THE INHIBITION OF VOLUNTARY SACCADIC EYE MOVEMENT COMMANDS BY ABRUPT VISUAL ONSETS

Jay A. Edelman and Kitty Z. Xu

Dept. of Biology, The City College of New York
Convent Ave. at 138th St., New York, NY 10031

RUNNING TITLE: Inhibition of voluntary saccade commands

 Correspondence should be addressed to
 Jay A. Edelman, Ph.D.
 J526, Marshak Science Bldg.
 The City College of New York
 Convent Ave. at 138th St., New York, NY 10034
 e-mail: jedelman@sci.ccny.cuny.edu

No. of Figures: 9  No. of Pages: 30

KEY WORDS: Saccade, voluntary, reflex, latency, express, delayed, distractor, human

ACKNOWLEDGMENTS: Supported by: NIGMS GM00816-28 (SCORE) and NIH/NCRR 5G12 Rr03060 (RCMI)
ABSTRACT

Saccadic eye movements are made both to explore the visual world and to react to sudden sensory events. We studied the ability for humans to execute a voluntary (i.e. non-stimulus driven) saccade command in the face of a suddenly appearing visual stimulus. Subjects were required to make a saccade to a memorized location when a central fixation point disappeared. At varying times relative to fixation point disappearance, a visual distractor appeared at a random location. When the distractor appeared at locations distant from the target virtually no saccades were initiated in a 30-40 ms interval beginning 70-80 ms after the distractor appearance. If the distractor was presented slightly earlier relative to saccade initiation then saccades tended to have smaller amplitudes, with velocity profiles suggesting that the distractor terminated them prematurely. In contrast, distractors appearing close to the saccade target elicited express saccade-like movements 70-100 msec after their appearance, though saccade endpoint was generally little affected by the distractor. An additional experiment showed that these effects were weaker when the saccade was made to a visible target in a delayed task and still weaker when the saccade itself was made in response to the abrupt appearance of a visual stimulus. A final experiment revealed that the effect is smaller, but quite evident, for very small stimuli. These results suggest that the transient component of a visual response can briefly but almost completely suppress a voluntary saccade command, but only when the stimulus evoking that response is distant from the saccade goal.
INTRODUCTION

Saccadic eye movements can be classified as reflexive, made in response to a sudden sensory event, or voluntary, made at will to a sensory element, generally a visual object, that is part of a visual scene. An exploration of the visual scene will occasionally be interrupted by the sudden appearance of a visual stimulus, which may reflexively elicit a saccadic eye movement towards it. Studying how sudden events interfere with ongoing behaviors is difficult because it requires quantification of the behavioral importance of maintaining an ongoing action relative to the assessed importance of sensory events. Nonetheless, various studies have examined the competition of these voluntary and reflexive processes. The ability for abrupt visual onsets to capture attention has been studied for close to twenty-five years (e.g. Egeth and Yantis 1997; Yantis and Jonides 1984; 1990). Such work has examined both “covert” capture of attention, studying how peripheral visual attention is manipulated by suddenly appearing visual targets, as well as “overt” capture of attention or “oculomotor capture”, studying how suddenly appearing visual stimuli can elicit inappropriate saccades when subjects are instructed to direct saccades as part of an ongoing behavioral process, such as visual search (Theeuwes et al. 2003; Theeuwes et al. 1999).

But, the sudden appearance of distracting stimuli can interfere with or delay goal-directed saccades without itself attracting gaze. Walker and colleagues showed that a distracting stimulus can increase the mean latency of a saccade triggered by the appearance of a target whose location is known in advance (Walker et al. 1997) (see also Corneil and Munoz 1996; Lévy-Schoen 1969). The appearance of distracters delayed the initiation of saccades when presented far from the target. If presented near the target, however, these distracters influenced the amplitude of the saccade, leaving latency unaffected. The effect of the distracter on overall saccade latency is somewhat weaker if the distracter is presented shortly before or after the target (Walker et al. 1995). Subsequent studies on this “remote distractor effect” have
examined how the presence of the distracter can influence saccadic trajectory (e.g. Doyle and Walker 2001).

Left unclear from these studies was the precise temporal nature of these distractor effects, particularly whether these effects were due to a long-lasting inhibition of saccade-related activity, thus reducing the probability of saccade execution for some time, or whether instead the effect was dramatic, but short-lived. Taking a somewhat different experimental approach, Reingold and Stampe have complemented these studies of the spatial specificity of remote distraction by examining the temporal specificity of visual distraction (Reingold and Stampe 2004; 2002; Reingold and Stampe 1999; 2003; Stampe and Reingold 2002). In the experiment most closely resembling the present experiments, consisting of discrete trials, they showed that a visual stimulus consisting of two large, bright bars, extending the entire length of the screen, can cause a transient inhibition in saccade execution occurring around 70-100 ms after the appearance of the distractor. They have referred to this phenomenon as "saccadic inhibition" and speculated that it could be useful to vision by temporarily pausing ongoing natural saccade behavior in the face of sudden sensory events. Additional work has shown that large display-spanning distractors are not necessary for this transient saccade inhibition to occur. Reingold and Stampe (2004) showed that 10x10 deg. distractors appearing on one side or the other of the fixation point can inhibit saccades. Smaller distractors have also been shown to have this effect when presented at or near central fixation (Graupner et al. 2007; Pannasch et al. 2001; Sheliga et al. 2002). They can also inhibit saccades made during reading when presented away from the saccade goal (Reingold and Stampe 2003). However, while these studies helped elucidate the temporal nature of saccade distraction, they did not examine the spatial specificity of these effects in the manner of Walker et al (1997). Specifically, they left unclear whether saccade inhibition occurs irrespective of the distance between the distractor and the saccade goal, or whether, like the remote distractor effect, it causes inhibition only when distant from the saccade goal.
The principal aim of the present study was to explore, in conjunction, the spatial and
temporal aspects of interference of suddenly appearing distractors on saccade generation
(Expt. 1). We also investigated how interference with saccade commands depends on whether
the planned saccade is visually guided and on whether it's reflexive (Expt. 2a, 2b) Finally, we
examined how the effect of the distractor depends on its size (Expt. 3). Our findings support the
idea that the phenomenon of saccade inhibition results from interactions between transient and
sustained loci of activity present on a spatial neural map located in an area involved in saccadic
programming, such as the superior colliculus or frontal eye fields. We then attempt to integrate
the implications of these behavioral findings with those of recent neurophysiological data
obtained in recordings of saccade-related areas in the monkey.

