., by making the target location predictable or unpredictable). Here distractors appeared at a number of locations relative to the target under conditions in which the target location was either known (predictable), or not known (unpredictable), prior to its onset. Our analysis allowed the level of inhibition at the distractor location to be assessed across space at various points in time by examining the modulation of trajectory deviations as a function of response latency.

2. Method

2.1. Participants

There were six subjects participants in each experiment: five females and one male in Exp. 1 (18–32 years old); three females and three males in Exp. 2 (21–40 years old). All had normal or corrected to normal vision.

2.2. Apparatus and materials

The presentation of stimuli and eye-movement recording was controlled by two computers connected via a local Ethernet link in order to co-ordinate presentation and data collection timing. Eye movements were recorded using a head mounted video-based eye tracker (Eyelink, Sensomotoric Instruments) with a sampling frequency of 250 Hz. A complex diamond shaped central fixation stimulus, sides 1°, was used and ensured that the manipulation of visual events at central fixation were comparable in both experiments (see Fig. 1). The saccade target took the form of a cross (X) which was 1° square, with each line having a thickness of 6' of arc (see Fig. 1). The distractor was an unfilled circle (o) with a diameter of 1° and a line thickness of 6' of arc. Stimuli were presented on a 17″, 60 Hz color monitor. A chin rest was used to minimize head movements and maintain the viewing distance at 57 cm from the screen.

2.3. Design

In experiment 1, the target appeared 10° from fixation in one of four positions on the main diagonal (oblique) axes. The distractors, when present, appeared at the same eccentricity 45°, 90° or 135° away from the target in a clockwise or counter-clockwise direction. Thus there were 24 conditions with distractors, arising from the combination of four target positions, three target–distractor distances, and two target–distractor directions. In a further four conditions, the target was presented alone, without distractors. Distractors appeared simultaneously with the onset of the saccade target. Subjects completed four blocks of 84 trials in both experiments, producing a total of 336 trials (12 trials per condition) in each. In Exp. 2 the position of the target was cued in advance by an arrow prior to the onset of target and distractor. The arrow was created by removing lines from the fixation stimulus. In Exp. 1 the target was not cued but the same number of lines were removed from fixation to create a non-informative tilted 'hourglass' shape.

2.4. Procedure

Prior to each block of trials a calibration of the subjects' eye position relative to fixed points on the monitor was performed. The calibration procedure required the subjects to saccade to nine points in succession around the screen. In order to validate the eye positions recorded subjects again made saccades to the same nine points in succession. If landing position deviated by more than 0.5° then the procedure was completed again. Once the accuracy was within 0.5° a block of trials was completed.

