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RESEARCH ARTICLES

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Distractor modulation of saccade trajectories: spatial separation and symmetry effects

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Abstract The trajectories of saccadic eye movements can be modulated by the presence of a competing visual distractor. In the present study the trajectories of vertical saccades curved away from a single visual distractor presented in one visual field, but tended to be straight when two distractors were presented at mirror symmetric locations in both visual fields. The spatial nature of the mirror distractor effect was examined by presenting a second distractor at mirror and non-mirror locations. Saccade trajectories also tended to be straight with both mirror and non-mirror symmetrical distractors. The relationship between the distractor location and saccade curvature was examined in a third experiment by manipulating the distractor-to-target spatial separation. Although there was a tendency for greater curvature when the distractor was presented in the same hemifield as the target there was no clear relationship between curvature and distractor location. The results show that the distractor modulation of saccade trajectory is not highly spatially specific and that it can be balanced by a second bilateral distractor in the opposite visual field. The results are interpreted in terms of a model in which the initial saccade direction and curvature back towards the saccade goal are controlled by separate processes. Initial saccade direction is modulated by the inhibition of distractor locations within a 'motor map' specifying saccade direction. Curvature back towards the saccade goal may be attributed to a feedback system, with a separate representation of the visual target location, that enables an on-line correction of the saccade during mid-flight.

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Introduction

It has long been known that saccade trajectories may be curved (Dodge 1917; Von Helmholtz 1962; Yarbus 1967); furthermore behavioural studies have demonstrated that the magnitude and direction of curvature can be modulated by competing stimuli. Saccades in man have been found to curve away from an attended location (Sheliga et al. 1995a, 1995b, 1997; Tipper et al. 2001) and away from visual distractors (Doyle and Walker 2001; Tipper et al. 2001) and from auditory and somatosensory distractors (Doyle and Walker 2002). The magnitude of curvature is typically greatest when the distractor is presented in the same hemifield as the saccade target (e.g. Doyle and Walker 2001; Tipper et al. 2001) and can be increased when the distractor shares properties with the target such as colour (Ludwig and Gilchrist 2003). Under other conditions saccades in man have been shown to curve towards distractor stimuli. Frens et al. (1995) showed that visually guided saccades curved towards an auditory distractor in crossmodal conditions. In a visual search task McPeek and Keller (2001) showed that saccades in monkey were more likely to curve towards the goal of a subsequent saccade.

The modulation of saccade trajectories has been interpreted in terms of competitive interactions between representations of potential target locations within the neural structures involved in the selection of a saccade target (Sheliga et al. 1995b; Doyle and Walker 2001; McPeek and Keller 2001; Doyle and Walker 2002). Both Sheliga (1995b) and Tipper and colleagues (2001) have attributed the curvature of saccades away from a distractor location to the requirement to inhibit a saccade programme automatically generated when a subject 'attends' to the distractor location, so that a saccade can be made to another location. Furthermore, Doyle and Walker (2001) showed that saccade trajectories deviated away from a task-irrelevant distractor in the absence of covert attentional orienting. This was attributed to the distractor onset reflexively generating a saccade programme which must be actively inhibited causing the target-directed saccade to deviate away from the distractor location. More specifically, in this model the target and distractor are represented by large overlapping populations of activity on a common motor map. Saccade direction is determined by a competition via lateral connections between the two neural populations. As these two populations overlap, inhibition of the distractor population will impinge upon the activity of the population of neurons encoding the target, resulting in a shift of the peak of activity away from the distractor. Hence taking a weighted average of activity to determine the saccade direction will result in a trajectory that deviates away from the distractor location.

These models of saccade curvature are inherently spatial in nature; manipulating the number of distractors and their spatial separation from the saccade target should modulate the observed effects on saccade trajectory. The spatial nature of the competitive interactions between target and distractor on saccade trajectory will be examined in this study. One of the predictions arising from the model outlined is that reducing the spatial separation between the target and distractor would result in a greater overlap between the populations that encode their locations, producing greater effects on saccade trajectory. Furthermore, introducing a second distractor in the mirror position of the first distractor at an equal distance from the target will result in a third population of activity which will change the activity associated with the target position such that the peak of activity will shift back toward the

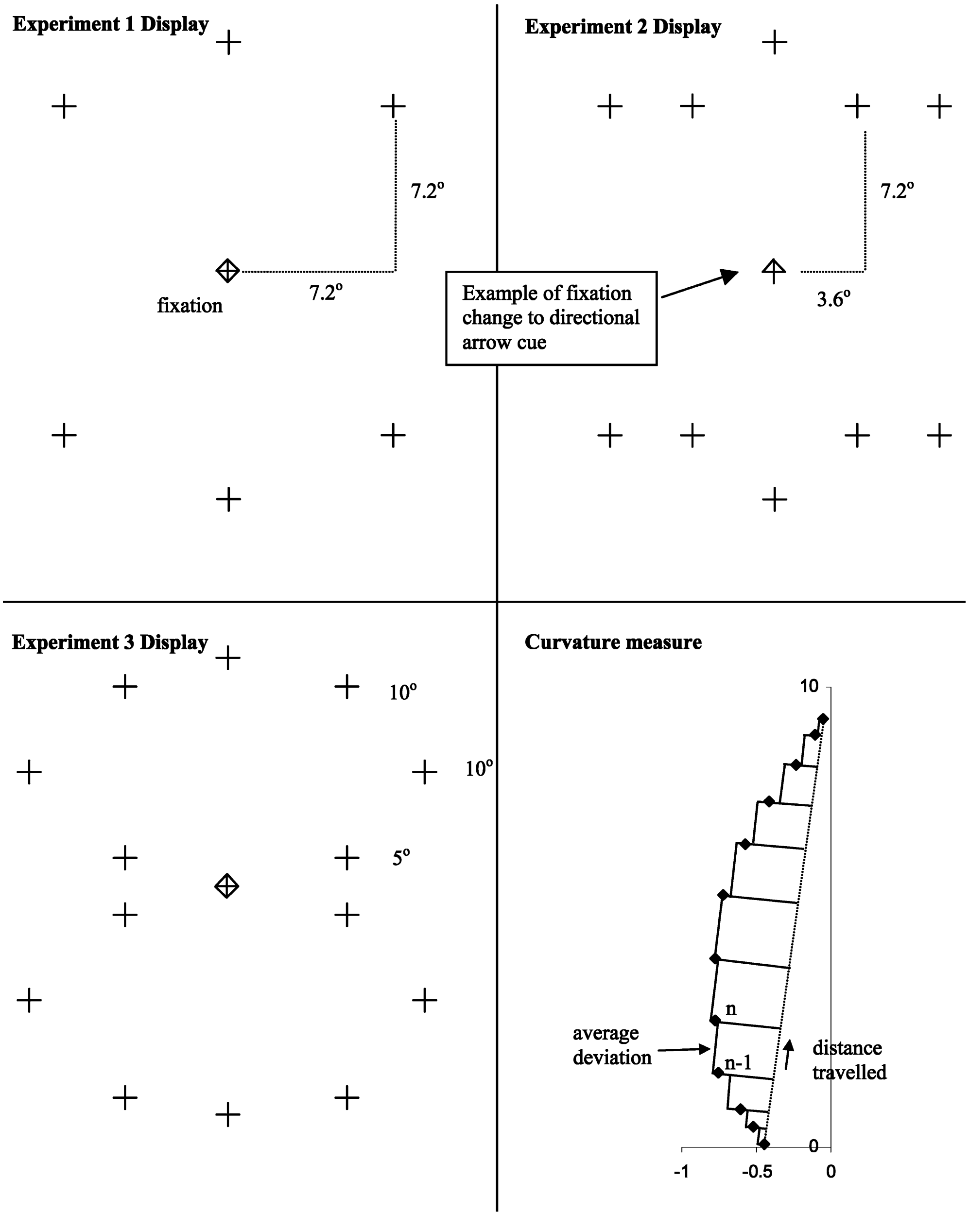

Fig. 1 The stimulus displays used for all three experiments are shown. *Crosses on the vertical midline* directly above or below fixation indicate possible target positions while all others represent possible distractor positions. The central fixation stimulus (Exp. 1 display) changed shape to an arrow cue (Exp. 2 display) that indicated the saccade target. The *figure to the bottom right* illustrates the method used to determine saccade curvature. Shown is an example saccade trace from Exp. 3. The curvature of saccade trajectory was computed by finding the area under the curve formed by the sampled curved saccade trajectory relative to the direct distance between start fixation position and landing position. In particular at sample point *n* the deviation perpendicular to the direction of the saccade at *n* and *n*−1 was averaged. This average was multiplied by the distance between *n* and *n*−1 along the direct route of the saccade

