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Research Report

The development of the spatial extent of oculomotor inhibition

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A R T I C L E   I N F O
Article history:
Accepted 25 August 2009
Available online 3 September 2009

Keywords:
Saccade
Trajectories
Remote distracter
Global effect
Superior colliculus

A B S T R A C T
Inhibition is intimately involved in the ability to select a target for a goal-directed movement. The effect of distracters on the deviation of oculomotor trajectories and landing positions provides evidence of such inhibition. Individual saccade trajectories and landing positions may deviate initially either towards, or away from, a competing distracter—the direction and extent of this deviation depends upon saccade latency and the target to distracter separation. However, the underlying commonality of the sources of oculomotor inhibition has not been investigated. Here we report the relationship between distracter-related deviation of saccade trajectory, landing position and saccade latency. Observers saccaded to a target which could be accompanied by a distracter shown at various distances from very close (10 angular degrees) to far away (120 angular degrees). A fixation-gap paradigm was used to manipulate latency independently of the influence of competing distracters. When distracters were close to the target, saccade trajectory and landing position deviated toward the distracter position, while at greater separations landing position was always accurate but trajectories deviated away from the distracters. Different spatial patterns of deviations across latency were found. This pattern of results is consistent with the metrics of the saccade reflecting coarse pooling of the ongoing activity at the distracter location: saccade trajectory reflects activity at saccade initiation while landing position reveals activity at saccade end.

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1. Introduction
Selecting an appropriate behavioural 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 et al., 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 (McPeek, 2006; Port and Wurtz, 2003; McPeek et al., 2003; Munoz and Istvan, 1998; Desimone and Duncan, 1995; Allport, 1993). Inhibition has generally proved difficult to study behaviourally because it results in no measurable output. However, direct evidence for such inhibition can be found by investigating how goal-directed movements are modulated when alternative stimuli must be inhibited (Findlay, 1982; McSorley and Findlay, 2003; McPeek et al., 2003, Ludwig and Gilchrist, 2003; McSorley et al., 2006; McPeek, 2006; Walker et
Inhibition elicited by competing stimuli can affect signals which drive saccadic eye movements, influencing where the eyes are directed (Findlay and Walker, 1999).

The path a saccade travels and where it eventually lands depend on the outcome of competition between possible motor responses, reflecting the relative neural activation at each stimulus site (van Opstal and van Gisbergen, 1989; Glimcher and Sparks, 1993). Saccade trajectories may initially deviate away from or towards distracting stimuli (McSorley et al., 2006), before landing somewhere between them (known as the global effect or centre of gravity effect; Findlay, 1982). The direction and extent of deviation in trajectory and landing position are fundamentally linked to both the development of distracter inhibition, as reflected in saccade latency, and the distance of the distracter from the target. Saccades which have a short latency tend to have trajectories (McSorley et al., 2006) and landing positions (Findlay, 1981; Chou et al., 1999) which deviate towards a distracter while saccades with longer latencies have trajectories which deviate away (McSorley et al., 2006) but land accurately on the target (Findlay, 1981; Chou et al., 1999). Stimuli that are presented close together tend to elicit saccades which land between them. This is true only when stimuli are relatively close together (within ±30 angular degrees) (Ottes et al., 1985; Walker et al., 1997; McSorley and Findlay, 2003; Findlay and Benson, 2006; Cruickshank and McSorley, 2009); otherwise, saccades are generally accurate. In contrast, the trajectory of a saccade has been shown to be sensitive to the presence of distracters at quite some distance from the target (from 27 to 135 angular degrees), but little is known about the effect of those in closer proximity (McSorley et al., 2004, 2005; van der Stigchel and Theeuwes, 2005; van der Stigchel et al., 2007).

Models of saccade trajectory control and landing position have been based on the idea of competitive interactions operating in a salience map encoding potential saccade targets (Godijn and Theeuwes, 2002; McPeek et al., 2003; McPeek and Keller, 2001; McSorley et al., 2004; Tipper et al., 2001). The intermediate layers of the superior colliculus (SC) are thought to form such a salience map with populations of neurons with large and broadly overlapping receptive fields forming a topographic representation of saccade direction (Mcllwain, 1991). A saccade is directed to the location represented by the area of maximum activity within this map (see Findlay and Walker, 1999). When separate populations of activity, associated with a target and distracter, are active, the overall activity profile can result in a saccade landing at an “average” of the two locations (Findlay, 1982). Similar explanations have been advanced to explain curvature towards a distracter location (McPeek et al., 2003; McPeek, 2006; McSorley et al., 2006): initial saccade direction is modulated by the competition between the target and distracter. If distracter-related activity is high when a saccade is initiated, there is a small shift in overall population of activity towards the distracter and the saccade will deviate towards the distracter location. By contrast, if the distracter-related activity is strongly inhibited prior to saccade initiation, then there is a small shift in the overall activity profile away from the distracter location producing a deviation of initial saccade direction away from the distracter (Aizawa and Wurtz, 1998; McPeek et al., 2003). In both cases, curvature back towards the saccade target may be due to further resolution of the competition between the distracter and target which takes place during the saccade. A location closer to the target then becomes the saccade goal and the saccade trajectory curves back towards it (Arai and Keller, 2005; McPeek, 2006; McSorley et al., 2004; Quaia et al., 1999; Walton et al., 2005).