METHODS
Subjects, eye movement recording, and visual stimulus display -- Four subjects (ages 20-43,
two naïve – N1, N2, two authors – A1, A2) participated in these experiments. Part of the
motivation for having naïve subjects participate in the task was that the authors, who both
participated as subjects, had considerable experience in saccade tasks, and reliably made
express saccades (latencies < 110 msec) in a gap task (Fischer and Ramsperger 1984; Saslow
1967). We speculated that such a tendency to make saccades of such short latency reflected
sensitivity to the sudden appearance of visual stimuli, and that the effects we found here could
reflect that sensitivity. To confirm that our naïve subjects did not make express saccades, we
ran them in a gap saccade task before and after their participation in this study. In neither
session did either subject make an appreciable number of express saccades.

Eye movements were recorded using an Eyelink II video-based eyetracker (SR
Reaersch), sampling at 500Hz. Stimuli were presented on a CRT monitor (Compaq P1220).
Stimulus presentation and data acquisition were controlled by a Macintosh G4 using C
programs that were written using the Vision Shell library (Raynald Comtois). The luminance of all stimuli was 100 cd/m², the maximum brightness setting of the monitor.

Subject setup and calibration -- Subjects' heads were stabilized with a bite bar. The Eyelink II apparatus was placed so that no part of it blocked the view of the screen. Calibration of eye position was performed using nine locations formed in a 3x3 grid. An eye position drift offset operation was performed at the start of each block of trials.

Experiment 1 – Inhibiting learned saccades—In this experiment subjects made saccades to the left or right as indicated by a central arrow. The task was similar to the “learned saccade task” of Bruce and Goldberg (1985) in that saccades were instructed to be made to a learned or memorized location at which no visible target was present (Fig. 1). The saccade goals were 10° to the left or right of the center of the display. Trials began with the presentation of a small central fixation arrow (‘>’, ‘<’, 0.5° from tail to head) pointed either left or right. Subjects were required to fixate this arrow within 500ms of its appearance. After central fixation had been achieved, the subjects were required to maintain fixation for 500-800ms, at which point the arrow disappeared, which served as the temporal cue for the subjects to make a saccade to the desired goal. The saccade had to be initiated within 500 ms of target disappearance, or else a loud beep would sound, and the trial was terminated. Data from such trials were not analyzed. Immediately after the saccade had landed, a small “feedback” stimulus, a spot of light (1° x 1°), appeared at the saccade goal for 300ms, during which subjects had to maintain fixation on it. This provided subjects information on their saccade accuracy.

There were two types of such trials in this block, both using the temporal schematics described above. In “Invisible Distractor” trials no distractor appeared (the reason why these trials were referred to as “invisible” is described below). In “Distractor” trials a bright square (2° x 2°) appeared at varying times relative to the disappearance of the fixation point, at varying locations on the screen. The temporal separation of fixation point disappearance and distractor appearance was fixed at one of four intervals, each separated from the next in duration by
30ms. To determine the range of timings for a subject, practice trials were run and the subject’s mean reaction time (i.e. interval between fixation arrow disappearance and saccade initiation) was calculated. Using this mean, intervals were set for each subject such that the average time between distractor appearance and saccade initiation was 85 ms, a typical time of maximum inhibition in the experiments of Reingold and Stampe (2002). For example, if a subject’s mean reaction time was 150 ms, then the intervals between fixation arrow disappearance and distractor appearance were set at 110, 80, 50, and 20ms, such that the expected intervals between distractor and saccade initiation were 40, 70, 100, and 130ms (the average of which is 85 ms). The distractor would disappear as soon as the saccade was initiated. The possible distractor locations lay on a circular locus centered on the fixation point, with a directional difference of 0º, 22.5º, 45º, 90º, or 180º from the position of the saccade goal, at an eccentricity equivalent to that of the saccade goal. The distractors appeared only in the upper hemifield.

Trials, varying in the location of the saccade goal and the presence, location, and timing of the distractor, were run randomly within a session. Within a session, 288 trials were run, 144 each with the left or right saccade goal. For each side’s set of 144 trials, 120 were Distractor trials and 24 were Invisible distractor trials. Of the 120 Distractor trials, 24 had distractors at each of the five positions relative to the saccade goal. For each of the 24 trials with a particular distractor position, there were six of each of the four possible fixation arrow disappearance / distractor appearance intervals, as specified above. Each subject participated in five identical sessions for a total of 1440 trials. Thus, across the entire data set, there were a total of 30 trials for each combination of saccade direction, distractor location, and distractor timing, along with a total of 240 Invisible distractor trials.

We also collected data for a follow-up to this experiment in which the distractors appeared in the lower instead of the upper hemifield (Expt. 1b). Otherwise, this follow-up was identical to Expt. 1.

Experiment 2a – Inhibiting visually guided delayed saccades
Experiment 2a was identical to Experiment 1 except that subjects made visually guided delayed saccades to a 2° x 2° square that appeared at the saccade goal 100 ms after the fixation arrow appeared. Subjects were still required to wait for the fixation arrow to disappear before making a saccade, making this a visually guided delayed saccade task (Fischer and Boch 1981). The square disappeared 300 ms after the end of the saccade made to it. Also, as there was a visible target at the saccade goal, in contrast to Expt. 1a, there were no trials with a 0° saccade goal / distractor angle difference. Thus, there were a total of 240 trials in each session. Again, five sessions were run for a total of 1200 trials. All four subjects participated in this experiment.

Experiment 2b – Inhibiting reflexive visually guided saccades

Experiment 2b was identical to Experiment 2a, except that the square at the saccade goal appeared coincident with the disappearance of the fixation arrow, and saccades were instructed to be made when this peripheral stimulus appeared, rather than when the central fixation stimulus disappeared, as was the case in Experiments 1 and 2a. This is thus similar to the remote distractor experiments of Walker et al (1997), except that distractors were generally presented after the saccade target rather than coincident with it. The same four subjects of Expts. 1 and 2a participated here.

Experiment 3 – Inhibiting learned saccades with distractors of various sizes

This experiment was identical to Experiment 1, except the only distractor location was opposite the saccade goal, and five different distractor sizes (all squares) were used (4°, 2°, 1°, 0.5°, and 0.25°). Within a session, 50% of trials had invisible distractors while the other 50% of trials had distractors of one of the five sizes. Six sessions were run. The two authors participated in this experiment.

Data analysis
Data analysis was performed using routines from Matlab (Mathworks) and SigmaStat (SYSTAT). All stated statistically significant differences were significant at $\alpha = 0.05$.

