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Evidence that indirect inhibition of saccade initiation improves saccade accuracy

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Abstract. Saccadic eye-movements to a visual target are less accurate if there are distracters close to its location (local distracters). The addition of more distracters, remote from the target location (remote distracters), invokes an involuntary increase in the response latency of the saccade and attenuates the effect of local distracters on accuracy. This may be due to the target and distracters directly competing (direct route) or to the remote distracters acting to impair the ability to disengage from fixation (indirect route). To distinguish between these, we examined the development of saccade competition by recording saccade latency and accuracy responses made to a target and local distracter compared with those made with an addition of a remote distracter. The direct route would predict that the remote distracter impacts on the developing competition between target and local distracter, while the indirect route would predict no change as the accuracy benefit here derives from accessing the same competitive process but at a later stage. We found that the presence of the remote distracter did not change the pattern of accuracy improvement. This suggests that the remote distracter was acting along an indirect route that inhibits disengagement from fixation, slows saccade initiation, and enables more accurate saccades to be made.

Keywords: eye movements, saccades, inhibition, remote distracter

1 Introduction

Owing to natural limitations of the visual system we must move our eyes to facilitate gathering visual information about our environment (Findlay and Gilchrist 2003; Land and Tatler 2009). The selection of the next target for our saccadic eye movements is the outcome of a competition between different potential visual targets (Allport 1993; Desimone and Duncan 1995; McPeek 2006; McPeek et al 2003; Munoz and Istvan 1998; Schall and Thompson 1999). The development of this competition can be shown through a modulation of saccade response time and landing position when other, distracting, stimuli must be inhibited: changes in when and where the eyes are directed reveals the state of the underlying neural competition at the time of saccade initiation (Findlay 1982; Findlay and Walker 1999; Glimcher and Sparks 1993; Ludwig and Gilchrist 2003; McPeek 2006; McPeek et al 2003; McSorley and Findlay 2003; McSorley et al 2006; van Opstal and van Gisbergen 1989). Saccades with shorter latencies are less accurate than those with longer latencies. This can be seen within the natural variations in latencies over the course of an experiment (Chou et al 1999; Findlay 1981), when a specific instruction to delay initiation is given (Chou et al 1999; Coëffé and O'Regan 1987; Ottes et al 1985) or when latencies are lengthened involuntarily by the presence of a remote distracter (McSorley and Findlay 2003).

In the latter case, Cruickshank and McSorley (2009) (also McSorley and Findlay 2003) showed that presence of a distracter close to the target (here called a local distracter), which would normally adversely affect saccade accuracy, has less of an influence on saccades to target in the presence of a distracter farther from the target (here called a remote distracter). We suggested that the remote distracter increases activity at fixation, thereby inhibiting the initiation of the saccade (known as the remote distracter effect) (Walker et al 1995,

1997). This followed the findings of Walker et al (1997) who showed that the extent of saccade latency increase depended upon the relative distance of the remote distracter and target from fixation, and not the direct distance of remote distracter from the target. An improvement in saccade accuracy could be explained as a consequence of the increase in latency allowing the competition that dictates the saccade landing position to be more fully developed (called here an 'indirect' route). An alternative hypothesis is that the remote distracter acts through some more 'direct' route, eg by impacting directly on activation within the competitive process by which the saccade target is selected thus leading to an improvement in accuracy. Certainly, it has been shown that a remote distracter reduces activity in SC at the target site through direct inhibitory interactions between the target and remote distracter locations, leading to an increase in saccade latency (Dorris et al 2007; Olivier et al 1999).

These different (indirect and direct) explanations for the effect of remote distracter on saccade accuracy predict differences in the temporal development of the underlying saccade competition when a remote distracter is added to a display containing a target and local distracter. For the indirect route the temporal development of the competition between the target and local distracter should be the same regardless of the presence of the remote distracter. Remote distracter presence would increase activity at fixation but not influence the slope of the developing competition. For the direct route, activity at the target and local distracter site will be affected by the presence of the remote distracter. This would predict an impact on accuracy of the saccade and on its temporal development.