actual target location. Thus the effect of this second distractor will be to 'balance' the neural activity in the saccade motor map straightening the saccade trajectory relative to either distractor presented alone. Shifting the position of the second distractor closer to the target will then be predicted to modulate the saccade trajectory away from the site of the second distractor due to the greater population overlap. The first experiment examined the influence of single and bilateral distractors presented at symmetrical locations in both visual fields on saccade trajectory. The second experiment examined the effect of shifting the spatial separation of the second distractor on saccade trajectory so the two distractors appeared at non-mirror symmetric locations. In the third experiment the effect of systematically varying the spatial separation between a target and a single distractor on saccade trajectory was examined.

To pre-empt the results somewhat, a second distractor was found to straighten saccade trajectories across a range of spatial separations. The spatial sensitivity of target driven saccades to the presence of a distractor was very high and distractors at all locations in the target hemifield modulated saccade trajectory. This effect was weaker only when the distractor was shown in the opposite hemifield to the target.

Experiment 1

The spatial nature of the competitive interactions between a visual saccade target and distractor were examined by introducing a second distracting stimulus in a mirror symmetric position. It was predicted that this would balance the inhibitory effect of a single distractor and thus straighten the saccade trajectory. The paradigm used required subjects to make a vertical saccade to a visual target that was presented above or below fixation. Saccade direction was indicated by the change of the central fixation stimulus to an arrow pointing up or down. Distractors appeared simultaneously with the change of the central fixation stimulus and could appear in the upper or lower visual field, in the left or right visual field, or bilaterally at mirror symmetrical locations in both the left and right visual fields (see Fig. 1). Thus, saccades could be regarded as being voluntary in nature and the distractors were entirely task-irrelevant (Doyle and Walker 2001).

Materials and methods

Subjects

Eight subjects, three male and five female with an age range of 20–56, took part in this experiment. All had normal or corrected to normal vision. One of the subjects was aware of the purpose of the experiment the remaining seven were naïve. Local ethical approval was obtained for this study and all experiments were conducted in accordance with the ethical standards described in the 1964 Declaration of Helsinki. All subjects who took part in these experiments gave their informed consent prior to inclusion.

Apparatus and materials

Eye movements were recorded using a head mounted video-based eye tracker (Eyelink, Sensomotoric Instruments) with a sampling frequency of 250 Hz. Stimuli were presented on a 17" colour monitor and took the form of a cross (+) which was 1 deg square, with each line forming the cross having a thickness of 6' of arc. The target cross appeared 10 deg directly above or below fixation. Distractors appeared to the left or right of the vertical midline in the same or opposite hemifield as the target 10 deg from fixation with an angular deviation of 45 deg from the vertical meridian (see Fig. 1). A chin rest was used to minimise head movements and maintain the viewing distance at 40 cm from the screen.

Design

Subjects were required to saccade to the upper or lower target cross depending upon a cue presented at fixation. Simultaneous with the cue either no distractor, a single distractor in one of the four locations, or two distractors both in the same or opposite hemifield to the target, were presented. Distractors could appear in both the same and opposite hemifield and did not therefore provide a sensory cue indicating target location. Thus, there were 12 distractor conditions and 2 no distractor conditions. Subjects completed 6 blocks of 70 trials each.

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 deg overall then the calibration procedure was repeated. Once the accuracy was within 0.5 deg a block of trials was completed.

Each trial began with the appearance of a central fixation stimulus. This took the form of a diamond with a cross in the middle (Walker et al. 2000). The upper and lower target crosses appeared 300 ms after initial fixation onset. A random delay of between 800 and 1,300 ms occurred after which two lines were removed from the fixation stimulus (i.e., the two lower lines or two upper lines) such that an arrow pointing up or down was formed. This arrow provided the subjects with the cue to move their eyes to that target location. If distractor/s were presented then they appeared simultaneous with the fixation change. After a delay of 1,000 ms, during which time a saccade should be made to the designated target, the display was blanked for an inter-trial delay of 600 ms.

Data analysis

Eyelink software identified saccade start and endpoints using 22 deg/s velocity and 8,000 deg/s^2 acceleration criteria. Further analysis of saccade metrics and dynamics were carried out using software developed in Matlab (Mathworks, Inc.).

Saccade amplitude, latency and overall direction were derived from the eye movement records for the first saccade in each record. Amplitude was defined as the shortest distance between saccade start and end point (in degrees of visual angle). Latency was defined as the interval between the change at fixation and saccade onset (ms). Direction was defined as the angular deviation of saccade direction taken from the initial fixation location to final endpoint.

Saccades were excluded from further analysis if

1. Latencies were less than 100 ms or greater than 2.5 standard deviations above the mean

2. Amplitudes were less than 2 deg or greater than 2.5 standard deviations above the mean
3. The direction of the saccade was greater than 15 deg either side of the target
4. Blinks occurred during the saccade

Once saccades had been identified the curvature of saccade trajectory was computed by finding the area under the curve formed by the sampled curved saccade trajectory relative to the direct distance between start fixation position and landing position [see Fig. 1 and Ludwig and Gilchrist (2002) for detailed description of measures of curvature]. In particular at sample point n the deviation perpendicular to the direction of the saccade at n and $n-1$ was averaged. This average was multiplied by the distance between n and $n-1$ along the direct route of the saccade. The use of the average goes some way to ameliorate effects of overestimating the actual curvature. In order to normalise across the varying amplitude of saccades the area measure was divided by the amplitude of the saccade. As saccade trajectories are never completely straight the area of curvature observed in no distractor (baseline) conditions was subtracted from that observed under distractor conditions. Thus, all measures of curvature reported here are in terms of the difference in curvature relative to the baseline natural level of curvature.

Results

Prior to analysis trials were excluded on the basis of latency (1%), amplitude (2.5%), direction (7%) and blinks (0%). Figure 2 shows the mean area differences by distractor location. The upper graph shows the results for saccades directed to the upper target and the lower graph shows the results for saccades directed to the lower target. Negative values represent curvature to the left and positive values curvature to the right. It can be seen that single distractors in the same hemifield as the target show a saccade trajectory which deviates away from the distractor, i.e., trials on which leftward distractors were present show rightward saccade curvature and vice versa. When both distractors are present this curvature is reduced relative to both single distractors; thus the saccade trajectory becomes straighter. A three way ANOVA was performed with saccade direction (up or down), hemifield (distractor in the same or opposite hemifield to the target) and distractor location within that hemifield (left, right or both) as factors. There was no main effect of saccade direction ($F_{(1,7)}$ <1) or distractor hemifield ($F_{(1,7)}$ = 1.8, p >0.05) but there was a main effect of distractor location ($F_{(1,7)}$ = 6.2, p <0.05). There were no significant interactions. A planned series of t-tests were performed to examine the main effects. It was found that curvature produced by the left and right single distractors was significantly different ($t_{(7)}$ = 2.9, p <0.05) with left distractors producing rightward curvature and right distractors producing leftward curvature. The curvature found when single distractors were presented was also significantly different from that found when both distractors are presented (left single distractor vs. both: $t_{(7)}$ = 2.5, p <0.05; right single distractor vs. both: $t_{(7)}$ = −2.9, p <0.05). Furthermore a one-sample t-test showed that curvature when both distractors were present was not significantly different from zero (zero being the average curvature found when no distractor was present). These results show that when two distractors were presented equidistant from the target, saccade trajectory was straightened relative to each distractor shown alone, to the extent that the trajectory did not significantly differ from that found when no distractor was presented.