*Calculation of saccade metrics* -- To compute the start and end of each saccade, a saccade velocity trace was obtained by differentiating the horizontal and vertical components of the eye position trace by a central difference algorithm implemented in Matlab and then using the Pythagorean theorem to calculate radial velocity as a function of time. The following algorithm for determining saccade latency was used in Matlab: the eye position trace just after the time of the cue to make a saccade (either target appearance or fixation point disappearance – see below) was examined to determine the first point at which velocity exceeded 35 deg/sec. Next, the trace was evaluated backward in time until the first point below 15 deg/sec was found. The end of the saccade was determined in an analogous manner, but with time reversed.

*Assessment of influence of distractors on saccade initiation* – To determine the influence of distractor timing on saccade initiation, we constructed histograms of saccade initiation as a function of time after the appearance of the distractor. Thus, if distractors at a particular location inhibited saccade initiation with a delay of, say, 80-120 ms, such histograms should show a “notch” at that delay where the probability of saccade occurrence dropped. To quantify this drop we calculated a continuous estimate of the probability of saccade occurrence, which replaced each saccade event in the histogram with a Gaussian kernel of standard deviation of 3 ms (analogous to how spike density functions are calculated for use in analyzing single-unit neurophysiological data, Richmond and Optican 1987). We then compared these continuous estimates for each condition in which a distractor appeared with the condition in which no distractor appeared.

The Invisible Distractor condition was run using an identical temporal framework as the other trial types, only with the distractors appearing black (i.e. matching the appearance of the background), so that they were invisible (hence the name). This is equivalent to randomly assigning each trial of the Invisible Distractor condition to one of the four possible temporal
intervals between distractor appearance and the cue to make a saccade (the disappearance of
the fixation point). This puts the histogram of saccade initiation on an equal footing for the
different trial types, such that if the visible distractors had no influence on saccade initiation,
their histograms of saccade initiation would look the same as that of the Invisible Distractor
trials. This approach has been used previously (e.g. Reingold and Stampe 2002). Next, we
calculated the maximum probability drop as the maximal difference between the curve for the
Distractor trials and the curve for the Invisible Distractor trials (Fig. 2) and noted the time relative
to distractor appearance at which this maximum drop occurred. We also assessed the duration
of this notch by calculating the half-width of this notch. This was done by noting the separation
in the times when the probability function for the distractor condition crossed a level
.corresponding to 25% of the total drop.

Saccade curvature -- If the effect of the distractor did not become manifest until late into
the saccade, a curved saccade might result. To assess this possibility, we defined saccade
curvature as the maximum perpendicular distance of any point on the saccade trajectory from a
straight line connecting the start and end points divided by the distance between the two points
(Smit and Van Gisbergen 1990). We then assigned a sign to this value depending on whether the
curvature toward the end of the saccade was toward the right (+) or the left (-).

RESULTS

Expt. 1 -- No visible target at saccade goal

We found that the presence of a visual distractor far away from the intended goal of the
saccade caused a transient inhibition in saccade generation that occurred 70 to 100 ms after the
appearance of the distractor. In contrast, when the distractor was presented close to the
saccade goal, it tended to elicit a saccade within 80-90 ms of its appearance, though the
saccade tended to land much closer to the intended saccade goal than to the distractor.
Histograms were constructed that reflected the probability of the time of saccade initiation with respect to the appearance of the distractor. They are shown for two subjects at the five different spatial relationships between distractor and saccade goal, along with the Invisible Distractor condition (Fig. 3).

The most noteworthy finding is the “notch” visible in the histogram showing saccade initiation with respect to the appearance of the distractor. This was present for all four subjects when the directional difference between saccade goal and distractor was 180 deg or 90 deg, and was present to a more modest extent when the spatial difference was 45 deg. We performed pair-wise comparisons between the Invisible Distractor condition and each of the other conditions using the Kolmogorov-Smirnov test. Distributions were significantly different for all four subjects when the target/distractor separation was 90 or 180 deg, for two subjects when the separation was 45 deg, and for three subjects when the separation was 22.5 deg. and 0 deg.

As described in Methods (Fig. 2), to quantify the characteristics of the notch for the larger saccade goal/distractor spatial separations we calculated a continuous probability density estimate of the distribution of saccade latencies, and compared this estimate using trials of a particular saccade goal/distractor angle with that of the Invisible Distractor trials (Fig. 4). We also computed the half-width of the density estimate of the notch (see Methods). The mean peak reduction in saccade probability was 93% when separation was 180 deg, 91% at 90 deg, and 65% at 45 deg. The mean half-width of the notch was 49 msec for a 180 deg. separation, 44 msec for 90 deg. and 25 msec for 45 deg. The time of the minimum of this notch ranged from 82-105 msec when separation was 180 deg. and 79-92 msec when the separation was 90 deg. To confirm that the probability of saccade occurrence was lower in this notch than in the same time interval when no distractor appeared, we compared these two probabilities using a z-test for proportions. We found significant reductions in probability of saccade occurrence for all four subjects for each of the 45, 90, and 180 deg separations. Finally, we confirmed the dependence
of the magnitude of inhibition on the goal/distractor separation across the four subjects with a one-way repeated measures ANOVA (p < 0.001). A multiple comparisons procedure (Student-Newman-Keuls) revealed that the effects across the different saccade goal / distractor separations were all significantly different from each other, except for the difference between the 90 and 180 deg separation conditions. A similar repeated analysis procedure performed for analyzing the temporal duration of the inhibition (just for 180, 90, and 45 deg. separations) also showed a dependence on angular separation; multiple comparisons showed that the duration of the inhibition was significantly shorter in the 45 deg. condition than in the other two conditions.

When the distractor appeared at the saccade goal (0 deg. separation) or else when the separation was small (22.5 deg) the distractor tended to elicit a saccade within 80-100 ms rather than suppress it, as depicted by the large peak in the distribution of saccade initiation times relative to distractor appearance in Fig. 3. There was a significant increase in the number of saccades made between 80 and 100 ms after distractor appearance for three of four subjects for the 0 deg separation condition and for all four subjects in the 22.5 deg. separation condition. Overall, there was a 117% increase in the proportion of saccades in that time window for 0 deg separation and an 88% increase in the proportion of saccades for trials with a 22.5 deg separation. The time of this peak averaged 87 ms for 0 deg. separation and 89 ms for 22.5 deg. These times are well within the range of human express saccade latencies (Edelman et al. 2007; Fischer and Ramsperger 1984) and are virtually identical in timing to the notch described above, when distractors appeared far away from the saccade goal.