Here we examine these different predictions by taking advantage of a fixation gap paradigm (Ross and Ross 1980; Saslow 1967) which involuntarily induces changes in the latency of saccades (speeds or slows eye movement responses) and is known to be independent of other distracter effects (McSorley et al 2006, 2009; Walker et al 1995). This allows us to examine the change in accuracy of target driven saccades in the presence of either a single local distracter or both a local and a remote distracter over a wide range of saccade latencies.

2 Method

2.1 Observers
Eight naive observers participated in the experiment. Observers ranged in age from 19 to 21 years. All observers had normal, or corrected to normal, vision. Local ethical approval was obtained for this study, which was conducted in accordance with the standards described in the 1964 Declaration of Helsinki. All participants gave their informed consent prior to inclusion.

2.2 Apparatus and materials
Stimuli were vertically oriented Gabor patches with a spatial frequency of two (target) or four (distracter) cycles per degree (cpd), with a standard deviation of 0.3 deg and a mean luminance of 23 cd/m^2. All stimuli were presented on a grey background also with a mean luminance of 23 cd/m^2. Eye movements were recorded using a head-mounted, video-based, eye-tracker with a sampling rate of 500 Hz (Eyelink II, SR Research), recording monocularly from observers' right eyes. Stimuli were presented in greyscale on a 21" colour monitor with a refresh rate of 75 Hz (DiamondPro, Sony). The stimulus presentation was handled by in-house software developed from example code provided by SR Research. Head movements were constrained with a chin-rest, which held the participant so that their eyes were in line with the horizontal meridian of the screen, at a viewing distance of 1 m. The eye-tracker was calibrated using a standard 9 point grid, carried out at the beginning of the experiment and after any breaks where the observer removed their head from the rest or removed the eye-tracker. Calibration was accepted only once there was an overall difference of less than

0.5 deg between the initial calibration and a validation retest; in the event of a failure to validate, calibration was repeated.

2.3 Design

Stimuli were presented 8 deg of visual angle from fixation at an angular offset of 10 deg (see figure 1 for an example with targets shown to the right of fixation). A target and distracter were always present in one of two possible locations: 10 deg above horizontal or 10 deg below (eg if the target appeared above then the distracter was in the down position and vice versa). In the opposite hemifield a single remote distracter was present on half of the trials. This appeared on the horizontal meridian, 4 deg from fixation. Distracters and target stimuli appeared simultaneously. For half of the observers (four) the target appeared only on the left while the remaining half saw targets only on the right. The fixation spot was removed from the display either before (gap, denoted by negative numbers) or after (overlap) target onset at stimulus onset asynchronies (SOAs) of −150, −75, 75, or 150 ms relative to target onset. For each SOA there were 4 conditions: 2 possible target/distracter positions (10 deg above or below the horizontal meridian) and 2 possible remote distracter states (absent or present). Observers completed 2 blocks of 80 trials, producing a total of 160 trials (10 trials per condition) each.
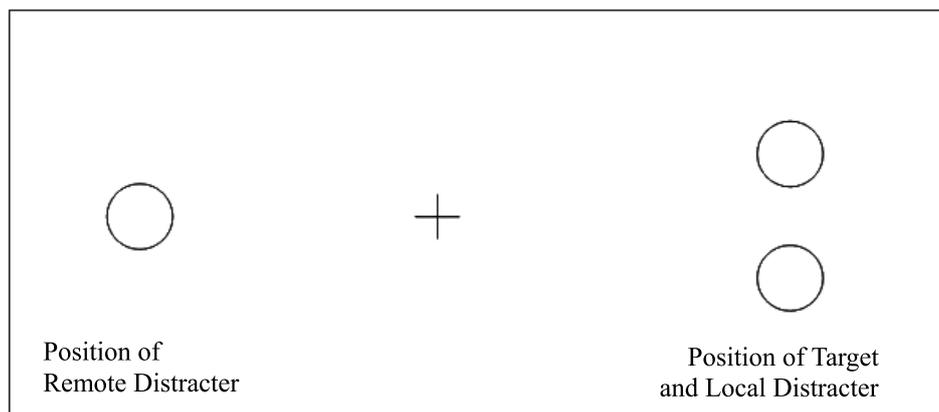
Figure 1. Targets were restricted to appear on the right or left hand side of the screen for two separate groups of four observers. In the example display shown, the target appears on the right, 10 deg of visual angle from fixation, at an angular offset of 10 deg above or below the horizontal meridian. A distracter, local to the target, also appears on the right in the mirror-opposite place to the target across the horizontal meridian. In 50% of trials a further, remote, distracter will appear to the left of fixation, on the horizontal meridian 10 deg of visual angle from fixation.