A three-way ANOVA examined saccade latencies with saccade direction (up and down), distractor hemifield relative to the target (same and opposite) and distractor condition (left, right and both). The mean latency for the target alone condition was subtracted from latencies for distractor present conditions, thus giving a relative latency value. There was no main effect of direction ($F_{(1,7)}$ <1) or distractor condition ($F_{(1,7)}$ <1). However, hemifield was found to be significant ($F_{(1,7)}$ = 10.8, p <0.05) with latencies to targets with same hemifield distractors being

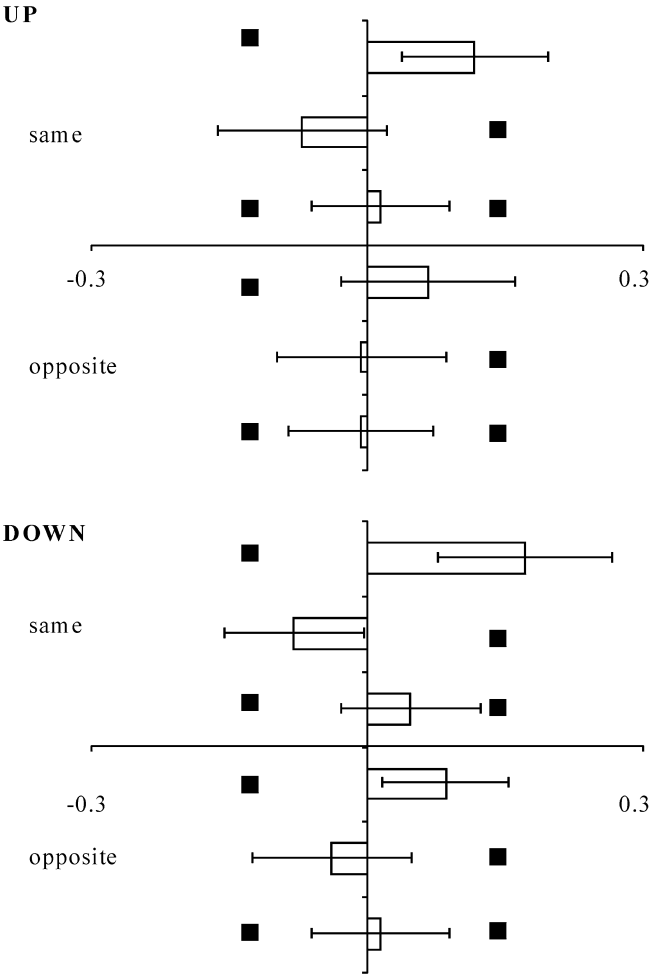

Fig. 2 The mean area difference of curvature by distractor condition in Exp. 1. The *upper graph* shows upward directed saccades and the *lower graph* downward directed saccades. Target position has been normalised to the up position. The graphs are arranged to mirror the display. The *top three bars in each graph* show saccade curvature found when distractors were on the left, right or both sides of the target in the same hemifield. The *bottom three bars* show the same sequence when distractors were in the opposite field to the distractor. Relative distractor position is indicated by *black squares; same* and *opposite* refer to distractor location relative to the target; thus distractors can appear in the same or opposite hemifield as the target

quicker than saccades to targets when distractors are in the opposite hemifield (no distractor: up 302 ms, down 324 ms; same hemifield distractor: up 228 ms, down 307 ms; opposite hemifield distractor: up 303 ms, down 322 ms). Thus saccades to targets with distractors in the same hemifield were quicker than saccades to single targets (in the no distractor condition), while saccades to targets with distractors in the opposite hemifield did not show any difference to single targets.

Saccade amplitudes were found to be longer when directed to the target in the downward position (up 8.3 deg, down 9.8 deg); however, there was found to be no effect of distractor presence or number.

Discussion

The results show that when two visual distractors appeared at mirror symmetric positions in both visual fields, curvature of the saccade trajectory was significantly straightened relative to when a single distractor appeared. This provides support for the model described in the introduction where competing populations of neural activity overlap on a common motor map. The inhibition of activity associated with single distractors produces saccade trajectories that deviate away from the distractor locations. When distractors appear bilaterally a balancing of neural activity results in straighter saccade trajectories.

Experiment 2

Experiment 1 showed that the introduction of a second bilateral distractor can influence saccade trajectory and results in saccades become straighter. This effect was explored further by manipulating the spatial separation of the second distractor and the target so distractors appeared bilaterally at mirror and non-mirror symmetric locations. The second distractor was presented equidistant, as in Exp. 1, or closer to the target than the first distractor. We questioned whether the underlying population of neural activity would be "unbalanced" when the second distractor was closer to the target, as the overlap between the populations encoding the second distractor and target would be greater than is the case for the first distractor and target. Thus, as with a single distractor, this would result in saccade trajectories that would deviate away from the nearest second distractor location.

Materials and methods

All methods are the same as Exp. 1 except where noted.

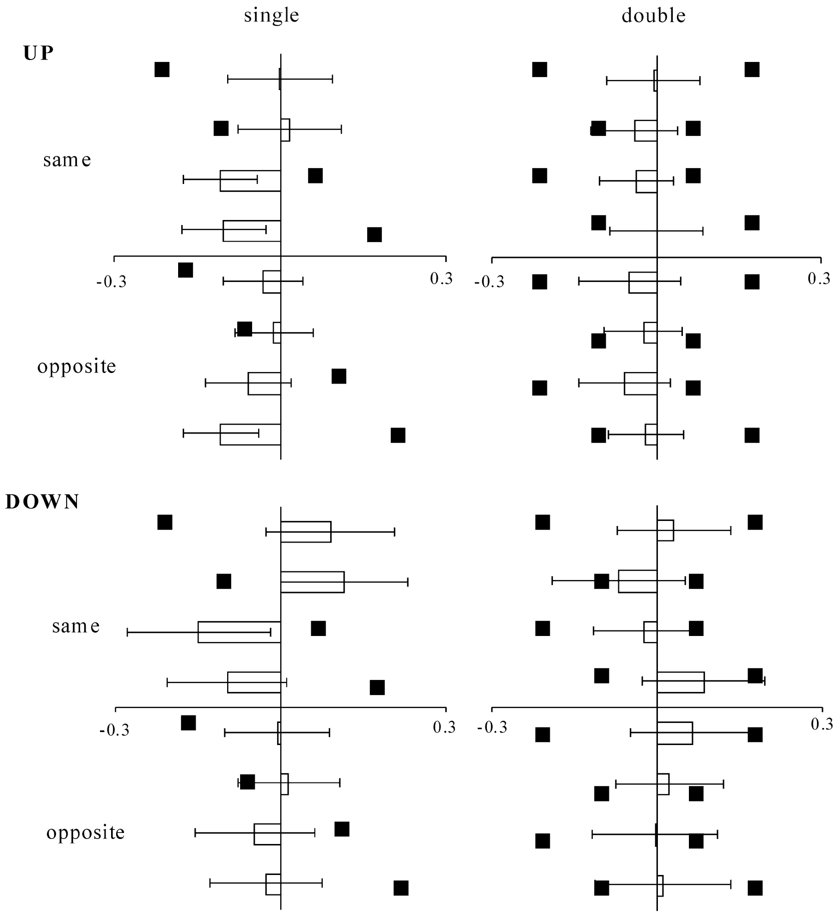

Fig. 3 The mean area difference of curvature by distractor condition in Exp. 2. *Upper and lower graphs* show saccade curvature for up and down targets respectively. Both target positions have been normalised to the up position. *Graphs on the left* show saccade curvature found when a single distractor was present and *those on the right* show saccade curvature found when two distractors were present. The *squares that accompany each bar* represent the distractor positions running from leftmost to rightmost position in the single distractor conditions and balanced to unbalanced in the bilateral distractor conditions; *same* and *opposite* refer to distractor location relative to the target

Subjects

Six subjects, all male with an age range of 25 to 38, took part in the experiment. All had normal or corrected to normal vision. Two of the subjects were authors (EM and RW) and were aware of the purpose of the experiment; the remaining four were naïve.