Each trial began with the appearance of the central fixation stimulus that was displayed initially for 300 ms, after which time lines were removed from the fixation stimulus such that a non-directional hourglass (Exp. 1), or an arrow pre-cue (Exp. 2), remained. This ensured that the manipulation of visual events at central fixation (required for presentation of arrow-cue) was similar in both conditions. This detail was important as saccade latency is affected by the onset or offset of a stimulus at central fixation (Walker, Kentridge, & Findlay, 1995). A delay of
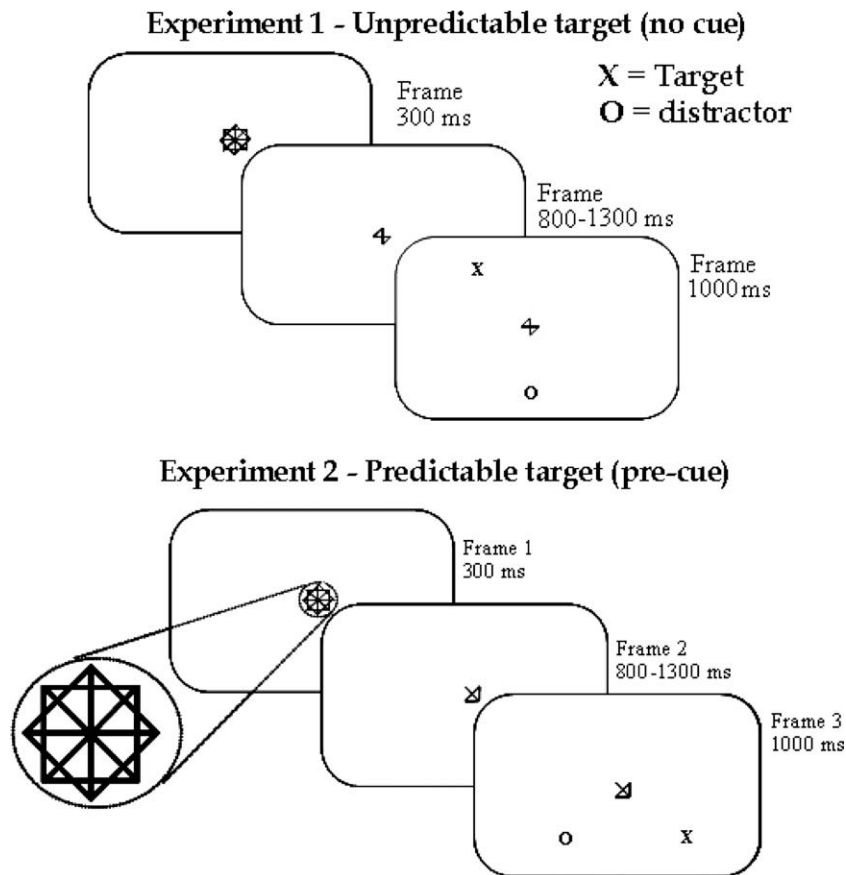
Experiment 1 - Unpredictable target (no cue)

Experiment 2 - Predictable target (pre-cue)

Fig. 1. Saccade to target task. Observers were asked to saccade to a cross which could appear 10° from fixation on one of the principle obliques (i.e., 45°, 135°, 225° or 315°). A distractor circle, if presented, appeared at 45°, 90° or 135° clockwise and counter-clockwise of the target. The upper figure (Exp. 1) shows a target at 135° with a distractor at 135° counter-clockwise of its position. The lower figure (Exp. 2) shows a target at 315° with a distractor at 90° clockwise of its position. The complex fixation cross is highlighted in the lower figure. This allowed the removal of the same number of lines to reveal a non-directional stimulus (an hourglass as illustrated in the upper figure) or a 100% valid directional cue (an arrow as illustrated in the lower figure).

800–1300 ms then occurred followed by the onset of the target and distractor, or target alone in no distractor conditions. Subjects saccaded to fixate the target as soon as the target appeared. A window of 1000 ms was allowed for making the saccade. The display was then blanked for an inter-trial interval of 600 ms.

2.5. Data analysis

Eyelink software identified saccade start and endpoints using a 22 deg/s velocity and 8000 deg/s acceleration criterion. The instantaneous velocity and acceleration were calculated and compared across two successive samples recorded at 250 Hz. If either was above threshold then a saccade was indicated as having initiated. The endpoint of the saccade was detected when the velocity or acceleration dropped below threshold. Further analysis was conducted offline using Matlab (Mathworks, Inc.).

Saccades were excluded from further analysis: if the direction of the saccade was greater than 15° either side of the target; if amplitudes and saccade latencies were 2.5 standard deviations away from the mean; or if blinks occurred during the saccade.

The maximum trajectory deviation of each saccade relative to the direct path between fixation and landing position was found (Ludwig & Gilchrist, 2002). As saccade trajectories are never completely straight, the trajectory deviation observed in no distractor (baseline) conditions was subtracted from that for distractor conditions. Trajectories deviating toward the distractor were assigned positive values and those deviating away from the distractor neg-

ative values. Trajectory deviation towards or away from the distractor was calculated for each factorial combination of target position and fixation offset time. Results are considered in terms of distractor distance from the target thus data are collapsed across target position (across the four principle obliques) and distractor direction (clockwise or counter-clockwise).