2.4 Procedure

Observers were familiarised with the target and distracter stimuli. Following this an introductory block of up to 20 trials was presented to introduce observers to the timing and spatial configuration of the experimental trials. Observers were instructed to move their eyes 'as quickly and accurately as possible' to the target Gabor patch, ignoring distracters. Trials began with a central fixation cross (+) subtending 0.5 deg of visual angle, presented for a varying duration of between 800 and 1300 ms. Gap trials included a blank screen, shown for either 150 ms or 75 ms, after offset of the fixation cross; overlap trials had no blank screen. This was followed by the onset of the stimuli which were displayed for 1 s. In gap trials no fixation cross was present with the stimuli; in overlap trials the first 75 ms or 150 ms of stimuli also included the fixation cross, thereafter none. Finally, a blank screen was shown for 500

ms, followed by the reappearance of the fixation cross. Once the observers eyes were fixated (within ±0.5 deg of visual angle from fixation) the next trial commenced.

2.5 Data analysis

A parser integral to the eye-tracking software was used to identify saccade start and endpoints using a 22 deg s^{-1} velocity and 8000 deg s^{-2} acceleration criteria (SR Research Ltd). Further analysis was undertaken using in-house 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 trial. Amplitude was defined as the horizontal component of the distance between eye start and end point (in degrees of visual angle). Saccade latency is the interval between the onset of the target and the initiation of the saccade (in ms). Direction was defined as the angular deviation of saccade direction taken from the initial fixation location to final endpoint in polar coordinates. Saccade accuracy was defined as the angular deviation between the target and saccade landing position eg a value of zero shows a saccade landing at the centre of the target, while 10 deg shows a saccade landing toward the distracter position. Saccades were excluded from further analysis if their amplitudes were less than two degrees (1.5%), latencies were less than 50 ms or greater then 500 ms (classed as not being a reaction to the appearance of the stimuli, 0.01%), or a blink occurred during the saccade (0.25%).