Design

Four more distractor positions were added to the four used in Exp. 1. These were at the same elevation but shifted horizontally so that they were closer to the target (see Fig. 1). When bilateral distractors were presented they were always shown in the same hemifield (upper or lower), in either the same or opposite hemifield to the saccade target. The two distractors could appear at equal distance from the target (balanced condition) or one could appear closer to the target (unbalanced condition). Thus, there were eight single distractor conditions, four balanced distractors (both distractors near or both distractors far in either the same and opposite hemifield to the target) and four unbalanced distractor conditions (one distractor near the target the other in the far position, i.e., left near and right far or right near and left far, in the same or opposite hemifield to the target). Overall there were 16 distractor conditions and one single target alone condition for both upward and downward target directed saccades giving 34 conditions. Subjects completed four blocks of 102 trials that took approximately 1 h.

Results

The exclusion criteria outlined in the method excluded 14% of trials (7% latency; 2% amplitude; 5% direction; and blinks 0%). Figure 3 shows the mean area of curvature by distractor condition. Upper and lower graphs show saccade curvature for up and down targets respectively. Graphs on the left show saccade curvature found when a single distractor was present and those on the right show saccade curvature found when two distractors were present. The squares which accompany each bar represent the distractor positions running from leftmost to rightmost position in the single distractor conditions and balanced to unbalanced in the double distractor conditions. It can be seen that, in general, saccade trajectories were straighter when two distractors were present. This effect is clearest for downward saccade targets and is also observed for upward saccade targets although the influence of the left distractor is much reduced.

It is important to consider the results in terms of the influence of a second distractor relative to a single distractor. We therefore modelled the influence of the second distractor by subtracting the curvature found when two distractors were present from saccade curvature found when a single distractor was present. The following notation is used to explain the subtractions performed: L is left, R is right, F is far, N is near and brackets are used to denote two distractor conditions. The influence of a second distractor shown on the right at near and far eccentricity respectively was found by subtracting (RN +LF) from LF single and (RF+LF) from LF single. The same subtraction was performed for the LN single distractors. Equivalently, to find the influence of the second distractor shown on the right at the far and near eccentricities the same pattern of subtractions were performed; however, it is important to note that one of the same two distractor conditions was subtracted as the balanced distractor condition is the same in both cases. Thus (LF+RF) was subtracted from RF single, and (LN

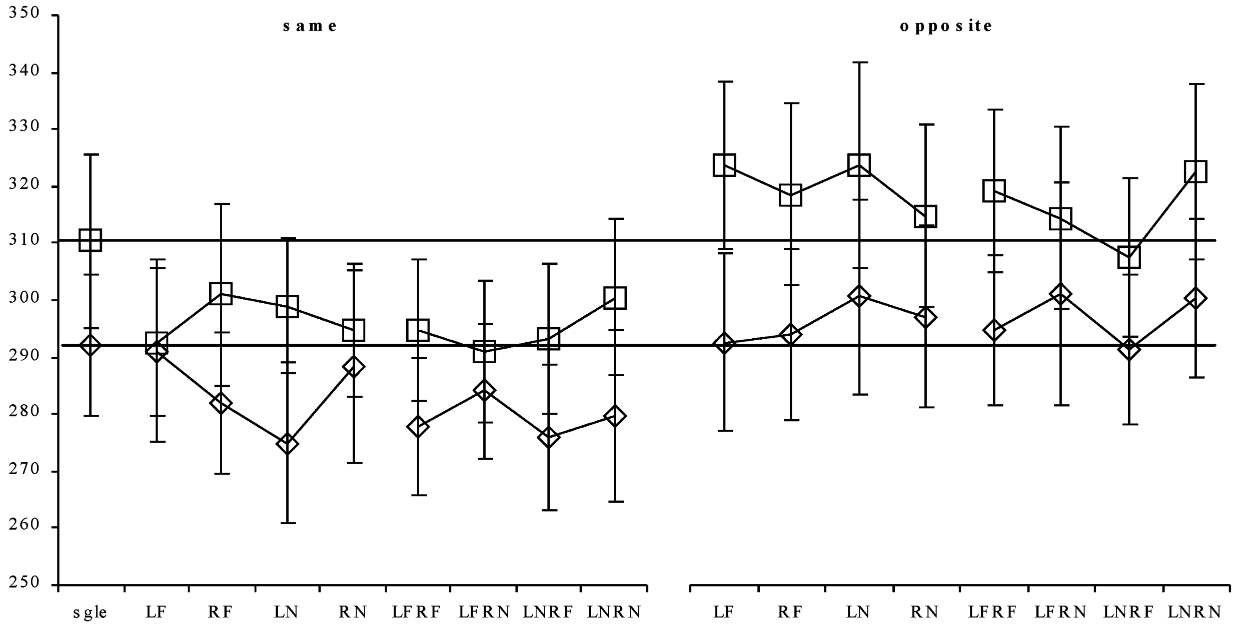

Fig. 4 The mean latencies of saccades by condition in Exp. 2. The *left side of the figure* shows the mean latencies for conditions in which there was no distractor present, or when distractors appeared in the same hemifield as the target. The *right side* shows mean latencies when the distractor was in the opposite hemifield to the target. The data marked by a *diamond shape* are upward directed saccades and those marked with a *square* are downward saccades. The single data points *to the left of the upper graph* show target alone latencies (these are also represented by *two dotted lines* running through the figure), while those clustered *to the right* show single distractors and bilateral distractors respectively

+RF) was subtracted from RF single. The same subtraction was then performed for the RN single distractors. The distractor positions and their influence on saccade curvature were thus considered purely in terms of balanced or unbalanced distractors. This can be examined graphically by comparing curvature when a single distractor was shown, to curvature shown when a second distractor was present (see Fig. 3).

It was hypothesised that the balanced distractor conditions should show greater straightening of trajectory than the unbalanced distractor conditions but this was not found to be the case. A five way ANOVA with saccade direction (up or down), distractor hemifield relative to the target (same or opposite), side of distractor (left or right), distance of first distractor from target (near and far) and second distractor condition (balanced and unbalanced) revealed that there was no main effect of direction ($F_{(1,5)} < 1$) or hemifield ($F_{(1,5)} = 1.7$, $p > 0.05$). There was a main effect of side of distractor ($F_{(1,5)} = 12.8$, $p < 0.05$) but no main effect of first distractor distance ($F_{(1,5)} = 3.1$, $p > 0.05$) or the second distractor condition ($F_{(1,5)} < 1$). There was a significant target by side by hemifield interaction ($F_{(1,5)} = 9.6$, $p < 0.05$) which indicates that leftward distractors shown in the same hemifield as the upper target produced less curvature. A series of planned comparisons were performed in which it was hypothesised that saccade curvature would be greatest with single distractors than with balanced and unbalanced distractors. Furthermore, it was hypothesised that saccade curvature would be greater in the unbalanced than balanced distractor conditions. Saccade curvature with a single distractor was found to differ from curvature found with both balanced and unbalanced distractors (left distractor vs. balanced and unbalanced distractors—$t_{(5)} = 3.3$, $p < 0.025$; right distractor vs. balanced and unbalanced distractors—$t_{(5)} = -3.4$, $p < 0.025$). There was no difference in curvature for the balanced and unbalanced distractor conditions ($t_{(5)} = -0.7$, $p > 0.05$).