Distractor influence on saccade direction – Despite the intention to make a saccade to a particular location, it would seem possible for the sudden appearance of the distractor to elicit a saccade directly to the distractor itself. We found that when the directional difference between the saccade goal and distractor was at 180 deg, one of the four subjects (N2) made a large number of saccade errors, with approximately 30% of the saccades landing close to the
distractor. The proportions of errors for the other three subjects at the 180 deg. separation and for all four subjects at the 90 deg. separation were less than 5%.

One could speculate that with smaller distances between targets and distractors, saccade endpoint could be influenced by the distractor, especially since the data on saccade initiation described above indicated that saccades were being triggered by the appearance of the distractor. However, even when this distance was small saccades overall landed much closer to the desired goal than to the distractor. We calculated a “distractor angular percentage gain” by dividing the upward deflection in saccade angle with respect to the horizontal meridian by the angular distance of the distractor from the horizontal meridian. Thus, if a saccade in the 45 deg. condition landed directly on the distractor then the distractor angular percentage gain would be 100%, whereas if it landed at the desired goal (along the horizontal meridian), this measure would be zero. For saccades initiated between 80 and 100 ms after the distractor, we found that distractor angular gain tended to be very small, on average 21%, 11%, and <1% for 22.5, 45, and 90 deg. separations, respectively. These values largely reflect the gains of one subject, N2, which were much larger than that of the others, though even for this subject gains were less than 50% (22.5 deg: 44%, 45 deg.: 31%).

Though the spatial effect of the distractor was generally small, we compared these saccades to those initiated within 30 ms of distractor appearance (a time frame in which the distractor presumably has no effect on the saccade). The differences were significant for all four subjects when the distractor distance was 22.5 deg and for two of four subjects when the distance was 45 deg (t-test). Given these small gains, one might suggest that saccades were initiated towards the distractor and then bent back towards the saccade goal. An analogous analysis of saccades maximally affected and non-affected by the distractor, as described above, showed that saccade curvatures were small for all trial types (curvature index, unaffected: 0.035, 22.5 deg: 0.039, 45 deg: 0.038).
As described above, the sudden appearance of a distractor opposite the saccade goal reduced the likelihood of initiating a saccade within approximately 80 ms of its appearance. The probability of initiating saccades within 40-80 ms of distractor appearance did not generally decease significantly, but, given the duration of a typical saccade of 10 deg in amplitude (~40-50 ms), saccades initiated within 40-80 ms after target appearance could be in progress when the distractor made its presence felt. Thus, it is possible that the kinematics or endpoint of such saccades could be different from saccades made with no distractor.

Indeed, when the distractor was opposite the saccade goal (180 deg separation) there was a tendency for saccades initiated 50-75 ms after distractor appearance to be more hypometric than saccades initiated at other times. We compared the amplitude of saccades initiated within 20 ms of the beginning of the reduction in saccade probability (typically 50-70 ms after distractor appearance) with the amplitude of saccades occurring within 25 ms of the distractor’s appearance. Amplitudes were significantly reduced in this later period for all four subjects (p < 0.05, two-tailed t-test), with an average reduction in amplitude of 28% (Fig. 5).

Interestingly, a comparison of peak velocity between these two sets of saccades revealed much smaller differences than one would expect given their relative amplitudes. The overall percentage decrease in velocity (12.5%) was much smaller than that of saccade amplitude (28.5%), suggesting that these saccades were higher in peak velocity than what would be normal for their amplitude. Fig. 6 contrasts, for two subjects, the velocity profiles of saccades with relatively small amplitudes (N2: < 5 deg; A2 < 7.5 deg) that were initiated between 50 and 75 msec after distractor appearance with those of saccades not affected by the distractor. That the small amplitude saccades achieve relatively high velocities before suddenly slowing down is consistent with the idea that the distractor, while not delaying the saccade, has prematurely terminated it. Note also for subject N2 eye velocity picks up approximately 25 ms
after the small amplitude saccades end, a velocity profile reminiscent of saccades interrupted by electrical stimulation of pontine omnipause neurons or of the rostral superior colliculus (Keller 1977; Keller and Edelman 1994; King and Fuchs 1977; Munoz et al. 1996).

Distractor influence on saccade amplitude and kinematics – distractor located at saccade goal

The presence of a distractor at the saccade goal also had an effect on saccade kinematics, in this case increasing saccade velocity. As mentioned above, when the distractor appeared at the saccade goal it had a tendency to elicit the saccade very rapidly, with a latency typical of express saccades. Saccades initiated 60-80 after distractor appearance had a higher velocity than saccades initiated 0-25 msec after distractor appearance. This increase was highly significant for all four subjects ($p < 0.0001$, two-tailed t-test) and averaged 23.8% across all four subjects (Fig. 7).

Surprisingly, for the three subjects who initiated a considerable number of saccades >100 msec after distractor appearance, it was evident that the velocity of saccades made at longer delays decreased substantially. For each of these three subjects we compared the peak velocity of saccades in the bin at which saccades were initiated most frequently (see fig. 3) with peak velocities of the following bin. The peak velocities in the earlier bin were significantly higher for all three subjects ($p < 0.0001$, two-tailed t-test), by an average of 13.7%. In contrast, the amplitude of saccades varied little as a function of the time between distractor appearance and saccade initiation (Fig. 7).

Experiment 1b – Can distractors appearing in the lower visual field also inhibit saccades? To reduce the number of possible conditions in Experiment 1 distractors were presented only in the upper visual field. We chose the upper visual field because we surmised that, as saccade latencies to the upper visual field are generally smaller than those to the lower visual field (Goldring and Fischer 1997), the effect of suddenly appearing distractors could be stronger. Although this maneuver increased the statistical power of our analyses, it left open the
question of whether distractors in the lower visual field could also transiently inhibit saccades. To test this, we repeated Experiment 1 but instead flipped visual stimuli about the horizontal meridian so that all distractors appeared either in the lower visual field or along the horizontal meridian. The two authors served as subjects.

We found an effect on saccade likelihood very similar to that found for Experiment 1. The reduction in saccade likelihood was again similar to that found for Experiment 1, with maximum decreases of saccade initiation of 87%, 84%, and 63% for distractor / saccade goal separations of 180 deg, 90 deg, and 45 deg, respectively. These decreases were all significant ($p < 0.05$, $z$-test of proportions) for both subjects.