The commonalities of the model underlying landing position and trajectory control have not been fully explored. Both are suggested to show the state of active inhibition of the competing stimuli within the same mechanisms but both show differences in their behavioural outcomes (e.g., path curvature away but accurate saccades). Furthermore, there has been little work examining the effect on saccade trajectory deviations of presenting distracters at close distances, such as those used in exploring landing positions (i.e., within the 30° window surrounding the target) and because of this it is unclear what the relationship is between the control of saccade landing position and its path. Only van der Stigchel and Theeuwes (2005) have placed a distracter within this window (at 27 angular degrees from the target). They found deviations in trajectory and landing position toward the distracter.

The experiment reported in this paper examines this impact of close distracters in greater detail. We report the metrics (landing positions and trajectories) of target-directed vertical saccades (“up” and “down”) in which the distance of a competing stimulus was manipulated from close proximity (10 angular degrees) to far away (120 angular degrees). We also show differences in their behavioural outcomes (e.g., path curvature away but accurate saccades). Furthermore, there has been little work examining the effect on saccade trajectory deviations of presenting distracters at close distances, such as those used in exploring landing positions (i.e., within the 30° window surrounding the target) and because of this it is unclear what the relationship is between the control of saccade landing position and its path. Only van der Stigchel and Theeuwes (2005) have placed a distracter within this window (at 27 angular degrees from the target). They found deviations in trajectory and landing position toward the distracter.
used a fixation-gap paradigm to vary saccade latency: fixation is removed from the display at various stimulus onset asynchronies (SOA) relative to the onset of the experimental display (Saslow, 1967; Ross and Ross, 1980). This is known to produce effects on latency which are independent of other distracter effects (Walker et al., 1995; McSorley et al., 2006). This manipulation allowed us to measure the time course of distracter-induced saccade deviation and the effects on landing position and trajectory, in a systematic way, across a number of spatial locations.

2. Results

The mean saccade latency (its reaction time) was calculated as the difference between stimuli onset and saccade onset. Fig. 1 shows mean saccade latency for each fixation SOA, collapsed across subjects, for baseline (no distracter—NONE) and distracter trials. A negative SOA means fixation was removed prior to stimuli onset by 150 or 75 ms (a gap) while a positive SOA indicates fixation was removed 75 or 150 ms after stimuli onset (an overlap). A zero SOA means fixation was removed simultaneous with stimuli onset. A two-factor ANOVA (Distance × SOA) showed an increase of latency across gap condition (main effect of SOA: F(5, 25)=34.1, p<0.01). Latencies were also found to increase as the distracter was shown at greater angular deviations from the target, despite being the same distance from fixation (main effect of distance: F(4, 20)=67.24, p<0.01). From Fig. 1, it can be seen that latencies of saccades to targets with close distracters were as quick, or quicker, than baseline (no distracter) saccades, while targets with far distracters elicited slower saccades. Indeed, post hoc tests show that the 10° distracter location resulted in quicker saccades while 60° and 120° positions lead to significantly longer saccades (all p’s<0.05). No interaction was found (F(20,100)=1.2, p>0.05), showing that the change in latency observed in distracter trials was comparable across gap condition.

