The influence of onsets and offsets on saccade programming

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Abstract. When making a saccadic eye movement to a peripheral target, a simultaneous stimulus onset at central fixation generally increases saccadic latency, while offsets reduce latency ('gap effect'). Visual onsets remote from fixation also increase latency ('remote distractor effect'); however, the influence of remote visual offsets is less clear. Previous studies, which used a search task, found that remote offsets either facilitated, inhibited, or did nothing to saccade latencies towards a peripheral target. It cannot be excluded, however, that the target selection process in such search tasks influenced the results. We therefore simplified the task and asked participants to make eye movements to a predictable target. Simultaneously with target onset, either one or multiple remote stimulus onsets and offsets were presented. It was found that peripheral onsets increased saccade latencies, but offsets did not influence the initiation of a saccade to the target. Moreover, the number of onsets and offsets did not affect the results. These results suggest that earlier effects of remote stimulus offsets and of the number of remote distractor onsets reside in the target identification process of the visual search task rather than the competition between possible saccade goals. The results are discussed in the context of models of saccade target selection.

Keywords: eye movements, remote distractor effect, saccadic response times

1 Introduction

Studies of oculomotor control have consistently found that the latencies of saccades initiated towards a peripheral target are reduced if the stimulus at fixation is extinguished around the time that the target appears (Saslow 1967; Rolfs and Vitu 2007). Moreover, the offset of a fixation stimulus has been shown to increase the number of so-called 'express saccades', which have a short latency around 100 ms (Fischer and Boch 1983; Fischer and Weber 1993). The reduction in latency with fixation offsets ('gap effect') has been attributed to the disappearance of the stimulus acting as a warning signal, especially when presented slightly before target onset, by providing a temporal cue about the onset of the visual target (Reuter-Lorenz et al 1995; Ross and Ross 1980). The offset of a visual fixation stimulus is also thought to reduce activity in neurons involved in maintaining fixation (Munoz and Wurtz 1993a, 1993b). The reduction of activation at fixation is expected to result in a faster initiation of a saccade to a target, both because of a reduction of lateral interactions between the activity at fixation and at the target position, allowing for target activity to reach a critical threshold earlier (Trappenberg et al 2001), and because fixation is released even in the absence of lateral inhibition, with the consequence that fixation activity drops below a critical threshold more quickly, allowing for a faster onset of the saccade (Findlay and Walker 1999). By contrast, saccade latency is increased when a visual onset appears remote from the target location, with the greatest increase observed for onsets occurring around the time the target is presented [Walker et al (1995); however, see Bompas and Sumner (2009)]. This so-called 'remote distractor effect' (RDE) appears to be an automatic process, as it also occurs in situations where the target location is known in advance and, as a consequence, the

saccade planning process does not involve discriminating between the target and distractors (Walker et al 1995).

Given these results, the question arises whether the offset of distractors remote from the saccade target will produce a similar facilitation effect as observed for visual offsets at central fixation, or whether, instead, they increase latencies, just like remote distractor onsets. Faster responses could be expected, as there is no a priori reason why the offset of a peripheral stimulus would not provide a temporal cue to indicate the onset of the target and would not lead to a reduction of competition in the oculomotor map. Furthermore, it has been suggested that the inhibitory influence of fixation neurons, thought to be involved in the gap effect, extends beyond the immediate fixation region to at least 10 degrees from fixation (Dorris et al 2007; Gandhi and Keller 1999; Walker et al 1997), and therefore remote 'gaps' could have similar effects as stimulus offsets at fixation. In fact, evidence for a facilitation of saccadic responses in the presence of irrelevant peripheral offsets was obtained in a study comparing the effects of either one or seven offsets on goal-directed saccades (Todd and van Gelder 1979). Even though the target stimulus could be presented at only one of two possible locations in both conditions, the additional six irrelevant offsets resulted in a decrease of saccadic latencies to the target (see also, Rolfs and Vitu 2007). In addition, the offset of an attended peripheral stimulus, located away from a central fixation stimulus, has been shown to facilitate the production of short latency 'express saccades' (Braun and Breitmeyer 1988; Mayfrank et al 1986). The observed reduction in latency and increase in the frequency of express saccades are consistent with remote visual offsets acting as a temporal cue and reducing fixation-related activity which, otherwise, would have inhibited saccade initiation.