3. Results

Fig. 2A shows mean saccade curvature for Exp. 1 (unpredictable targets) and Exp. 2 (predictable targets). Saccades trajectories deviated away from the distractor, for all cue conditions and distractor distances. A mixed factor ANOVA was performed to examine the effect on saccade trajectories of distractor location (three levels), with experiment as the between subjects factor. The ANOVA showed a significant main effect of target–distractor distance ($F(2,20) = 8.5$, $p < 0.05$) on saccade trajectory deviation, but no effect of experiment ($F < 1$) and no interaction ($F(2,20) = 1.2$, $p > 0.05$). A trend analysis shows a significant linear fit to distance ($F(1,10) = 12.8$, $p < 0.05$). Thus, when target position was either unpredictable (Exp. 1) or predictable (Exp. 2) saccades deviated away from the distractor location and the magnitude of the deviation diminished with increasing distractor distance from the target.

Mean saccade latency is shown in Fig. 2B. A mixed factor ANOVA was performed to examine the effect on saccade latency of distractor location (3 levels), with experiment as the between subjects
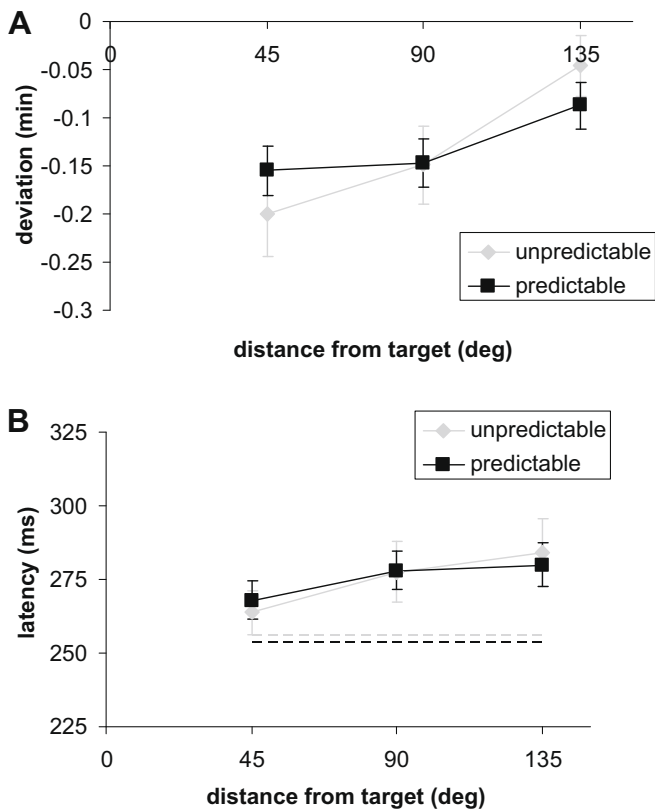
A

B

Fig. 2. Mean saccade trajectory deviation (A) and latency (B) made under unpredictable (gray) or predictable (black) target conditions grouped across target direction. Saccade trajectory deviation and latency are shown as function of distractor distance from target. For trajectory deviation negative values indicate curvature away from the distractor location. The dashed flat line indicates the no deviation point (A); or the mean saccade latencies found under the no distractor present condition (B). Error bars are standard deviations of the mean.

factor. The ANOVA showed a significant main effect of distractor location ($F(2, 20) = 10.98$, $p < 0.05$) on saccade latency, but no effect of experiment ($F < 1$) and no interaction ($F < 1$). A trend analysis shows a significant linear fit to distance ($F(1, 10) = 14.1$, $p < 0.05$). Saccade latency therefore increased as distractor-to-target separation increased.

It is noticeable that average saccade latencies recorded in each experiment were found not to differ. It might have been expected that saccade latencies elicited after the cue information provided in Exp. 2 would have been quicker as target search should not be necessary. One explanation for this is that the cue was not used by the participants. To test this possibility saccade accuracy was examined. While it may be the case that latencies did not differ, it would be expected that accuracy should improve with the addition of the cue. The average direction error (angular deviation) relative to each target position was found for each distractor position (including no distractor). This was then averaged across the four target positions. Accuracy did indeed improve when the cue was present (Exp. 1 no cue: none −1.11; 45°−0.95; 90°−0.87; 135°−1.04; Exp. 2 pre-cue: none −0.62; 45°−0.19; 90°−0.56; 135°−0.47; accuracy is shown in angular degrees). A mixed factor ANOVA was performed to examine the effect on saccade accuracy of distractor location (four levels), with experiment as the between subjects factor. The ANOVA showed a significant main effect of experiment ($F(1, 10) = 9.1$, $p < 0.05$), but no effect of distractor ($F(3, 30) = 1.2$, $p > 0.05$) and no interaction ($F < 1$). Accuracy was found to be

significantly improved with the presence of the pre-cue suggesting is was being employed by participants in performing this task.