It is possible that the straightening of saccade trajectories found when two distractors are present relative to single distractor conditions may be due to differences in saccade latencies. Thus, the presence of two distractors may increase latency and therefore trajectories may be straighter as there is more time for the target location to become more clearly defined (in terms of underlying encoding activity). Figure 4 shows the mean latencies by condition. Overall latency is quicker for upward directed saccades than downward saccades (Honda and Findlay 1992). Latency is reduced when a distractor appears in the same hemifield as the saccade target but is not influenced by a distractor in the opposite hemifield. Critically, there is no difference in latency for the single and double distractor conditions.

Saccade amplitudes show the same pattern as found in Exp. 1 with downward directed saccades being longer than for those directed upwards (up 8.1 deg, down 8.9 deg).

Discussion

The results of Exp. 2 have confirmed that saccade trajectories straightened when two distractors were shown in both visual fields relative to a single distractor condition and there was a trend for greater curvature of saccades when the distractor appeared in the same hemifield as the saccade target. The spatial separation between the bilateral distractors did not have a modulatory effect on saccade trajectories and there was no difference in curvature for mirror-symmetric and non-mirror symmetric bilateral distractor conditions. The bilateral distractor effect does not appear to reflect differences in saccade latency between the single distractor or bilateral distractor conditions as latency was comparable in the single and bilateral distractor conditions.

Experiment 3

The results from Exp. 2 suggest that the coding of target and distractor positions is very coarse. In order to further examine the spatial influence of distractors on saccade curvature a single distractor was presented at systematically greater distances from the saccade target in Exp. 3. If the presence of a distractor has a fine spatially specific affect on saccade trajectory, then a steady decline in saccade curvature should be observed as distractor distances from the target increase. However, the results of Exp. 2 suggest that the target and distractor are more coarsely coded and thus differences in the curvature of saccade trajectory should only be seen between more extreme target to distractor spatial separations (e.g. same and opposite field effects). Indeed previous experiments have found some evidence that distractors in the opposite hemifield have little consistent effect on saccade trajectories (Tipper et al. 2001).

Saccade dynamics have been found to be affected through inhibition operating between fixation and more eccentric positions (Walker et al. 1997). Saccade trajectories may be similarly affected and it may be the distractor separation from fixation, or the distractor separation from the saccade target that is critical for the modulation of saccade trajectory. Systematically varying the distractor-to-target spatial separation enables these effects to be examined. To this end distractors shown in the same hemifield as the target were arranged to be either close to target, close to fixation or at equidistant positions. Furthermore, the distractors shown in the hemifield opposite to the target were at the same distances from fixation as the same hemifield distractors (see Fig. 1). If distractor-to-fixation distance was the primary influence on saccade trajectory then distractors in the same and opposite hemifield should have the same influence on saccade trajectories.

Exp. 3 was performed to investigate the nature of the spatial resolution of the distractor modulation of saccade trajectory by systematically varying the spatial separation between distractors and the target and fixation location and quantifying the effects on saccade curvature. In order to prevent the distractor location from cueing the target direction distractors were shown either in the same or opposite hemifield. Distractor location is therefore more simply discussed in terms of distance from fixation and its hemifield position relative to the target. The opposite hemifield distractors also afford a test of whether distance from the target or distance from fixation is of primary importance in the modulation of trajectory. If the distance of the distractor from fixation determines saccade trajectory then the same and opposite hemifield distractors should have the same influence on saccade curvature when presented at the same eccentricity.

Materials and methods

All methods are the same as Exp. 1 except where noted.

Subjects

Six subjects, five male and one female with an age range of 25–38, took part in the experiment. All had normal or corrected to normal vision. Two of the subjects were authors (EM and RW) and were aware of the purpose of the experiment and four were naïve.

Design

The viewing distance was 57 cm. Distractor positions were either close to the target (5 deg from target and 10 deg from fixation), equidistant between the target and fixation (10 deg from both) or close to fixation (10 deg from target and 5 deg from fixation), to the

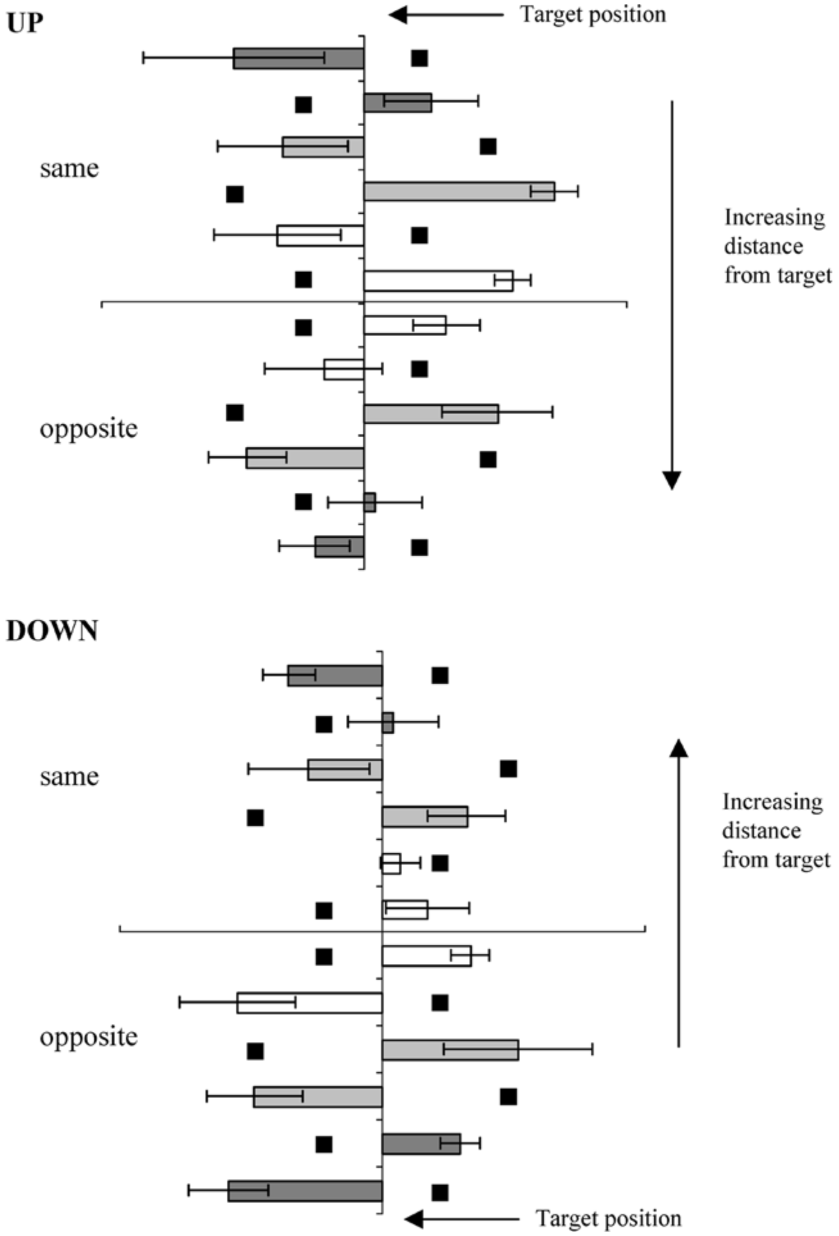

Fig. 5 The mean area difference of curvature by condition for Exp. 3. Curvature is shown separately for upward (*upper graph*) and downward (*lower graph*) directed saccades. Each graph represents physical space with *each bar* showing the saccade curvature associated with each distractor at progressively greater distances from the target. Relative distractor positions are indicated by *black squares; same* and *opposite* refer to distractor location relative to the target

left or right of the vertical midline (see Fig. 1). There were 12 possible distractor locations plus an additional no distractor condition for both upward and downward directed saccades giving 26 possible conditions. Subjects completed five blocks of 104 trials.