Studies investigating the influence of distractor onsets and offsets in 'oculomotor capture' paradigms have, however, produced conflicting findings regarding the effects of distractor offsets. In such paradigms, the focus is not on whether irrelevant stimuli increase or reduce saccade latencies, but instead, whether stimuli unrelated to the task 'capture the eyes', ie induce an eye movement to the distractor stimulus rather than the target. Typically, a search paradigm is used, in which participants have to locate a target among a set of distractors. For example, Boot et al (2005) investigated oculomotor capture by task-irrelevant onsets and offsets when participants searched for a target letter among an array of distractors. Simultaneously with target onset, a new letter was presented or one of the already present distractors was removed. Whereas the appearing distractor captured the eyes in about 30% of the trials, no such oculomotor capture occurred for disappearing distractor items. Moreover, saccades to the target, when the eye was not captured by the distractor, were delayed for distractor onsets, but not for offsets. By contrast, similar, strong effects of distractor onsets and offsets were found in a search task in which participants were required to make an eye movement to a target that changed contrast (Ludwig et al 2008). Compared with baseline, in which no distractor was present, larger numbers of incorrect initial saccades were observed both to onsets and offsets, in addition to longer saccadic latencies to the target on trials where the distractor was successfully ignored. To summarise, remote offsets have either been shown to reduce latencies (Todd and van Gelder 1979; Rolfs and Vitu 2007), to increase latencies (Ludwig et al 2008), or to not affect latencies (Boot et al 2005).

Studies investigating the effects of remote stimulus offsets so far have relied on saccade tasks in which the target had to be located among a set of distractors. In contrast, studies investigating the effects of remote distractor onsets have shown robust influences on latency also under conditions in which there is a clearly defined saccade goal (Edelman and Xu 2009; Walker et al 1997). The question arises whether the effects of remote offsets are restricted to a saccade selection task, or whether they also occur when the target is highly

predictable, just as in the RDE. We investigated this issue by presenting remote visual distractor onsets and offsets in a remote distractor paradigm with a fixed target location. Participants were presented with a predictable target to which they had to make an eye movement. Simultaneously with target presentation, one or more distractor stimuli appeared or disappeared from the screen.

Besides comparing onsets and offsets, the experiment also investigated whether the number of distractors influences the size of the RDE. Previous research found that when the number of irrelevant distractor onsets in a visual search task is increased, saccadic latencies to the target become longer (McSorley and Findlay 2003). However, it is not clear whether this effect of the number of distractors is due to increased uncertainty about the target location, or whether the additional distractors impose stronger inhibition on target-related signals in the saccade motor map. By varying the number of distractors for a predictable saccade target, it can be established whether more distractors automatically result in stronger inhibition, or whether these distractors need to be possible saccade goals for the effect to occur.

2 Methods

2.1 Participants
Twelve participants (1 male, 11 female, age range 18–40) took part in the experiment. Two of the participants were the authors, whereas the others were students at Royal Holloway, University of London, naive to the purpose of the experiment, who participated for course credit. All participants reported normal or corrected-to-normal vision. Before the experiment, participants were informed about the general purpose of the experiment after which they signed a consent form. The study was approved by the Royal Holloway Psychology Department's local ethics committee.

2.2 Apparatus
A 2400 AMD Athlon PC and the experimental builder software package (SR Research Osgood, ON, Canada) presented the stimuli on a 21 inch CRT screen with a refresh rate of 100 Hz. Eye movements were recorded with an Eyelink II (SR Research Osgood, ON, Canada) video-based eye tracker in pupil only mode at 500 Hz. Eye movements of the right eye were analysed.