**Experiment 2: Do visual stimuli at the saccade goal mitigate distraction?**

The results described above show that saccades made to a blank location are inhibited by the sudden appearance of a visual distractor when it appears at a position with a large angular separation from the location of the saccade goal. On one hand, it is possible that the inhibition is an inevitable consequence of the appearance of the sudden onset. However, it is also possible that the inhibition is a net result of competition between saccade-related processes present at the saccade goal with those present at the distractor location. If so, inhibition occurs because a command to make a saccade to a blank location is simply not robust enough to resist the effect of a transient burst of activity that codes for visual stimuli or saccades to a distant location. If so, it is possible that the effects of the inhibition would be ameliorated by boosting the command signal for the intended saccade.

One way to do this is to present a visual stimulus at the goal, since it has been demonstrated that saccades to visual targets are accompanied by more activity than saccades to blank space (Edelman and Goldberg 2001; 2003) (Everling et al. 1999). We tested this possibility using two modifications of Expt. 1. First, we had subjects make a saccade to a visual stimulus that had been present at the saccade goal for several hundred msec (visually guided...
delayed saccade task, Expt. 2a), and second we had subjects make a reflexive saccade to a visual stimulus that suddenly appeared at the saccade goal (Expt. 2b). Given that a visual stimulus was now present at the saccade goal, unlike Expt. 1, we did not run trials in which a distractor appeared at the saccade goal.

**Experiment 2a – Distracting saccades made to a stable visual target** - The effect of the distractor was somewhat less strong here than for Experiment 1a, though we observed some decreases in saccade probability even for trials with a small distance (22.5 deg) between the distractor and the saccade goal (Fig. 8). Compared to the Invisible Distractor condition, the mean peak reduction in saccade probability was 74% when separation was 180 deg, 78% at 90 deg., and 65% at 45 deg, and 41% at 22.5 deg. We found significant reductions in probability of saccade occurrence at the time of the notch for 3/4 subjects at the 180 deg. separation, for all subjects at the 90 and 45 deg. separations, and for 2/4 subjects at the 22.5 deg. separation. We tested the dependence of the magnitude of inhibition on the angle of separation across the four subjects with a one-way repeated measures ANOVA on ranks (p = 0.002). Multiple comparisons showed differences between the 22.5 deg. separation and each of the other three separations. Across the four subjects, the mean half-width of the notch in saccade probability was slightly smaller for the 22.5 deg separation than the other three separations grouped together (180 deg: 35 msec, 90 deg: 37 msec, 45 deg: 37 msec, 22.5 deg: 15 msec, t-test, p = 0.025). For the smallest distractor / saccade goal separation of 22.5 deg, there was a less distinct peak of saccades at a time 80-100 msec after distractor appearance than was observed in Expt. 1. The proportion of saccades made in the 22.5 deg. condition in this time interval compared to the Invisible Distractor condition did not change appreciably, as different subjects showed varying amounts of excitation and inhibition during this time window.

As in Expt. 1a, the effect of the distractor on the endpoint of saccades elicited between 80 and 100 ms after distractor appearance was quite small, with an average distractor angular gain (as defined for Expt. 1) of 15%, 6%, and -2% for 22.5, 45, and 90 deg. separations.
respectively. Curvatures were also small (curvature index, unaffected: 0.037, 22.5 deg: 0.035, 45 deg:0.045).

Experiment 2b -- Saccade triggered by a suddenly appearing visual target  The effect of the distractor on saccade metrics was substantial, though still smaller than that found in Experiments 1 and 2a (Fig. 8). The mean peak reduction in saccade probability was 62% when separation was 180 deg, 50% at 90 deg., 49% at 45 deg, and 29% at 22.5 deg. We found significant reductions in probability of saccade occurrence at the time of the notch for 3/4 subjects at 180, 90, and 45 deg. separations, and for 1/4 subjects at 22.5 deg. separation. As in Expt. 1a, we confirmed the dependence of the magnitude of inhibition on the goal/distractor separation across the four subjects with a one-way repeated-measures ANOVA (p = 0.003). Multiple comparisons showed differences between the 180 deg separation and each of the 45 and 22.4 deg separations. The mean half-width of the notch was similar to those found in Experiment 2, though slightly less for 45 deg (180 deg: 36 msec, 90 deg: 24 msec, 45 deg: 32 msec, 22.5 deg: 16 msec). A one-way repeated measures ANOVA of notch duration across the four subjects showed a dependence on separation (p = 0.01), with significant differences found between the 22.5 deg. condition and each of the 45 and 180 deg. conditions. Unlike Expt. 1, but similar to Expt. 2a, at the smallest distractor / saccade goal separation of 22.5 deg, there was no distinct peak of saccades at a time 80-100 msec after distractor appearance.

As in Expt 1a, and 2a, the effect of the distractor on saccade endpoint in Experiment 2b was small. The average distractor angular gain (as defined for Expt. 1 and 2a) was 9%, -1%, and -1% for 22.5, 45, and 90 deg separations respectively. Saccade curvatures were similarly low (curvature index, unaffected: 0.037, 22.5 deg: 0.040, 45 deg:0.040).

Comparison of amount of inhibition across trial types – We wished to compare the size of the saccade inhibition effect for the different levels of visual activation (Learned Saccade -- Expt. 1, Visually guided saccade --Expt. 2a, Suddenly Appearing Target --Expt. 2b) at the
saccade goal. To do this we compared the magnitude and duration of the reduction of saccade probability caused by the distractor as a function of the trial type and target / distractor spatial separation across the four subjects. We conducted a two-factor repeated measures ANOVA using trial type and target / distractor separation as factors. As in all three experiments the magnitude of the inhibition was largest when the saccade goal / distractor separation was 180 and 90 deg we only considered trials with those two separations. Confirming many of the observations described above, we found a main effect of trial type (p = 0.002), as well as a significant interaction between task and separation (p = 0.035). A multiple-comparisons procedure (Student–Newman-Keuls) confirmed that the reduction was largest for the Learned saccade task (Expt. 1), intermediate in the Visually guided task (Expt. 2a), and lowest in the Reflexive saccade task (Expt. 2b). The reduction was also significantly larger for 90 deg than 180 deg in the Reflexive task, suggesting that this was the source of the interaction.

An analogous analysis of the effect of target condition and target/distractor separation on the duration of the reduction revealed a main effect with separation (p < 0.028), but not task (p > 0.3). Multiple comparisons revealed a significant increase in duration in the Learned Saccade task (Expt. 1) relative to the Reflexive saccade task (Expt. 2b).

Experiment 3 -- Does the magnitude of transient inhibition depend upon distractor size?