The maximum trajectory deviation of each saccade relative to the direct path between fixation and landing position was calculated and the trajectory deviation observed in no distracter (baseline) conditions was subtracted from that for distracter conditions. Trajectories deviating toward the distracter were assigned positive values and those deviating away from the distracter negative values. To examine the effect of saccade latency on saccade trajectory deviation, the latency distribution across all target–distracter conditions, for each subject, was quartiled: the mean saccade trajectory deviation was determined for successive 25% portions of the saccade latency distribution (data were not separated by fixation-gap intervals). The mean deviation and latency for each quartile were averaged across subjects. These are plotted in Fig. 2a. The ordinate shows the average curvature, and the abscissa shows latency quartiles. A two-factor ANOVA (Distance × Quartile) shows a main effect of distance (F(4, 20)=6.4, p<0.05) and quartile (F(3, 15)=5.1, p<0.05) and an interaction between them (F(12, 60)=2.7, p<0.05). These are driven by the differences in the pattern of saccade trajectory deviations elicited by distracters close to the target at 10° and 20° compared with those further away (30°, 60° and 120°). A series of one-factor ANOVAs were performed to examine each distracter distance separately. These show that there was no effect of saccade latency on the extent of trajectory deviation for the closest distracters (10° and 20°), although there was a
trend for longer latency saccades to produce straighter paths when made in the presence of the 20° distracter (10°: F(3,15)=2.2, \( p>0.05 \); 20°: F(3,15)=3, \( p=0.062 \)). Distracters further away evoke a significant decrease in the extent of trajectory deviation toward them as the latency of the response increases (30°: F(3,15)=6.0; 60°: F(3,15)=3.4; 120° F(3,15)=3.6, \( p<0.05 \)). In summary, distracters close to the target produce similar deviations towards them at all saccade latencies. For distracters further away, a linear pattern was found, very like that reported by McSorley et al., (2006): quicker saccades tended to deviate towards the distracter while slower saccades deviate away.

Landing position data were treated in the same way as trajectory data. The angular deviation of the saccade landing position, for each trial, was subtracted from the actual position of the target. As with trajectory deviations, the mean angular deviation was determined for successive 25% portions of the saccade latency distribution. The mean angular deviation and latency for each quartile were averaged across subjects (see Fig. 2b). The ordinate shows the average landing position deviation, and the abscissa shows latency quartiles. A two-factor ANOVA (Distance×Quartile) shows a main effect of distance (F(4, 20)=7.4, \( p<0.01 \)) but no effect of quartile (F(3, 15)=2.6, \( p>0.05 \)) and no interaction between them (F<1). This shows that landing position is pulled toward the distracter when the distracter is less than 30 angular degrees from the target. Outside of this area, landing position seems much less affected and largely accurate over all latencies (Ottes et al., 1985; Walker et al., 1997).

3. Discussion

Deviations in the trajectory and landing position of a saccadic eye movement have been taken to be measures of the same processes involved in the neural competition which underlie the selection of the next target. However, previous work has shown that these measures have different patterns of spatial sensitivity (e.g., McSorley et al., 2004). This study directly investigated the temporal development of the spatial sensitivity of the inhibitory processes underlying saccade trajectory and landing position deviations across a range of distracter locations. Different patterns of deviations were found for saccade trajectory and their final landing positions, depending upon distracter distance. When a distracter is close to the target (10 angular degrees), trajectory and landing position deviate towards the distracter at all saccade latencies. Increasing the distance between target and distracter produces separable effects. Saccade trajectory deviations were found to depend upon saccade latency. Short latency saccades deviated toward the distracter while longer latency saccades straightened (20° and 30° separation) then progressively deviated away from the distracter position (60° and 120° separation). Deviations in saccade landing position showed no such dependency on the response time, deviating toward the distracter similarly with small separations from the target (10°, 20° and 30°) or not at all when the target to distracter separation was larger (60° and 120°). These different patterns of deviation suggest that saccade trajectory and landing position are not the outcome of the same aspects of neural competition involved in saccade selection; we propose they reflect the ongoing development of the neural competition.

3.1. The development of saccade competition

Models of saccade trajectory control and landing position outlined in the introduction were based on the idea of competitive interactions, operating in a salience map, encoding potential saccade targets (Godijn and Theeuwes, 2002; McPeek et al., 2003; McPeek and Keller, 2001; McSorley et al., 2004; Tipper et al., 2001). It was suggested that both deviations in landing position and trajectory were due to an imbalance in the relative neural activation of the competing stimuli, which ultimately reflects the inhibition at the distracter location. However, our data (and that from others) do not support a strong relationship between the extent of trajectory deviation and the final landing position (see also McSorley et al., 2004; Port and Wurtz, 2003; van der Stigchel et al., 2007). From this it has been suggested that the trajectory and landing position of saccades may be controlled by separable processes: McSorley et al (2004) examined the relationship between distracter-to-target spatial separation on saccade landing position and curvature over very broad separations (45° and above) and reported a coarse relationship between the trajectory deviation and landing position, i.e., saccades curving away from the distracter were likely to land away and those deviating toward were more likely to land between target and distracter. However, the lack of a precise relationship led McSorley et al (2004) to suggest a separation in the mechanisms underlying control of saccade trajectory and landing position. They suggested that the initial direction of a saccade reflects the combined activity of the target and distracter representations, and the curvature back toward the target involves a separate feedback system that provides an on-line error correction mechanism that may involve a separate input from the FEFs or cerebellum to the brainstem saccade generator (Port and Wurtz, 2003; Quaia et al., 1999).