2.3 Stimuli
Figure 1a illustrates the stimulus sequence (in reverse contrast), showing, in this particular example, a trial with the target appearing on the left together with three distractor onsets or offsets. Illustrations of target screens for other numbers of onset and offset distractors are shown in the figure 1b. Stimuli were presented in white on a black background. On onset trials (figure 1a, top-left), the fixation cross (0.3 deg of visual angle in width and height) was presented in isolation and, after a variable delay (between 1200 and 1600 ms), the target (a triangle of 0.4 deg in width and height) appeared at a distance of 5.7 deg from the centre of the screen. Simultaneously with the target, one, two, or three distractors (filled circles of 0.4 deg in diameter) appeared, also at 5.7 deg from the centre of the screen, at any of four positions (left, right, above, or below fixation) not occupied by the target. In the offset condition, three distractors were presented simultaneously with the fixation symbol and one or more disappeared when the target was presented (figure 1a, top-right). A blank screen presented for 1000 ms separated the trials.

2.4 Design
In half of the trials, the distractors appeared together with the target (onset trials), and in the other half of the trials, the distractors were presented together with the fixation cross, but they were removed from the screen at the moment the target appeared (offset trials). The number of distractors that could appear or disappear was equal to zero, one, two, or

Onset condition   Offset condition

(a)

Other stimulus screens

1 onset / 2 offsets

2 onsets / 1 offset

(b)
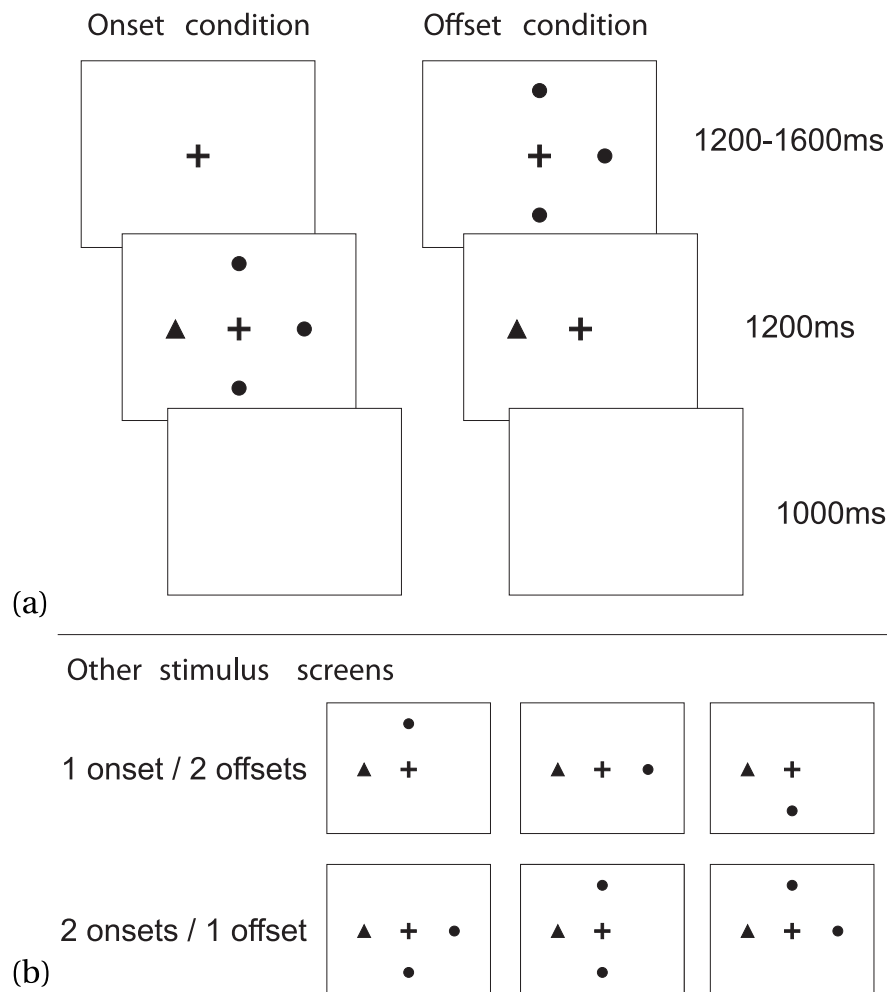
Figure 1. (a) Illustration of the stimulus sequence in the distractor onset (left) and offset (right) conditions (shown in reverse contrast). In the onset condition, a fixation symbol, presented in isolation, was followed by a predictable saccade target (the triangle on the left) and one, two, or three distractor stimuli (filled circles). In the offset condition, the distractors were presented simultaneously with the fixation symbol after which one, two, or three distractors were removed when the target appeared. (b) Possible target stimulus screens for one and two distractor onsets and offsets.