Results

Trials were excluded on the basis of latency (1%), amplitude (3%), direction (3%) and blinks (0%). Figure 5 shows the mean area of curvature for each condition, for upward (upper graph) and downward (lower graph) directed saccades. Each graph represents physical space with each bar showing the saccade curvature associated with each distractor at progressively greater distances from the target. A four way ANOVA was performed with saccade direction (up and down), hemifield of distractor relative to the target (same and opposite), side of distractor (left or right) and distance of the distractor from the target (close to fixation, equidistant between fixation and target or far from fixation). This revealed that there was no significant main effect of saccade direction ($F_{(1,5)} = 1.1$, $p > 0.05$), of the hemifield of the distractor relative to the target ($F_{(1,5)} < 1$) and distance of the distractor from the target ($F_{(1,5)} < 1$) on saccade trajectories. The side of the distractor was found to be significant ($F_{(1,5)} = 36.3$, $p < 0.05$) as was a hemifield by side interaction ($F_{(1,5)} = 10.9$, $p < 0.05$). Saccade trajectories thus deviate away from the location of a single distractor especially when shown in the same hemifield as the target. There were no other significant interaction effects.

In order to examine the influence of the distractors upon saccade latencies the mean saccade latency to each target was subtracted away from the latency observed in distractor conditions (separately for each subject). A four way ANOVA was performed with these difference latencies with the same factors as those used in the previous curvature analysis (i.e., direction, target to distractor hemifield, side and distance of distractor). This revealed no significant main effects but a hemifield by distance interaction was found to be significant ($F_{(1,5)} = 19.8$, $p < 0.05$). This was a result of saccades being faster when a distractor was shown in the same hemifield at progressively closer proximity to the target location.

Saccade amplitudes were found to be longer when directed downwards (up 8.1 deg, down 10 deg), but this was not systematically related to distractor position. The overall direction of saccades to the upper field target was affected by distractor side, but not by distractor-to-target or distractor-to-fixation spatial separation. Figure 6 shows that on average saccades in the upper field curved away from the distractor and also tended to land away from the distractor. The cluster of the upper field saccades in the top right and bottom left quadrants of the scatter plot show that angular deviation was not monotonically affected by distractor distance from target or fixation. Overall direction and curvature for lower field (downward) saccade curvature can be seen to be unrelated.

Discussion

The results show that saccade trajectories curved away from the location of a single distractor but the magnitude of the effect was not influenced by either the distractor-to-target, or distractor-to-fixation distance. There was a weak effect of distractors in the target hemifield producing more curvature than those in the opposite hemifield. Overall, the results suggest that the encoding of target and distractor locations is very coarse and does not vary with distractor spatial separation.

The reduction in saccade latency observed here and the previous two experiments with distractors in the same hemifield as the saccade target (cf. Doyle and Walker 2001) could be accounted for in terms of non-spatial warning signal effects (Ross and Ross 1980) enabling the earlier triggering of a voluntary saccade. Voluntary saccades made on the basis of a symbolic cue, as was the case in this study, are known to have longer latency than saccades made following the abrupt onset of a visual target (Walker et al. 2000; Doyle and Walker 2001). A latency facilitation effect was observed with same hemifield distractors in all three experiments here that

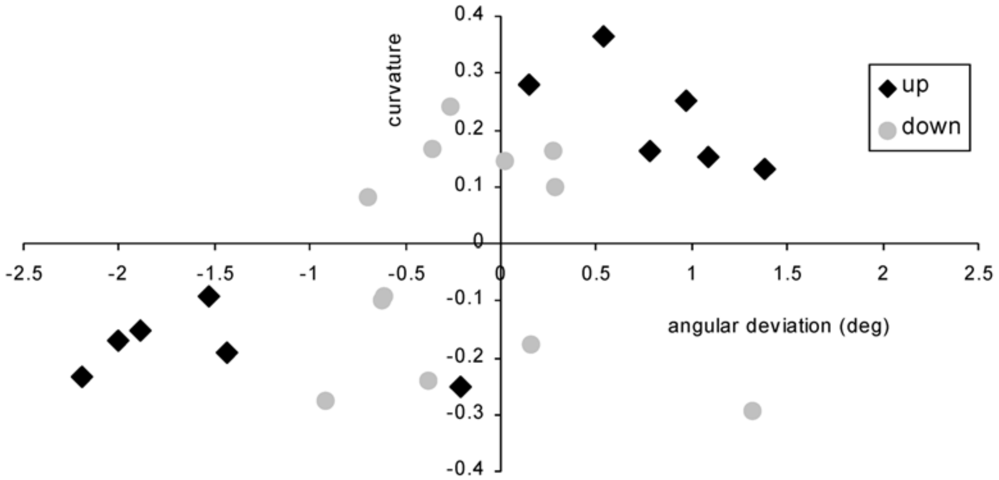

Fig. 6 The curvature of the saccade plotted as a function of its landing position indicated by angular deviation from target. Angular deviation is shown on the *abscissa* and curvature on the *ordinate*. *Positive deviation* on either axis shows a rightward deviation and a *negative value* a leftward deviation. *Each point* shows the average curvature and angular deviation found for each distractor condition. An effect of distractor distance from fixation or saccade target would be revealed by a steadily decreasing relationship between curvature and angular deviation. This was not observed

increased as the distractor approached the saccade target (Exp. 3). This facilitation could be due to the distractor acting as a non-spatial warning signal (Ross and Ross 1980) enabling the early triggering of the saccade 'go signal' in less time than is required for voluntary saccades. Although distractors in the opposite hemifield would also be expected to provide a similar warning signal this effect may be masked as in this case the stimulus operates like a remote distractor that increases saccade latency. A similar account has been proposed to explain a latency facilitation effect observed when an auditory distractor is presented along with a visual saccade target, that decreases as the spatial separation between the target and distractor increases (Frens et al. 1995).

Saccade amplitudes were consistently found to be longer when directed to the lower visual field target in all three experiments. We suggest that this may be related to the observed latency differences between saccades directed to the upper and lower visual field targets. Saccades directed to the lower visual field were generally longer in latency than those directed to the upper target for all three experiments. Lower visual field targets were thereby targeted more effectively due to the saccade being initiated later when presumably the target was more finely resolved (McSorley and Findlay 2003). Furthermore we suggest that the different pattern of angular deviation for upper and lower directed guided saccades is also a function of this latency and resolution trade-off.

General discussion

In a series of experiments presented here the spatial nature of distractor effects on saccade trajectories was examined. In the first experiment the trajectories of vertical saccades made to a single target tended to be straight, but curved away from a single distractor presented in either the left or right hemifield. Saccade trajectories became straighter when two distractors appeared bilaterally and simultaneously at mirror symmetrical locations in both visual fields. A second experiment examined the spatial nature of the mirror distractor effect by presenting two distractors bilaterally in both visual fields at mirror and non-mirror symmetric locations. Saccades again deviated away from single distractors and became straight with both mirror and non-mirror symmetrical bilateral distractors. The third experiment further examined the spatial nature of the distractor effect on saccade curvature by manipulating the distractor-to-target and distractor-to-fixation spatial relationship. Saccade trajectories deviated away from single distractors but the magnitude of the effect was not influenced by either the distractor-to-target or distractor-to-fixation distance. In all three experiments similar effects were observed for saccades made to targets in the upper and lower visual fields. However, distractors in the target hemifield had a greater effect than did those in the opposite hemifield in the third experiment only. Thus saccade trajectory control is very sensitive to the presence of a competing visual distractor but is not sensitive to its precise spatial location. This suggests that the effect of distractors on saccade trajectory are coarsely coded.