The relationship between saccade latency and saccade deviation is shown in Fig. 3. The latency distributions for each subject were first grouped into bins of 25% (quartiled). The deviation within each bin was then averaged across subjects. Thus, the curvature is shown for the quickest 25% of saccades, through to the slowest 25% of saccades. A mixed factor ANOVA was performed on saccade trajectory deviation with distractor distance (three levels) and latency (four levels – quartiles) as a within subjects factors and experiment as the between subjects factor. There was a significant main effect of distractor location ($F(2, 20) = 9.4$, $p < 0.05$), a significant main effect of quartile ($F(3, 30) = 3.2$, $p < 0.05$) and a significant interaction between them ($F(6, 60) = 2.5$, $p < 0.05$). No other effects were found to be significant. The main effect of distractor location reflects the same relationship as in Fig. 2: trajectory deviation away from the distractor increases as its distance from the target decreases. The main effect of quartile shows that saccade trajectories deviate away from the distractor more as saccade latency increases, though this starts to diminish for the longest latencies. This pattern is confirmed by a trend analysis showing a significant linear and quadratic relationship between saccade latency and trajectory deviation (Linear: $F(1, 10) = 17.35$, $p < 0.05$; Quadratic: $F(1, 10) = 6.7$, $p < 0.05$). The interaction between distractor location and quartile shows that the pattern of trajectory deviation differs across distractor location. Further trend analyses of the quartile patterns separately for each distractor location showed that a quadratic trend best described the relationship between saccade latency and trajectory deviation at 45° and 135° (45°: $F(1, 11) = 15.2$, $p < 0.05$; 135°: $F(1, 11) = 6.2$, $p < 0.05$) while a linear trend best described the relationship at 90° $F(1, 11) = 4.34$, $p < 0.05$). Examination of Fig. 3 suggests saccade elicited to the target when distractors are close to (45°) and far from (135°) produce trajectory deviations which increase then diminish as latency increases (shown by the quadratic trends). On the other hand, saccades elicited when distractors are at the intermediate position (90°.) show a continuous increase in trajectory deviation with increasing saccade latency (shown by the linear trend).

4. Discussion

We have examined the changing shape of inhibition over time. The direction and magnitude of saccade trajectory deviation was observed when a competing distractor was presented along with the saccade target. Deviation away from the distractor was taken as a measure of inhibition of a saccade to the distractor. The aim was to examine the development of inhibition resulting from competition between the target and distractor. Distractor inhibition was examined when the target location was either predictable or unpredictable and under conditions in which the spatial separation between target and distractor was manipulated.