three. In the case of one or two appearing or disappearing distractors, the position of the distractors was varied across conditions such that each position was occupied equally often. In half of the trials, the target appeared on the left of fixation; in the other half, on the right of fixation. Each combination of trial type (onset, offset), number of appearing or disappearing distractors (zero, one, two, or three), and target location (left, right) was presented three times per block. The order of the trial types and the number of appearing or disappearing distractors was randomised. The direction of the target (left or right), however, was kept constant during each half of the block. Each participant performed three blocks, resulting in nine repeated measurements per stimulus combination per participant.

2.5 Procedure

Participants were tested individually. They were seated at a distance of 57 cm from the computer screen with their head position restrained by a combined forehead-and-chin rest. They were instructed to look at the fixation cross in the centre of the screen until the onset of the target (triangle) stimulus at a predefined location left or right of fixation.

Before each experimental block, the nine-point calibration procedure of the Eyelink II system was performed, in which participants were asked to fixate each of the calibration dots presented in sequence on the computer screen. The calibration was repeated until the recorded eye positions were aligned to the three-by-three grid on which the calibration points were presented. The three experimental blocks were preceded by a practice block of twelve trials. In the first half of each block the target always appeared on one side of fixation (left or right), and in the other half of the block on the other side. The side on which the target was going to appear was indicated before each half of the block by a text message on the screen, after which a drift correction was performed, in which participants looked at a centrally presented dot and pressed the spacebar of the computer keyboard to correct for influences of small head movements on the recorded eye position. Blocks (practice and experimental) were separated by a short break. The experiment took about 20 mins to complete.

2.6 Data analysis

Trials with first saccades in the opposite direction of the target, with a first saccade amplitude of less than 2 deg, of more than 8 deg (overshoots) and with a vertical deviation of more than 2 deg were excluded from the data analysis as well as trials in which the first saccade contained a blink and saccades with response times faster than 80 ms (anticipations) and slower than two times the standard deviation above the mean. These criteria led to the exclusion of on average 11.89% of the trials per participant (3.36% for too fast and 1.56% for too slow response times, 5.10% for too short and 2.37% for too long saccade amplitudes; categories not mutually exclusive). In only 2.49% of the trials, the saccade was excluded uniquely because it was in the wrong direction (either it was in the opposite direction or it deviated too much from the horizontal). Visual inspection showed that most of these saccades were made by a small number of participants and that direction errors were mostly due to the vertical component of the saccade being slightly above threshold. Moreover, if a saccade was directed towards one of the remaining three directions (eg leftward, upward, or downward, for a rightward target), only in about half of the cases (0.75% of all trials) it was targeted at a distractor onset or offset, whereas in the other cases the direction seemed to be unrelated to stimulus presentation. This suggests that oculomotor capture occurred only sporadically.