The present study has confirmed that saccade trajectories curve away from a visual distractor presented in one visual field, and has further shown that they become straighter when distractors appear in both visual fields. However, the distractor modulation is not highly spatially specific. Models of curved trajectories have invoked the idea of localised areas of inhibition operating on populations of neurons encoding the distractor location (Doyle and Walker 2001, 2002; Tipper et al. 2001). Our results show that the underlying coding of target and distractor positions is coarse and that the influence of the distractor may only weaken when the distractor is shown at very large distances in the opposite hemifield to the saccade target. In addition, if distractor influence produces the initial deviation of saccade direction by a process of inhibition within a saccade motor map then curvature back towards the target must involve a separate process. If not, then saccade end point would be expected to be influenced by the distractor in a similar way and saccades would tend to land at an intermediate position away from the target instead of curving back towards the actual target location as was observed. In the experiments reported here the vast majority of saccades were correctly directed to the target (i.e., the vast majority of saccades were within 15 deg of either side of the target) and the landing position was not systematically influenced by the presence of the competing distractor (see Fig. 6). Models need to account for these two processes as well as the weak spatial nature of the observed distractor effects.

Initial deviation and coarse coding

In our model (shown in Fig. 7) in common with others initial saccade direction is determined by the weighted average of activity in a motor map encoding the location of all visual stimuli (Sheliga et al. 1995a, 1995b, 1997; Tipper et al. 2001). The activity on the motor map is determined by the competitive interactions between overlapping neural populations that encode each of the spatially separate visual stimuli. However, the nature of these competitive interactions varies somewhat across the different models. Sheliga et al. (1995b) attributes curvature away from the distractor position to a classic centre-surround organisation of lateral connections in which adjacent neurons excite each other while those farther away inhibit each other. However, Tipper and colleagues (Houghton and Tipper 1996, 1999; Tipper et al. 2000, 2001) suggest that this organisation of lateral connections would result in curvature toward the distractor only and that a second stronger inhibitory process termed "reactive inhibition" (a self-inhibiting feedback process that results in more powerful distractors receiving greater levels of self-inhibition) was required to bring the level of activity below baseline level. The consequence of the localised region of inhibition is the deviation of saccade trajectory away from the distractor location. In our model saccade direction is also determined by the weighted average of neural activity in the saccade motor map associated with visual stimuli (cf. McIlwain 1986, 1991). A saccade is made to the location of highest activity at the point at which a separate ‘go’ trigger signal (not shown) is given for an eye movement to be initiated (see Findlay and Walker 1999). When a target and distractor are presented two separate populations of activity result. For a saccade to be made to the designated saccade goal a population of activity must be selected as the target and activity associated with the distractor is then inhibited by lateral interactions within the salience map. The consequence of the region of inhibition is that the peak of neural activity on the salience map shifts away from the distractor region and the saccade vector deviates away from the location of the distractor.

The model described in Fig. 7 relies on a salience map for the control of initial saccade direction that can be modulated by a competing distractor. Neurophysiological studies have shown that populations of neurons in the intermediate layers of the superior colliculus (SC) form such a salience map for the translation of visual inputs for an oculomotor command. For any saccade a large population of collicular neurons are active (Munoz and Wurtz 1995) with the peak of activity corresponding to a specific saccade amplitude while more distant neurons will discharge with a decreased level of activity. The SC receives excitatory and inhibitory inputs from cortical regions such as the lateral intraparietal region (LIP) and the frontal and supplementary eye fields (FEF and SEF). As such it can be regarded as a ‘funnel’ through which the cortex mediates an influence on the selection of a saccade

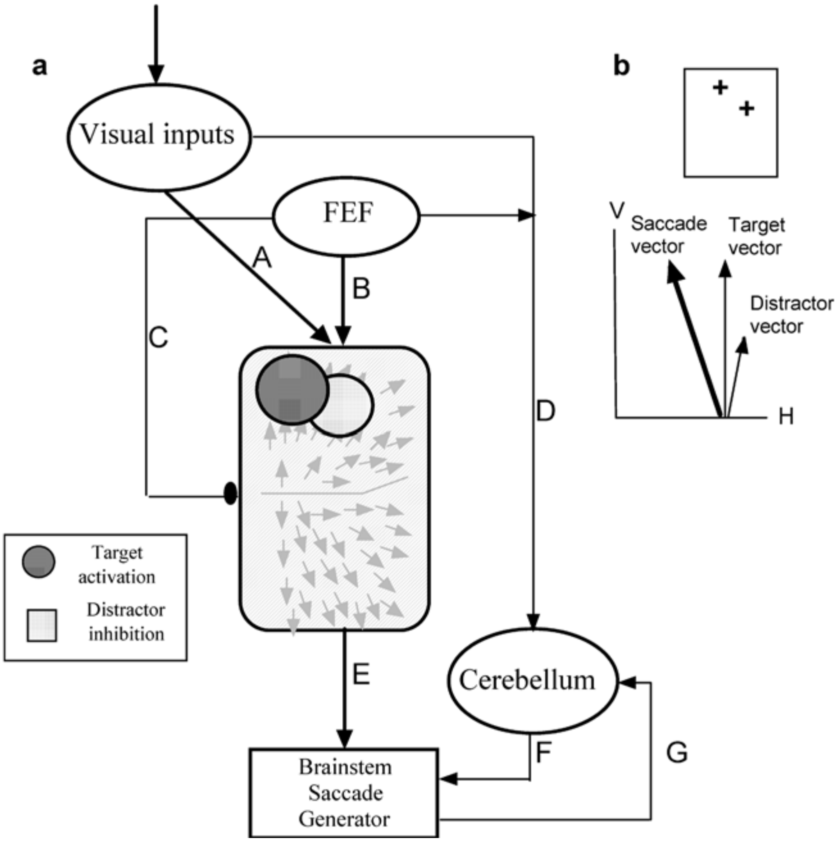

Fig. 7 a Schematic diagram of the network of regions involved in saccade generation for the model used to account for saccade deviation and curvature (n.b. only one side of the network is shown) (*SC* intermediate layers of the superior colliculus—the *arrows* indicate the topographically organised movement vectors, *FEF* frontal eye fields). The cortical visual inputs to the intermediate layers of the SC are shown (*A*) along with a signal from the FEFs that may ‘select’ a population of activity as the desired saccade target (*B*). The neural activity associated with a vertical saccade target in the upper visual field is shown along with an overlapping population of inhibited neurons associated with a distractor in same visual field (see **b**). The distractor inhibition is the consequence of lateral interactions within the SC but may also involve an additional inhibitory input from the FEFs (not shown). *C* Inhibitory signal from FEFs to all non-target regions of SC; *D* independent target position signal for feedback loop; *E* output from colliculus conveying saccade amplitude and direction to brainstem saccade generator; *F* drive signal from cerebellum that modulates trajectory as part of a feedback loop (comparing target position signal from FEFs with current eye position signal *G* from SC). It is important to note that a vertical saccade depends on the outputs from both the left and right colliculi. As the distractor is presented in only one visual field there is an imbalance in the overall direction vector signal reaching the brainstem saccade generator, resulting in a deviation in saccade direction away from the distractor location. Curvature back towards actual target position is attributed to an additional drive signal from the cerebellum that provides a comparison of desired and actual eye position signals. **b** Schematic representation of a vertical target and the same hemifield distractor with the associated movement vectors. The activity associated with a vertical saccade target is strong and the activity associated with the distractor inhibited (below a threshold level) that results in the overall population of activity producing a saccade vector that deviates away from the distractor target (Wurtz 2000). The FEFs send a topographically organised projection to the intermediate layers of the SC and microstimulation studies have shown that collicular neurons are excited when FEF regions encoding similar vectors are stimulated, while neurons in surrounding areas are inhibited (Schlag-Rey et al. 1992). This functional organisation provides a possible source of top-down modulation for selecting a saccade target and inhibiting a competing distractor stimulus. When more than one visual stimulus is presented a higher-level signal may be required to 'select' one population of activity as the desired saccade target and an inhibitory signal inhibits all non-target locations (Schlag-Rey et al. 1992). As the level of activity associated with the saccade target increases a further process of lateral inhibition (Munoz and Istvan 1998) results in the population of neurons encoding the distractor being inhibited below a threshold level. A consequence of the region of inhibition is that the peak of neural activity on the salience map shifts away from the distractor region and saccade direction deviates away from the location of the distractor.