Under both predictable and unpredictable target conditions saccade trajectories were found to deviate away from distractors and the magnitude of this deviation increased as the distance between the target and distractor decreased (McSorley et al., 2004; van der Stigchel & Theeuwes, 2006). The relationship between trajectory deviation and saccade latency showed that, regardless of whether the target location was unpredictable or predictable, inhibition of distractors increased over an extended period of time, and in some cases then diminished again. Specifically, inhibition was found to diminish at longer latencies for distractors close to and far from the target (45° and 135°) but not for intermediate distractors (90°). We suggest that oculomotor inhibition is best explained as being due to a common underlying mechanism involving an initial
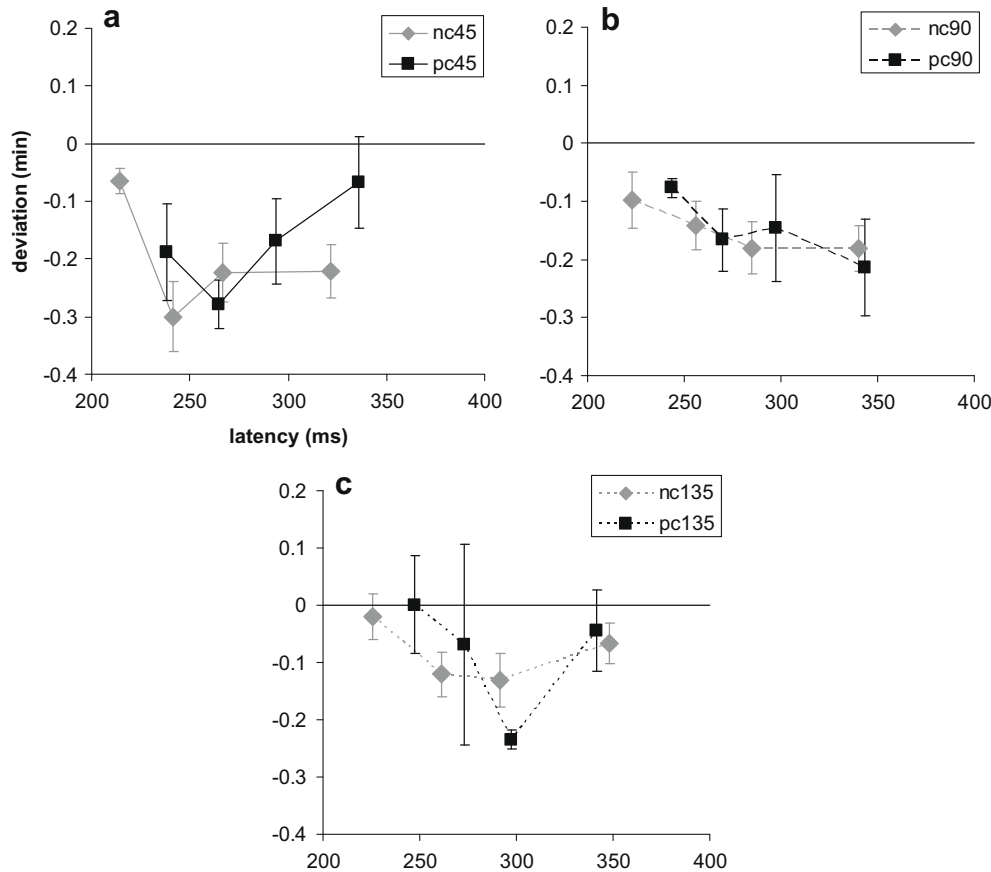
Fig. 3. Saccade curvature is shown as a function of quartiled saccade latency. For clarity these have been grouped by distractor distance from target (45°, 90° and 135°). This is indicated in the figure legends which show the condition (no cue, nc; and pre-cue, pc) and distractor distance. Gray data points and connecting lines show results from unpredictable target experiment while black shows results from the predictable target experiment. The curvature elicited from the quickest 25% of saccades progressively to the slowest 25% of saccades is shown from left to right. The absissca shows latency in milliseconds and the ordinate shows curvature in terms of deviation towards (positive values) or away (negative values) from the distractor. The lines on the graphs show the trajectory deviation found at each distractor distance from target. The solid flat line at zero indicates the no deviation point for reference. Error bars are standard error bars.

increase in strength, followed by a subsequent decrease. The intermediate, 90°, distractor location would then represent a special case. We suggest that the sustained increase in the inhibition of the intermediate distractor may arise because this distractor is also a potential target location. If baseline activation at potential target locations was higher than at other locations, perhaps due to a top–down influence, then inhibition of such locations might take longer to reach a maximum compared to distractors at other, non-target locations. Thus we would expect saccades to the intermediate distractor location to also show decreasing inhibition at longer latencies than those we recorded. The lack of effect of the cue in this case suggests that its effect is not felt at distractor locations but only impacts on the indicated target location. This may be the result of the remaining uncertainty about the distractor location.