3 Results

Figure 2 shows mean saccade latency for each SOA, collapsed across subjects, dependent upon contralateral distracter presence. A two-factor ANOVA (SOA by distracter) showed a monotonic increase in saccade latency as SOA turns from a gap to an overlap between fixation and stimuli onset [main effect of SOA: $F_{3,21} = 34.4$, $p < 0.01$]. While maintaining this pattern
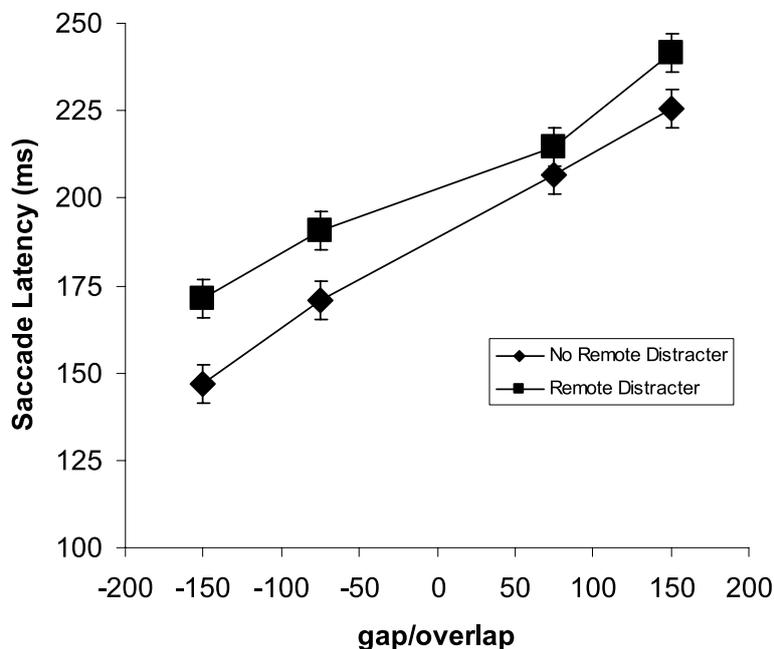
Figure 2. Saccade latency (ms) is shown as a function of fixation marker stimulus onset asynchrony (SOA) (ms). Saccade latency was found to increase as the SOA of the fixation marker changed from a gap (−150 and −75) to overlap (75 and 150). This gap effect pattern was the same regardless of remote distracter presence. Remote distracter presence induced an overall slowing of saccade latency showing a similar remote distracter effect regardless of SOA. Repeated measures error bars are shown (Loftus and Masson 1994).

(ie no interaction: $F<1$), saccade latency increased further when the contralateral distracter was present compared with its absence [main effect of distracter: $F_{1,7} = 14.1$, $p<0.01$].
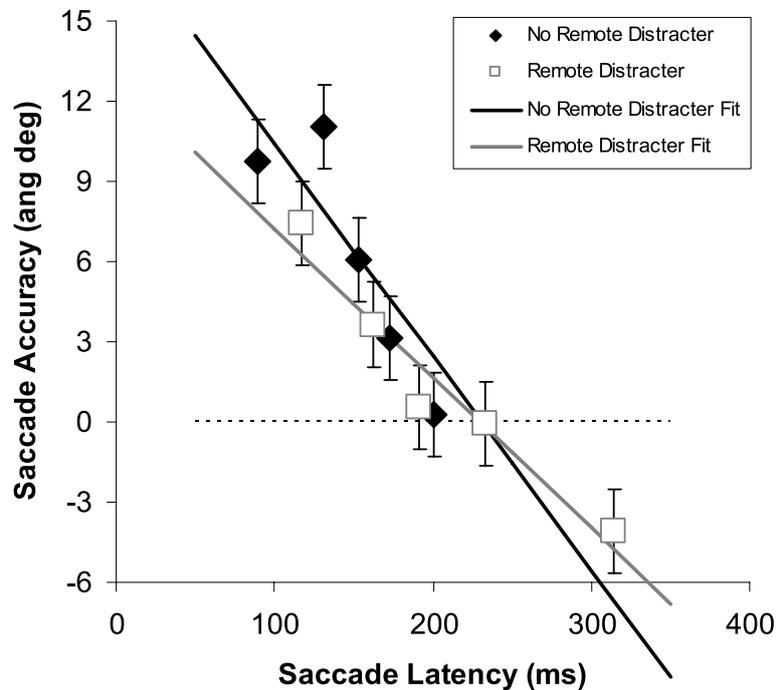
Figure 3. Saccade accuracy (in terms of angular deviation from the centre of the target stimulus) is shown as a function saccade latency depending on remote distracter presence. Mean accuracy was determined for successive 20% portions of the saccade latency distribution from shortest to longest. These are plotted across the means of those latency bins. Accuracy was found to improve as latency increased whether a remote distracter was present or not. The fits shown are linear and show no significant changes in slope or intercept when the remote distracter was present. The accuracy improvements found in the presence of the remote distracter reflect a similar temporal development of saccade competition as found when only the local distracter was present. Repeated measures error bars are shown (Loftus and Masson 1994).