The absence of a tight coupling between distractor location and saccade curvature in the present study may be a consequence of the large populations of SC neurons (estimated at around 25%; Munoz and Wurtz 1995) with broad receptive fields that are involved in the control of saccade direction. The inhibitory process involved in suppressing distractor-related activity appears to be broad with a rather weak spatial gradient. The inhibition appears to be greatest when the distractor is in the target hemifield but does not appear to result in a small well localised region of inhibition for the distractor location alone. When bilateral distractors are presented in both visual fields the level of inhibition in both the left and right collicular maps may be balanced so saccades tend to be straight. As the spatial resolution of the inhibitory process is weak there are no observable effects of presenting bilateral distractors at symmetric or non-symmetric locations.

The involvement of the colliculus in the deviation of saccade trajectory and the lack of a highly spatially-specific inhibitory effect has been revealed by reversible localised deactivation techniques. Aizwa and Wurtz (1998) and Quaia et al. (1998) examined the influence of localised inhibitory influences on saccades by injecting a GABA agonist (muscimol) in the intermediate layers of the colliculus to inactivate buildup neurons associated with a saccade of a certain direction and amplitude. They found that the localised area of inactivation resulted in saccades that reached the target but with highly consistent curved trajectories. Most interestingly saccades were found to start out in the wrong direction right from movement initiation and there was no suggestion of the trajectory being straight until it approached the inactivated region. This finding indicates the coarse nature of inhibitory effects on saccade direction and is a likely consequence of distributed population encoding within the saccade motor map. One model of the control of saccade trajectory (Aizawa and Wurtz 1998) was based on the idea that a 'moving hill' of buildup neuron activity in the collicular map provides current information about eye position. The moving hill refers to the spread of activity from buildup neurons in caudal regions of the colliculus that moves rostrally during the saccade and has been incorporated into models of saccade generation as the part of the feedback loop (neural integrator) (Optican 1995). The results of the reversibly deactivated studies did not support the view that the SC is the site of the neural integrator (Aizawa and Wurtz 1998; Quaia et al. 1998) and more recent single cell recording studies have not demonstrated a rostral spread of buildup cell activity in the colliculus (Soetedjo et al. 2002). The moving-hill hypothesis and the involvement of the colliculus in the on-line control of saccade trajectory have not been supported by these neurophysiological findings.

Control of saccade trajectory

Coarse regions of inhibition within the collicular motor map can, therefore, account for the initial deviation of saccade direction but cannot explain the deviation of trajectory back towards the target location (as saccade endpoint would be expected to be modulated by the presence of the distractor). Thus in any spatially based inhibitory model, including ours, saccade landing position must be encoded by a separate mechanism that encodes target location independently of the distractor influence. As direct visual feedback is not available during a saccade (due to saccadic suppression; Burr and Ross 1982) one possibility is that a corrective signal driving the saccade back towards the target in mid-flight (Mays and Sparks 1980) arises from a separate high-level signal (Doyle and Walker 2001) that may be used as a "desired" position signal to compare to the actual eye position signal thus providing an error signal. Minimising the error signal, via a feedback mechanism, drives the saccade toward the target (Robinson 1975). Thus saccades would be initially misdirected away from the distractor and then curve back toward the target position.

Two structures that could provide an additional input to the brainstem saccade generator for the control of final saccade landing position are the frontal eye fields and the cerebellum (Robinson and Fuchs 2001). The FEFs are thought to send a direct projection to the brainstem saccade generator that bypasses the colliculus (Schiller et al. 1980) that could provide an additional signal of target location. The functional nature of this projection has been questioned, however, on the basis of more recent reversible deactivation studies of the SC and FEFs (Hanes and Wurtz 2001) and there is no evidence to suggest that a *direct* FEF to brainstem pathway is involved in the on-line control of saccade trajectory.

A more parsimonious account of curved trajectories has attributed the control of saccade direction and trajectory to separate pathways one involving the colliculus and the other involving the cerebellum (Quaia et al. 1999). The cerebellum receives an indirect input from the frontal and supplementary eye fields and the superior colliculus that could provide information about the position of the saccade target. In Quaia et al.'s (1999) model populations of burst and buildup neurons in the colliculus (driven by cortical inputs) specify target location in retinotopic co-ordinates and provide the directional drive signal to the brainstem saccade generator controlling saccade direction. The spatial characteristics of the collicular neurons are not thought to be under the control of feedback mechanisms and do not change during a saccade and cannot therefore account for trajectories curving back towards the target. A second pathway from the cerebellum to the brainstem provides an additional directional drive signal, monitors the progress of the saccade and chokes off the outputs from both pathways, which signals the end of the saccade. The cerebellum monitors saccade progress (acting as a displacement integrator) and adjusts the directional drive signal to compensate for directional errors thus producing a control over saccade trajectory. In terms of our model inhibitory processes acting on populations of collicular neurons would result in the initial deviation of saccade direction, and the curvature of the saccade back towards the target would be attributed to the second pathway involving the cerebellum. This feedback loop has been incorporated into the model shown in Fig. 7a, which contains an independent target position signal, that would not be influenced by the presence of a competing distractor, for the control of trajectory back towards the saccade target.

In some situations, such as visual search, saccades are found to curve towards distractors rather than away as was observed here. McPeek and Keller (2001) reported that the trajectories of incorrect saccades deviated toward the location of a subsequent secondary corrective saccade. Thus, when a saccade is made to stimulus A and subsequently a second saccade is made to stimulus B with a short inter-saccade interval, the trajectory of the first saccade is influenced in an excitatory manner by the second saccade programme. The short inter-saccadic interval is taken as evidence of parallel programming of two saccades (see also: Hallett and Adams 1980; Theeuwes et al. 1998, 1999; McPeek et al. 2000; McPeek and Keller 2001; Godijn and Theeuwes 2002), indicating that more than one response can be simultaneously represented by the oculomotor system. In much the same manner as Sheliga et al. (1995b) and Tipper and colleagues (2001) curvature towards a distractor has been interpreted in terms of lateral interactions between separate neural populations involved in encoding the target and distractor stimulus (McPeek and Keller 2001). If the population of neurons encoding the second stimulus location becomes sufficiently active just prior to the first saccade it will add to the activity of the target population and result in a deviation toward the subsequent saccade target (McPeek et al. 2003). It is important to note that deviation of saccade trajectory toward the goal of a subsequent saccade goal may not be the same as deviation towards a distractor. It is possible that curvature away from a distractor is observed in paradigms where highly predictable target locations are used that may enable greater inhibition of the distractor than is the case with less predictable targets as is the case in visual search (Doyle and Walker 2001; McPeek et al. 2003).

In summary, the results presented here have provided supporting evidence for a model of saccade trajectory in which the overlap between separate populations of cells encoding target and distractors determine initial saccade direction as described in Fig. 7. Furthermore, the results also suggest that the spread of these neural populations is very coarse with distractors presented at large spatial separations from the target still affecting target directed saccade trajectories. Consideration of the physiology of saccade control suggests that the SC controls the initial deviation of saccade direction through competitive lateral interactions and that the cerebellum provides a feedback signal for the on-line control of trajectory so that saccades curve back toward the target location.

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