It might be expected that the presence of the cue would give rise to another pattern of trajectory deviations in the 90° distractor case. If this location is a potential target site then when the cue reveals the actual target site then the higher activity at the non-target site can be reduced. However, as the distractor site is not revealed, and it is the imbalance in activation at non-target locations which results in trajectory deviations, we suggest that in all cases when the cue reveals the target location, activity at all non-target locations is reduced prior to stimuli onset uniformly because the position of the distractor is unknown. Importantly, the relative activity between the possible distractor does not shift. Thus the activity at for the 90° distractor location is still relatively higher then the other distractor locations. Because

of this the pattern of trajectory deviation (which is driven by relative activity at non-target sites) is the same in both cued and non-cued cases.

We show a time-varying inhibition scheme which could account for our results in Fig. 4. The activation levels at target and distractor sites are shown as a function of time (c.f. Thompson, Hanes, Bichot, & Schall, 1996). After stimulus onset, the activation of the target site and distractor site rise from their respective baselines. The potential target locations (solid 'target' line and dotted 'distractor' line) have a higher baseline resting level of activation than non-target locations ('solid 'distractor' line) due to top down influences dependent on the task demands. The shape of the activation functions at the distractor locations is the same but the time course varies due to this difference in the initial baseline activation level. Over time, distractor locations are subject to increasing inhibition (in this case the target location wins) and their activation starts to diminish. If a saccade is triggered during the initial period when activation at the distractor location is higher than baseline its trajectory would then deviate toward the distractor. Alternatively if the inhibition of the distractor continues and drops below the baseline of other locations the trajectory would start to deviate away until a maximum point of inhibition is reached. The inhibition is then assumed to drop back to the baseline rather than saturate. The general pattern of results shown in Fig. 3 can be attributed to activity levels depicted in the outline box on Fig. 4. At the average saccade latency, inhibition of the distractor location would be near-maximal, and saccade trajectories would consis-
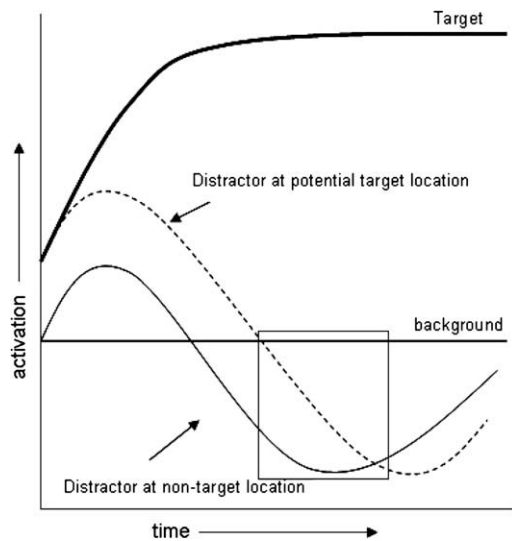
Fig. 4. Schematic diagram of the activation at non-target sites which results in saccade trajectory deviations. Activation at target and distractor sites increase when stimuli are displayed. On correct trials the activation at distractor sites initially increases but then diminishes due to inhibition from the target site before tending back to zero. When activation at the distractor site is high relative to background, saccade trajectories deviate toward the target, when lower they deviate away. The dashed and solid distractor lines show activation when the location is a potential target site or not respectively. Activation is higher when the location is a potential target site. Therefore, both the onset and the ending of the inhibition process that produces curvature away are delayed. The unfilled box highlights the portion of the curves which show similar patterns to the results in Fig. 3.

the distractor (Walker et al., 2006). This difference between studies may be due to differences in the mean saccade latencies. It is known that there is a predictive relationship between saccade trajectory deviation and saccade latency (McSorley et al., 2006). The trajectories of saccades with latencies less than approximately 200–220 ms. tend to deviate towards the distractor while those with latency greater than 200 ms. deviate away. In the experiment reported here saccade latencies are of the order of 260–280 ms. so would be expected to produce deviation away from the distractor. In contrast, the saccades reported in Walker et al. (2006) are much shorter at approximately 210 ms. It is interesting to note that the 45° distractor condition employed here is the same as that used by Walker et al. (2006) and yet the latencies recorded here are about 60 ms longer. We suggest that the increase in latencies reported in this condition are due to a general lengthening of saccade latencies in all conditions – including the no distractor baseline conditions, which is likely to be due to greater task difficulty because of the larger number of potential distractor locations or more cautious observers.