To examine the effect of saccade latency on saccade accuracy (the angular error of the saccade landing position relative to the target position), the latency distribution was quintiled for each contralateral distracter condition, separately for each subject. The mean saccade accuracy deviation and its corresponding mean latency were determined for successive 20% portions of the saccade latency distribution (data were not separated by fixation gap intervals). These were averaged across subjects and are shown in figure 3. It is clear that, as the latency of the saccade increases, its corresponding accuracy improves. To explore this relationship further the best linear fits were determined for each contralateral distracter condition separately for each subject. All data were well captured by these fits except for one observer in the NO remote distracter condition [$r^2 = 0.1$; mean r^2 otherwise: absent = 0.41 (range 0.2 to 0.78); present = 0.7 (range 0.27 to 0.91)]. Two separate one-sample t-tests show that slopes from all subjects in both contralateral distracter conditions significantly differ from zero [absent: t(7) = −4.5; present: t(7) = −5.5, p<0.01] indicating that accuracy improves as saccade latency increases. A paired t-test shows no difference between the slopes for each distracter condition [t(7) = 1.3, ns] suggesting that the contralateral distracter improves saccade accuracy by increasing the latency of the saccade in the similar manner to that which occurs when the distracter is absent. The overall linear fits to each remote distracter condition are plotted on figure 3.

4 Discussion

When making saccades to targets which have distracting stimuli close by, we find an accuracy benefit gained from the presence of a visual distracter remote from their location (see also Cruickshank and McSorley 2009; McSorley and Findlay 2003). Remote distracter effects on accuracy have been ascribed to a lengthening of the saccadic response time made in its presence. We find that manipulation of saccade latency showed an improvement in saccade accuracy as latency increased. The addition of the remote distracter did not change the pattern of improvement; rather, presence of remote distracter appears to increase latency and access the competition between the target and local distracter at a later time, thus producing more accurate saccades. This suggests action of the remote distracter is indirect (Walker et al 1997): the temporal development of saccade competition does not change as the remote distracter does not directly influence it. We suggest that remote distracters act along an indirect route which impairs disengagement from fixation, perhaps via long range inhibitory interactions (Gandhi and Keller 1995) which serve to increase activity around fixation, and inhibit the initiation of the saccade. This allows competition between the local distracter and the target to be more developed prior to its reaching a critical threshold for movement initiation allowing more accurate saccades to be made. A direct route, in which the remote distracter interacts more directly with target and local distracter and therefore impacts on the competition taking place between them, would have predicted the temporal development of saccade competition would be modified in some way by remote distracter presence. Our data do not fit with this explanation (see also the findings of Cruickshank and McSorley 2009; McSorley and Findlay 2003).

It is interesting to note that accuracy improves until saccade latency is around 200 ms at which point there is some suggestion in figure 3 that it worsens again (that is, landing position starts to deviate away from the target in the opposite direction to the local distracter). This is very similar to the pattern of deviations found in the trajectories of target driven saccades made in the presence of a distracter (Godijn and Theeuwes 2004; McSorley et al 2006, 2009; Walker et al 2006). Saccade trajectories are found to deviate toward the distracter location when they have a short latency but deviate away as latencies increase. The saccade latency at which the direction of trajectory deviation changes from toward to away from the distracter (ie when the trajectory is straight) is also around 200 ms. The few data reported in this paper which support this similarity are suggestive, but further work exploring longer saccade latencies would be necessary to establish the temporal development of the inhibition of the local distracter on saccade landing position.