A broad correlation between trajectory and landing position was also reported by van der Stigchel et al (2007). However, they interpreted this as possible evidence for a common mechanism underlying saccade metrics. Indeed recent models of saccade metrics would seem to suggest a concatenation of the different interpretations of trajectory and landing position deviations (Walton et al., 2005; Arai and Keller, 2005). These models support the idea that trajectory and landing position show the outcome of the same processes but at different times, i.e., trajectory deviates because of the state of inhibition at the distracter site prior to saccade onset but then curves toward its final landing position as the inhibition subsides. This idea could account for the results reported here and those by both McSorley et al (2004) and van der Stigchel et al. (2007): the initial direction of a saccade (either towards or away from a distracter) reflects the combined activity of target and distracter locations at saccade initiation while the curvature back towards the target also reflects this combined activity but over the period of time from saccade execution to its landing. This would need to involve a separate feedback system which updates the position of the eye from the ongoing competition between target and distracter. This provides an on-line error correction mechanism that may
involve the frontal eye fields or cerebellum (Arai and Keller, 2005; McPeek, 2006; Port and Wurtz, 2003; Quaia et al., 1999; Walton et al., 2005). In terms of our results, the overall differences between trajectory and landing position deviations reflect the different levels of inhibition at each distracter site at saccade initiation and then during its movement.

The scheme outlined suggests that deviations in trajectory and landing position represent different time slices of the underlying competition that determines the saccade target. The differences in the effect of distance from target to distracter on trajectory and landing position suggest that the pooling of activity in the oculomotor system may be much larger than is usually suggested from landing position studies alone. Landing position is influenced by distracters presented less than 30° away from the target, not by those farther away (Ottos et al., 1985; Walker et al., 1997). However, the deviations in saccade trajectory show an influence of the distracter when it is much farther away, suggesting that activity is pooled over a large distance. If trajectory and landing position represent the same underlying competition at different points in time, this suggests that the windows over which they are computed are of the same large magnitude. The differences in influence of distracters may arise because the resolution of the competition to determine the final landing position is reached more quickly when the distracter is further away, resulting in more accurate saccades.

Similarly it can be speculated that the metrics of other motor systems, such as the trajectory and final position in reaching or pointing with the arm (Tipper et al., 2001; Welsh and Elliott, 2005; Song et al., 2008), could also be taken to reveal changes in the underlying neural competition which determines target selection. Indeed, work in this area has shown that the trajectory of reaching and pointing movements is influenced by the presence of distracters, deviating either toward or away from their position (ibid). This conception of behavioural movement suggests that the selection of a direction of movement is not fixed prior to its execution in a serial fashion (Tanji, 2001; Koechlin et al., 2003), rather the movement is subject to further processing which takes place during the execution of the movement itself. The ongoing processing of visual information and its influence on motor planning and selection is felt throughout the movement and may even extend to further movements, if a behavioural sequence is required, as is often the case in our day to day activities.

3.2. Distracter effects on saccade latency

One other observation from the present study is that of the effect of distracter distance on saccade latencies. Saccade latencies were not only affected by the gap manipulation but also by the distance between distracter and target. Latencies increased as the separation increased. Saccades to targets with close distracters were quicker than to target alone, while those further away elicited progressively slower saccades. This suggests a remote distracter effect: Walker et al (1997), in a very thorough study, showed that target-directed saccade latencies are increased when a distracter is presented outside of the 30° window known to affect landing position. Furthermore, their results show that iso-eccentric distracters elicit the same increase in saccade latency to a target. They suggest that the extent of this slowing is a function of the ratio of distracter distance from fixation to target distance from fixation. However, the latencies recorded here do not fit this pattern. The ratio of our distracter and target distances from fixation are the same regardless of the angular deviation of the distracter; hence, the RDE should be the same. The increase in latencies we report here suggests that the distance of the distracter to the target influences saccade latency, perhaps in conjunction with the distance from fixation. This is in line with the results reported by Dorris et al (2007; Olivier et al., 1999). They found that visual signals which were close together interacted with strong excitation while those further away inhibited each other. Therefore, much as landing position and trajectory are subject to the underlying neural competition between stimuli, we suggest that the increase in latency reported here is also due to this competition. When the distracter is close to the target, its activity merges with that of the target; thus, a trigger threshold for the initiation of the saccade (Hanes and Schall, 1996) is reached more quickly, producing short saccade latencies, averaging saccades and trajectories which deviate toward the target. When the distracter is farther away from the target, its activity is inhibited; hence, latencies are longer, saccades are more accurate and trajectories deviate away.