In conclusion, we have shown that inhibition of competing motor responses is slow to develop and spatially coded. The same underlying mechanisms appear to be involved as the pattern of inhibition is similar regardless of the predictability of the target location and distance of the distracting motor response.

Acknowledgment

tently deviate away from distractors. The solid 'distractor' line therefore shows an inflexion resembling Fig. 3a and c while the dotted 'distractor' line shows a consistent drop with trajectory deviation steadily increasing, resembling Fig. 3b.

The overall observed pattern of trajectory deviation is indicative of an inhibitory process combining feed forward and top–down processes. These converging processes operate to select a single saccade target location from among competing stimuli. In the unpredictable situation the inhibition of the distractor location can only commence following the onset of the stimuli and after the target and distractor have been discriminated. However, in the predictable situation, inhibition can be applied prior to onset of a predictable stimulus. Specifying the target location could produce a top–down inhibition of all other locations. Any further inhibition, which presumably produces saccade trajectory deviation away from the distractor, must occur after its position is revealed. In both cases inhibition may involve local competitive inhibition between target and distractor locations in a neural motor map, leading to the gradual suppression of the distractor location (McPeek, 2006; McPeek et al., 2003; Port & Wurtz, 2003; Walton, Sparks, & Gandhi, 2005), coupled with a top–down inhibition of the distractor, in order for the activity associated with it to be suppressed below surrounding baseline activity. This produces a shift in the target-related activity to drive the saccade trajectory deviation away from the distractor location. The inhibitory influence of the frontal eye fields on saccade-related neurons in the superior colliculus, may be attributed to activity of local inhibitory interneurons (Munoz & Istvan, 1998), excitation of fixation neurons located in more caudal regions of the SC (Sommer & Wurtz, 2000) or via inhibitory projections from the substantia nigra (c.f. Schlag-Rey et al., 1992).

The finding of trajectory deviation away from the distractor when the target is unpredictable is different from our previous study showing unpredictable targets producing curvature towards

References

Aizawa, H., & Wurtz, R. H. (1998). Reversible inactivation of monkey superior colliculus. I. Curvature of saccadic trajectory. *Journal of Neurophysiology, 79*, 2082–2096.

Allport, A. (1993). Attention and control: have we been asking the wrong questions – A critical review of the last twenty five years. In D. E. Meyer & S. Kornblum (Eds.), *Attention and performance XIV: A silver jubilee* (pp. 183–218). Cambridge, Mass: M.I.T. XIV.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193–222.

Godijn, R., & Theeuwes, J. (2002). Programming of endogenous and exogenous saccades: Evidence for a competitive integration model. *Journal of Experimental Psychology: Human Performance and Perception, 28*, 1039–1054.

Godijn, R., & Theeuwes, J. (2004). The relationship between inhibition of return and saccade trajectory deviations. *Journal of Experimental Psychology, 30*, 538–554.

Koechlin, E., Ody, C., & Kouneiher, F. (2003). The architecture of cognitive control in the human prefrontal cortex. *Science, 302*, 1181–1185.

Ludwig, C. J. H., & Gilchrist, I. D. (2002). Measuring saccade curvature: a curve fitting approach. *Behavior Research Methods, Instruments and Computers, 34*, 618–624.

Ludwig, C. J. H., & Gilchrist, I. D. (2003). Target similarity affects saccade curvature away from irrelevant onsets. *Experimental Brain Research, 152*, 60–69.

McPeek, R. M. (2006). Incomplete suppression of distractor-related activity in the frontal eye field results in curved saccades. *Journal of Neurophysiology, 96*, 2699–2711.

McPeek, R. M., Han, J. H., & Keller, E. L. (2003). Competition between saccade goals in the superior colliculus produces saccade curvature. *Journal of Neurophysiology, 89*, 2577–2590.

McPeek, R. M., & Keller, E. L. (2001). Short-term priming, concurrent processing, and saccade curvature during a target selection task in the monkey. *Vision Research, 41*, 785–800.