The results of Experiment 1 suggest that the saccade inhibition demonstrated previously during a voluntary saccade task using display-spanning stimuli can also occur using a much smaller stimulus, a bright square of 2 deg width. This raises the question of whether the effect would exist for even smaller distractors. To test this, we repeated a modified version of Experiment 1 using five different sizes of distractors ranging in width from 0.25 deg to 4 deg. Distractors were presented on 50% of trials. Distractors always appeared opposite the saccade goal. The two authors served as subjects.

We found that even the smallest distractor (0.25 deg) inhibited saccade production. Indeed, for both subjects saccade inhibition was statistically significant for all distractor sizes (p
< 0.001, z-test on proportions, Fig. 9). However, the inhibitory effect had some tendency to increase as distractor size increased, and in particular, inhibition appeared weakest at the smallest square width. Across the two subjects, the mean peak reduction in saccade probability was 62%, 70%, 81%, 77%, and 90% for the square sizes of 0.25, 0.5, 1, 2, and 4 deg, respectively. A linear regression of the peak magnitude of the probability decrease as a function of the log of the distractor size showed a significant dependence of the effect of distractor size for one subject (A2, p = 0.003) and a similar, though non-significant, trend in the other subject (A1, p = 0.13).

DISCUSSION

These results provide clear evidence that the sudden appearance of a visual stimulus distant from an intended saccade goal can almost completely inhibit the generation of a saccade from 70-100 ms after the appearance of the stimulus, regardless of the subject’s desire to make a saccade. In contrast, when visual stimuli are presented near the saccade goal, the tendency for short-latency saccades to be elicited with an extremely short latency (express saccades) increases considerably, even for the naive subjects who have had shown little tendency to make express saccades in more conventional saccade tasks. This inhibition is strongest when the saccade is made to blank space, less strong when the saccade is made to a visual stimulus that has been present for several hundred ms, and still less strong when the saccade is elicited by the sudden appearance of a visual object. Inhibition occurs even when the distracting visual stimulus is quite small (0.25 x 0.25 deg) and occurs regardless of whether the distractor appears in the upper or lower visual field. There were few trials in which no saccade was made, suggesting that this inhibition only delayed saccades, but did not abolish the saccade program completely.

One might expect that the saccades of highly motivated human subjects should not be susceptible to the inhibiting effect of distractors, given that they have a spatially defined
movement goal. Indeed, highly focused spatial attention is the one behavioral state that has been shown to mitigate attentional capture by the sudden appearance of visual stimuli (Yantis and Jonides 1990). Yet, saccades do not seem similarly impervious. This was true even for the two authors (subjects A1 and A2), who were both well-experienced in eye movement tasks. Indeed, virtually all the findings of Experiments 1, 2a, and 2b held for both the experienced and naïve subjects.

Relation to previous studies of saccade inhibition and distraction

These results extend and clarify implications from work on the “saccadic inhibition” effect of Reingold and Stampe (1999, 2000, 2002, 2003, 2004) and Stampe and Reingold (2002). These previous studies have shown that a flash of the entire display, or else presentation of a large visual stimulus flanking a central fixation point, inhibited saccades for a short period of time. The presence of such a distracting stimulus can inhibit saccades whether they are made during reading (Reingold and Stampe, 1999, 2000, 2003, 2004), visual search (1999, 200), or more conventional saccade tasks (Reingold and Stampe 2002).

Other studies have shown that the abrupt onset of behaviorally irrelevant visual stimuli can delay saccade commands even when stimuli are small. Sheliga et al (2002) demonstrated that visual stimuli flashed at the location of fixation (superimposed upon a smaller visual stimulus already present at fixation) delayed a volitional eye movement during a centrally cued double saccade task. However, they found only minor saccadic delays when a visual stimulus was presented opposite the saccade goal, but superimposed upon an already visible stimulus. We speculate that the lack of an effect of the peripheral stimulus was due to there already being a visual stimulus at that location, as well as that the distractor was somewhat small (0.8x0.8 deg). It has also been shown that small stimuli presented at or near fixation can delay saccades during scanning of a complex visual scene (Graupner et al. 2007; Pannasch et al. 2001). Reingold and Stampe (2003) found that small stimuli could inhibit saccades when superimposed
on text and when appearing away from the saccade goal. Such inhibition has also been
described in a double-step task in monkey (Sommer and Tehovnik 1999).

However, these experiments did not examine whether small stimuli, distant from the
saccade goal, could inhibit saccades in a discrete-trial task in which the saccade goal was pre-
defined. Such a saccade command should have the greatest chance at defying saccadic
inhibition. Moreover, these prior studies did not systematically examine the strength of saccade
inhibition as a function of distractor size, distractor location, and saccade task. Our results
demonstrate that saccade inhibition can occur even when there is an explicit motor plan and
when the distractor is very small (0.25 x 0.25 deg) and not present foveally. Our experiments
are also the first to show that this inhibition is contingent on the distractor being at some
distance from the saccade goal, as distractors close to the saccade goal tended instead to
immediately trigger saccades.

Work on the remote distractor effect has shown that presentation of visual distractors
prior to the execution of an impending saccade can, depending on the spatial distance between
the saccade goal and the distractor, increase saccade reaction time or influence the endpoint of
the saccade (Walker et al. 1997). Of our experiments, Expt. 2b most closely resembles those of
Walker et al. (1997) in that the goal-directed saccade was a visually guided reaction-time
saccade. Our results are consistent with theirs, since we found saccade inhibition even in this
reflexive task. We also found that in this task saccades were almost always eventually made to
the saccade goal, which is also consistent with their findings.

Moreover, like previous studies of the remote distractor effect, we found that saccades
were much more likely to be delayed when distractors were presented far from the saccade goal
than when presented close to the saccade goal. However, unlike the present study, these
previous studies did not systematically vary the timing of the distractor, and thus could not
assess the precise temporal nature of the impact of distractors on saccade initiation. Our results
reveal that the remote distractor effect may, in large part, be a result of the short-duration inhibition of the saccade system shown here.

**The effect of distractors on saccade vector and kinematics**

Another similarity between our results and those on studies of the remote distractor effect is that distractors, even when close to the saccade goal, had little effect on saccade direction. However, the present result is more surprising given that the distractor tended to trigger the saccade very rapidly, such that the saccade had latencies in the express saccade range. This finding suggests that while the sudden visual appearance of the distractor triggers the saccade, the vector of the movement is still governed by the voluntary saccade command.