3.3. Conclusion

In conclusion, we have shown that the inhibition of competing oculomotor responses produces very different patterns in deviations of saccade trajectory and landing position. We propose that these are the result of a common competitive process which pools activity over a large portion of space at different periods of time. Saccade trajectory reveals the state of inhibition at the time of saccade initiation while landing position reflects the state of inhibition toward the time of saccade end. Our results show that the study of the movement of the eyes can also provide a valuable insight into the process of competition between different potential motor programs which take place before the selection of the saccade target and during the movement itself. We would hazard that the chains of behavioural movements we make while interacting with our built and natural environments also reflect these ongoing competitive interactions between the potential options with which we are provided on a day to day level.

4. Experimental procedures

4.1. Participants

Six observers participated, three female and three male with an age range of 18–32 years. All had normal or corrected-to-normal vision.

4.2. 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 II, SR Research Ltd) with a sampling frequency of 500 Hz. The central fixation stimulus was a small black circle with a white surround of 0.5° diameter. The saccade target was a black cross (+) which was 1 deg², the distracter was an unfilled circle (O) with a diameter of 1°. All stimuli were presented on a mid-gray background, on a 21-in. 75 Hz DiamondPro Sony colour monitor. A chin rest was used to minimize head movements and maintain the viewing distance at 57 cm from the screen.

4.3. Design

In experiment 1, the target appeared 10° from fixation, in one of two positions on the main vertical axis, i.e., "up" or "down". The distracters, when present, appeared at the same eccentricity 10, 20, 30, 60 or 120 angular degrees away from the target in a clockwise or counter-clockwise direction. The distracter and target stimuli appeared simultaneously. The fixation spot was removed from the display either before (denoted by negative numbers) or after target onset at stimulus onset asynchronies (SOAs) of −150, −75, 0, 75 or 150 ms relative to target onset. Thus, for each gap interval, there were 20 conditions with distracters: 2 possible target positions, 2 possible distracter directions (clockwise and counter-clockwise), and 5 possible target-distracter distances. In a further 2 conditions, the target was presented alone, without distracters. Subjects completed 2 sessions of 5 blocks of 110 trials, producing a total of 1100 trials (10 trials per condition) each.

4.4. 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 subjects to saccade to nine points, in a random order, around the screen. In order to validate the recorded eye positions, subjects again made saccades to the same nine points in a different random order. Calibration was only accepted once the difference between calibration and validation was less than 0.5° overall. Observers were instructed to make a saccade to the target and to ignore the distracters. Each trial began with the central fixation stimulus, displayed for a duration between 800 and 1300 ms. This was followed by the onset of target and distracter, if present. The display was then blanked for an inter-trial delay of 600 ms.

4.5. Data analysis

A parser integral to the eye-tracking software was used to identify saccade start and endpoints using a 22 deg/s velocity and 8000 deg/s² acceleration criteria (SR Research Ltd). Further analysis was undertaken using in-house software developed in Matlab (Mathworks Inc.). Saccade latency, trajectory, amplitude and overall direction were derived from the eye movement records for the first saccade in each trial. Amplitude was defined as the vertical component of the distance between eye start and end point (in degrees of visual angle). Saccades were excluded from further analysis if amplitudes were less than 2° of visual angle, saccade latencies were less than 50 ms or greater than 600 ms or blinks occurred during the saccade.

The two main metrics reported here are the trajectory and landing position (or angular) deviation of the saccade. The maximum trajectory deviation of each saccade relative to the direct path between fixation and landing position was determined (see Ludwig and Gilchrist, 2002). This was calculated by fitting a second-order polynomial to the saccade trajectory and finding the maximum point of angular deviation from the straight line which joined the saccade start position to its end position. As saccade trajectories are never completely straight, the trajectory deviation observed in no distracter (baseline) conditions was subtracted from that for distracter conditions. The deviation of saccade landing position was taken as the angular deviation of saccade end point from the true position of the target. In both cases, deviations toward the distracter were assigned positive values and deviations away from the distracter were given negative values. Trajectory and angular deviation were calculated for each factorial combination of target position and fixation offset time. Results are considered in terms of distracter distance from the target; thus, data are collapsed across target position (up and down) and distracter direction (clockwise or counter-clockwise).

Acknowledgment

The work was funded by a grant from the EPSRC (awarded to EM).

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