Our results fit well with recent models of saccade programming. In these models the competition which determines where and when saccades are directed is determined on motor maps which are organised topographically throughout the visual/motor system (Findlay and Walker 1999; Godijn and Theeuwes 2002; Kopecz 1995; Trappenberg et al 2001) like those identified in superior colliculus, frontal eye fields, and lateral intraparietal area. Visual areas of interest, such as different potential targets, are represented across these as neural peaks of activation with overlapping receptive fields (eg Bruce and Goldberg 1985; Goldberg et al 2006; Lee et al 1988), with excitatory connections to nearby receptive fields and inhibitory connections to those further away (Hikosaka 1989; Hikosaka et al 2000; Munoz and Istvan 1998; Sommer and Wurtz 2004a, 2004b; Wurtz and Sommer 2004). Competition between possible saccade targets takes place within these motor maps until a single area of activation exceeds threshold and the saccade is initiated to that point (Hanes and Schall 1996; Ratcliff et al 2007). The landing position of a saccade is a consequence of distributed population coding over large overlapping receptive or movement fields in the superior colliculus, which form a saliency map (Lee et al 1988; McIlwain 1986, 1991). When possible

visual targets are close together (within ± 20 deg), they activate overlapping movement fields, resulting in a single large peak of activity. In these cases saccades tend to land between the stimuli, at the peak of activation (this is known as the global effect or centre of gravity effect). The extent of the deviation in landing position reflects the relative neural activation at each stimulus site (Findlay and Benson 2006; Glimcher and Sparks 1993; Ottes et al 1985; van Opstal and van Gisbergen 1989; Walker et al 1997). Landing position deviations from the target arise when sites representing multiple stimuli are active and the saccade will land between them. A shorter latency saccade is generated when activation produced by the onset of the stimuli quickly exceeds threshold, resulting in inhibition of fixation activity. Owing to the overlapping receptive field properties of the saccadic system the landing position is likely to be influenced by activation produced by each stimulus close to the target location. Saccades will become progressively more accurate as the activation at the target location increases and that of the other stimuli diminishes through competitive processes which takes time, thus longer latency saccades are more accurate saccades.

Stimuli which are farther apart affect when the saccade is initiated but do not affect where the saccade lands (this is known as the remote distracter effect; Born and Kerzel 2008; Honda 2005; Ludwig et al 2005; Walker et al 1995, 1997). The remote distracter effect occurs even when observers know which side of fixation the target will appear on, suggesting that it is an automatic effect not subject to voluntary control (Benson 2008; Walker et al 1995, 2000). Walker et al (1997) found that the magnitude of the remote distracter effect diminishes with relative distance of the target and distracter from fixation, as opposed to distance of the distracter from the target. This led them to suggest that that the remote distracter acts via long range inhibitory interactions (as reported by Gandhi and Keller 1995) on cells in the rostral pole of the superior colliculus (Munoz and Wurtz 1995a, 1995b) by maintaining tonic activation and thus inhibiting when a saccade can be initiated (Munoz and Wurtz 1993). Contrary to Walker et al (1997), others have reported that increasing distracter distance from the target (rather than fixation) induces the remote distracter effect (Dorris et al 2007; Olivier et al 1999). They show that neuronal activity in superior colliculus at the target location is inhibited when distracters are shown at remote distances from the target. However, given the restricted set of distracter distances from target (two: near and far) and the timing differences between distracter and target onset (distracter was onset 200 ms prior to the target) employed by Dorris et al (2007), it is not clear which of these two explanations underlie the remote distracter effect. It is notable that our results fit better with the former explanation for an impact of the remote distracter on fixational disengagement. A further test of our findings would be to manipulate the position of the remote distracter (temporally and spatially) in the manner reported by Walker et al (1997). Our prediction is that the accuracy of the saccade should be dependent wholly on the latency of the saccade regardless of remote distracter placement.

In conclusion, we suggest that the involuntary increase in saccade latency induced by a remote distracter inhibits the onset of the saccade by increasing fixation related activation. As the competition between stimuli progresses the point of highest activation shifts towards the target. Thus, the involuntary increase in saccade initiation latency induced by the presence of a remote distracter improves target localisation by accessing the underlying competition which determines its identity at a later, and more finely resolved, stage of processing.

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