Our findings suggesting that the sudden appearance of visual distractors can prematurely terminate a saccade suggests that the influence of the distractor is not confined to simply determining whether a saccade is initiated or not, but can affect a saccade in progress. This adds further evidence to the idea that saccades, even in mid-flight, are still susceptible to competing saccade programs and new sensory events. (Becker and Jürgens 1979; McPeek 2006; McPeek and Keller 2002; McPeek et al. 2000; Port and Wurtz 2003).

When the distractor was near the saccade goal in Experiment 1, we found that saccades that appeared to be visually driven (i.e. made 70-100 ms after distractor appearance) tended to have higher velocities than when the saccades were unaffected by the distractor. This is not surprising, given that visually guided saccades tend to be faster than non-visually guided saccades (Edelman and Goldberg 2001; Edelman et al. 2006; Gnadt et al. 1991; Ohno et al. 2000; Smit and Van Gisbergen 1989; Smit et al. 1987; Van Gelder et al. 1997). However, we also found that velocities of saccades dropped somewhat as the interval between distractor and saccade initiation further increased. This would suggest that ultra short-latency saccades like express saccades might be slightly higher in velocity than saccades of slightly longer latency. We know of no study in human that has directly assessed this, though a study in monkey
showed that velocity of express and “regular” latency saccades were similar (Edelman and Keller 1996).

What is the role of saccadic inhibition in natural oculomotor behavior?

Although saccadic inhibition is now well documented, in the real world our strong sense is that the sudden appearance of a salient visual stimulus will draw the eye towards it. This has been demonstrated in studies of oculomotor capture, where a suddenly appearing visual stimulus can elicit a saccade to itself even though it is irrelevant to the task (Theeuwes et al. 2003; Theeuwes et al. 1999). Why are such saccades not observed in studies of saccadic inhibition? First, the distractors may be too large, even spanning the entire visual display (Reingold and Stampe 2000; Reingold and Stampe 2004; 2002; Reingold and Stampe 1999; Stampe and Reingold 2002), such that there is no distinct visual stimulus that can serve as a target. In the real visual world, objects are of modest visual extent, such as a car appearing from out of a hidden driveway, or an animal from behind a bush. Second, there may be a pre-defined saccade goal, as in the present study as well as previous studies (Walker et al. 1997)(Reingold and Stampe, 2002)(Sheliga et al. 2002). In contrast, in the real world there is generally no explicit, pre-defined saccade command. Third, distractors in saccadic inhibition tasks may not be highly salient, such as when they are presented within a cluttered visual field of text (Reingold and Stampe 2003). In such a case, their appearance may be sufficient to inhibit a saccade, but their level of salience may be insufficient to trigger a saccade to themselves. Finally, the distractor may appear too close to fixation to effectively elicit a saccade (Sheliga et al. 2002) (Graupner et al. 2007; Pannasch et al. 2001). Given these contrasts between laboratory scenarios and visual ecology, it is not clear whether saccade inhibition is a commonplace occurrence during natural oculomotor behavior.

The neurophysiology of saccade inhibition

Regardless of its natural frequency, the phenomenon of saccadic inhibition can serve as a useful tool for increasing our understanding of neural mechanics of oculomotor control
(Reingold and Stampe 2002). Our results provide a human behavioral counterpart to the recent neurophysiological study of Dorris et al. (2007) in macaque superior colliculus which showed that the appearance of a remote distractor far away from a saccade goal can cause a transient decrease in low-frequency activity in the deeper layers of the superior colliculus, while distractors appearing near the saccade goal increased activity, often resulting immediately in a saccade. A similar pause in collicular activity was found during a cued saccade task when a visual stimulus located at fixation changed shape (Li et al. 2006). A simple explanation of our findings and these physiological results is that the transient burst of visual activity temporarily inhibits neurons whose response fields are remote from the distractor. The duration of the high-frequency transient visual burst tends to be on the order of tens of milliseconds (Sparks and Hartwich-Young 1989), similar to the notch seen in our histograms of saccade initiation and pauses in low-frequency activity observed in neurons in the superior colliculus (Dorris et al. 2007; Li et al. 2006).

In contrast, recordings in the monkey lateral interparietal area (LIP) indicate that a behaviorally irrelevant distractor results in a contralateral visual transient, but has no inhibitory effect ipsilaterally (Bisley and Goldberg 2006; Powell and Goldberg 2000). This difference between collicular and LIP activity suggests that inhibition operates at the collicular level, as has been suggested previously (Reingold and Stampe 2002; Walker et al. 1997). Indeed, one might speculate that areas such as LIP, and possibly the frontal eye fields, maintain a voluntary saccade command signal even in the face of a visual distractor, but can only execute this command after the contralateral visual transient has died down.

It is unclear how these inhibitory influences are mediated across saccade motor maps. Whereas there has been speculation that intracollicular connections could play such a role (Munoz and Istvan 1998), at least for mediating competitions that existed in just one hemifield (and that thus map out to only one colliculus), recent evidence suggests that the kind of long-
range inhibition observed here could not be mediated by intrinsic collicular connections, and thus must rely on inputs from other, perhaps cortical, areas (Lee and Hall 2006).

We found that the effect of the remote distractor was weaker, though still quite evident, when a visual stimulus was present at the saccade endpoint (Expt. 2a), and still weaker when the goal-directed saccade was itself reflexive (Expt. 2b). This suggests that when the distractor is distant from the saccade goal, the voluntary saccade command and the distractor compete for access to the saccadic system. In our Experiment 1, a visual transient competed against the low-frequency activity induced by the command to make a voluntary saccade a blank location. Increased activity at a site on the map corresponding to the saccade goal due to the presence of a visual target (Experiment 2a), and further increases due to the actual appearance of a visual stimulus at the saccade goal (Experiment 2b), would further bias this competition toward the saccade goal, making the goal-directed saccade less and less prone to competition from the distractor. This is in accordance with the findings of Reingold and Stampe (2002) who showed that saccade inhibition was stronger when the goal-directed movement was an anti-saccade, in which no visual stimulus is present at the saccade endpoint, than when the goal-directed movement was a pro-saccade, and also stronger in an overlap task than in a gap task.

When a visual target was present at the saccade goal, we found less of a facilitatory effect for distractors appearing at a small (22.5 deg) angular distance from the saccade goal, than when no target was present at the saccade goal. This effect could be the result of inhibition of activity at this location by visual-related activity present at the saccade goal. Such flanking inhibition has been demonstrated in the frontal eye fields (Schall and Hanes 1993) and the superior colliculus (Li and Basso 2005).