McSorley, E., Haggard, P., & Walker, R. (2004). Distractor modulation of saccade trajectories: spatial separation and symmetry effects. *Experimental Brain Research, 155*, 320–333.

McSorley, E., Haggard, P., & Walker, R. (2005). Spatial and temporal aspects of oculomotor inhibition as revealed by saccade trajectories. *Vision Research, 45*, 2492–2499.

McSorley, E., Haggard, P., & Walker, R. (2006). Time-course of oculomotor inhibition revealed by saccade trajectory modulation. *Journal of Neurophysiology, 96*, 1420–1424.

Munoz, D. P., & Istvan, P. J. (1998). Lateral inhibitory interactions in the intermediate layers of the monkey superior colliculus. *Journal of Neurophysiology, 79*, 1193–1209.

Port, N. L., & Wurtz, R. H. (2003). Sequential activity of simultaneously recorded neurons in the superior colliculus during curved saccades. *Journal of Neurophysiology, 90*, 1887–1903.

Quaia, C., Aizawa, H., Optican, L. M., & Wurtz, R. H. (1998). Reversible inactivation of monkey superior colliculus. II. Maps of saccadic deficits. *Journal of Neurophysiology, 79*, 2097–2110.

Quaia, C., Lefévre, P., & Optican, L. M. (1999). Model of the control of saccades by superior colliculus and cerebellum. *Journal of Neurophysiology, 82*, 999–1018.

Schlag-Rey, M., Schlag, J., & Dassonville, P. (1992). How the frontal eye field can impose a saccade goal on superior colliculus neurons. *Journal of Neurophysiology, 67*, 1003–1005.

Sheliga, B. M., Riggio, L., Craighero, L., & Rizzolatti, G. (1995). Spatial attention-determined modifications in saccade trajectories. *NeuroReport, 6*, 585–588.

Sommer, M. A., & Wurtz, R. H. (2000). Composition and topographic organization of signals sent from the frontal eye field to the superior colliculus. *Journal of Neurophysiology, 83*, 1979–2001.

Tehovnik, E. J., Sommer, M. A., Chou, I-H., Slocum, W. M., & Schiller, P. H. (2000). Eye fields in the frontal lobes of primates. *Brain Research Reviews, 32*, 413–448.

Theeuwes, J., & Godijn, R. (2004). Inhibition of return and oculomotor interference. *Vision Research, 44*, 1485–1492.

Thompson, K. G., Hanes, D. P., Bichot, N. P., & Schall, J. D. (1996). Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. *Journal of Neurophysiology, 76*, 4040–4055.

Tipper, S. P., Howard, L. A., & Paul, M. A. (2001). Reaching affects saccade trajectories. *Experimental Brain Research, 136*, 241–249.

van der Stigchel, S., Meeter, M., & Theeuwes, J. (2006). Eye movement trajectories and what they tell us. *Neuroscience Biobehavioural Reviews, 30*, 666–679.

Van der Stigchel, S., Meeter, M., & Theeuwes, J. (2007). The spatial coding of the inhibition evoked by distractors. *Vision Research, 47*, 210–218.

van der Stigchel, S., & Theeuwes, J. (2006). Our eyes deviate away from a location where a distractor is expected to appear. *Experimental Brain Research, 169*, 338–349.

Walker, R., Kentridge, R. W., & Findlay, J. M. (1995). Independent contributions of the orienting of attention, fixation offset and bilateral stimulation on human saccadic latencies. *Experimental Brain Research, 103*, 294–310.

Walker, R., & McSorley, E. (2008). Distractor modulation of saccade trajectories. *Journal of Eye Movement Research, 2*(7), 1–13.

Walker, R., McSorley, E., & Haggard, P. (2006). The control of saccade trajectories: Direction of curvature depends upon prior knowledge of target location and saccade latency. *Perception and Psychophysics, 68*, 138–139.

Walton, M. M. G., Sparks, D. L., & Gandhi, N. J. (2005). Simulations of saccade curvature by models that place superior colliculus upstream from the local feedback loop. *Journal of Neurophysiology, 93*, 2354–2358.