It has been long known that only lesions of both the superior colliculus and frontal eye fields can completely eliminate saccades in monkey, whereas lesions of either structure alone does not cause a permanent loss in the ability to make saccades (Schiller et al. 1980). However, lesions of the superior colliculus, but not the frontal eye fields, wipe out express
saccades, the shortest latency saccades (Schiller et al. 1987). This finding has led to much speculation that short-latency saccades are generated by the superior colliculus whereas longer latency saccades are generated by the frontal eye fields and perhaps other cortical structures, though the pathway by which saccade-related signals reach the brainstem saccade generator without passing through the superior colliculus remains uncertain (Stanton et al. 1988). If this were true then one could think that a strong motivation to make a voluntary saccade should not be affected by an irrelevant remote distractor. If, as has been suggested, the distractor effects that we and others have found are mediated by the superior colliculus (Dorris et al. 2007; Reingold and Stampe 2002; Walker et al. 1997), then our findings suggest that the superior colliculus interferes with the production of voluntary saccades, and thus, at least in the intact human brain, the superior colliculus lies in the final common pathway for the generation of saccadic eye movements, whether they be reflexive or voluntary.

REFERENCES


**FIGURE LEGENDS**

Figure 1. Schematic of Expt. 1. Trials began with the appearance of a central fixation point in the form of an arrow indicating the desired direction of the upcoming saccade. The desired amplitude of the saccade was 10 deg. The disappearance of the arrow was the cue to make a saccade. At a time between this cue and the initiation of a saccade, a distractor could appear. To provide feedback on the accuracy of the saccade, a visual stimulus appeared at the saccade goal after the saccade landed. For more details see text.

Figure 2 – Schematic of analyses of saccadic inhibition effect. For each subject’s data for a particular target/distractor separation, a density function estimating saccade probability was calculated. This curve was then compared to an analogous one calculated for trials in which the distractor was invisible. We estimated the maximum decrease in saccade probability over time for each set of distractor trials relative to the Invisible Distractor trials, as well as the duration of
this reduction in probability. We also calculated the time of peak saccade occurrence. For more details see text.

Figure 3 – Histograms for Expt. 1 showing occurrence of saccades as a function of the interval between target disappearance and saccade initiation for two subjects. As a reference, at top are shown trials in which the distractor was not visible. Below this are histograms of data for each target/distractor separation, with leftward and rightward saccades grouped together.

Figure 4 – A) Probability density functions for different target/distractor separations are shown for one subject. As a comparison, these curves are each superimposed with the corresponding curve from Invisible Distractor trials. B) Maximum decreases in saccade probability are shown for the five target/separations for each of the four subjects. A value of 0% indicates that no distinct notch was found. C) Time of peak probability of saccade occurrence is shown for each of the five target/distractor separations and for each of the four subjects.

Figure 5 -- Plot of saccade amplitude as a function of the time between distractor appearance and saccade initiation for two subjects for Experiment 1. Data are from trials in which the distractor appeared opposite the saccade goal. Each dot corresponds to data for one saccade. The lines denote binned averages where the bins were of 20 ms width. Binned averages are shown only if there were at least six saccades in the bin.

Figure 6 -- Plot of mean radial saccade velocity as a function of time for two subjects in Experiment 1, showing mean velocity both for saccades that were unaffected by the distractor and those that had relatively small amplitudes (N2: < 5 deg; A2 < 7.5 deg). Data are from trials in which the distractor appeared opposite the saccade goal (180 deg. saccade goal / distractor separation).
Figure 7 – Plot of mean peak saccade velocity as a function of time of saccade initiation relative to the appearance of distractor for Experiment 1 for trials in which the distractor appeared at the saccade goal (0 deg. saccade goal / distractor separation). The symbols and lines represent 20 msec-width binned averages. Data for a particular bin are shown only if there were at least six saccades in the bin.

Figure 8 – Histograms of saccade occurrence for subject A2 for each target/distractor separation for Experiment 2a (left) and Experiment 2b (right). Other conventions as in Fig. 3A. B) Maximum decreases in saccade probability for Experiment 2a (left) and Experiment 2b (right). Other conventions as in Fig. 4B.

Figure 9 – Histograms of saccade occurrence for subject A1 for each target/distractor separation for Experiment 3. Other conventions as in Fig. 3A. B) Maximum decreases in saccade probability as a function of distractor size for Experiment 3.
Figure 1

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- **500-800 ms fixation period**
- **Distractor appears at 0 to ~160 msec prior to saccade**
- **Saccade initiated**
- **Visual feedback stimulus appears at saccade goal**
- **Distractor appears at 0 to ~160 msec prior to saccade**
- **500-800 ms fixation period**
Figure 2

Probability

Distractor - saccade interval (msec)

Maximum drop

Duration of drop
Figure 3

Number of saccades

Time between appearance of distractor and beginning of saccade (msec)

Invisible Distractor

0 deg

22.5 deg

45 deg

90 deg

180 deg

N1

A1

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Figure 4

A

Saccade probability

Target / distractor separation (deg)

Maximum probability reduction (%)

Time of peak probability of saccade occurrence (msec)

Saccade to blank location

B

C

Target / distractor separation (deg)

Time between appearance of distractor and beginning of saccade (msec)
Distractor opposite saccade goal

Saccade amplitude (deg)

N1

A1

Time between distractor appearance and saccade initiation (msec)
Distractor opposite saccade goal

Saccade radial velocity (deg/s)

N2

Small amplitude (terminated prematurely)

A2

Normal amplitude (unaffected by distractor)

Time relative to saccade initiation (msec)
Fig. 7

Distractor at saccade goal

![Graph showing peak saccade velocity (deg/s) over time between distractor appearance and saccade initiation.](attachment:graph.png)

- N1
- N2
- A1
- A2
A. Visually guided delayed saccade

- For each target/distractor separation (22.5, 45, 90, 180 degrees), the number of saccades is plotted against the time between the appearance of the distractor and the beginning of the saccade (msec).

B. Maximum probability reduction (%)

- Visually guided delayed and reflexive saccades are compared for each target/distractor separation (22.5, 45, 90, 180 degrees).
Figure 9

A

Invisible Distractor

Square Width:

0.25 deg

0.5 deg

1 deg

2 deg

4 deg

Time between appearance of distractor and beginning of saccade (msec)

Number of saccades

0 50 100 150 200

0 20

B

Maximum probability reduction (%)

0.25 0.50 1.00 2.00 4.00

Distractor size (deg)

0 50 100 150 200

0 20

A1

A2