2.7 Results

Figure 2 shows the saccadic latencies to the target as a function of the number of distractor onsets (green circles) and offsets (red diamonds). For onsets, longer latencies were found when one or more distractors were presented, compared with the no-distractor baseline condition (number of distractors = 0). For offsets, no differences were found between the conditions. These observations were confirmed by a two (onset / offset) by four (number of distractors) repeated measures ANOVA, showing a significant main effect of the number of distractors ($F(3,33) = 7.58$, $p = 0.001$), a significant main effect of the type of change (onset / offset; $F(1,11) = 16.25$, $p = 0.001$), and a significant interaction ($F(3,33) = 4.87$, $p = 0.007$). Posthoc tests revealed a significant effect of the number of distractors for the onset condition ($F(3,33) = 13.46$, $p<0.001$), with the fastest response times for the no-distractor condition ($F(1,11) = 25.93$, $p<0.001$). Response times did not differ significantly across the one, two, and three distractor conditions ($F(2,22) = 2.40$, $p = 0.11$). For offsets, latencies were not influenced by the distractors ($F(3,33) = 0.35$, $p = 0.79$).

To investigate whether the increased response times for the distractor conditions were due to a selective reduction of latencies within a particular range, the response time distributions for each of the conditions were compared (figure 3). A similar comparison was also made for the offset conditions. The top two plots of figure 3a show the response time distributions for each of the conditions. These distributions were obtained by sliding a 'window' of 100 ms
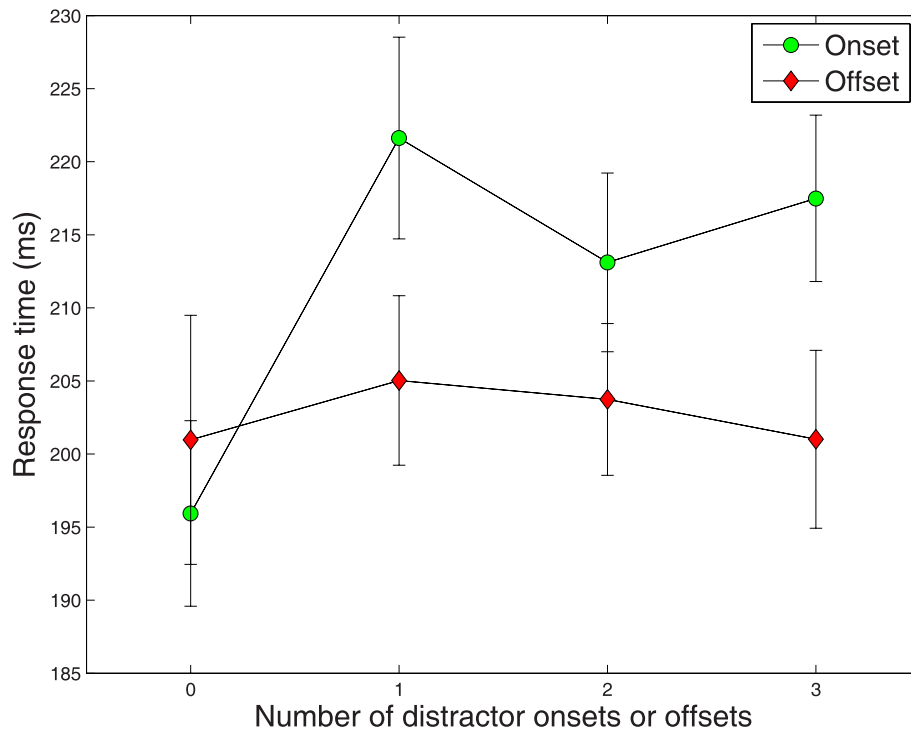
Figure 2. Average response time as a function of the number of distractors that were onset (green circles) or offset (red diamonds). Error bars show the standard error of the mean across 12 participants.

across the time line in steps of 2 ms and by determining the average number of observed saccades latencies within the window. In the middle two plots (figure 3b), the difference of the distributions between the distractor conditions and the respective baseline conditions (no distractor for onsets, all distractors remaining for offsets) is shown. For both distractor onsets and offsets, a reduction in the number of faster saccades (around 120–160 ms) appears to occur, indicated by the shift of the distribution towards higher values in the top two plots and the dip in the middle two plots of figure 3. Although both onset and offset distractors show a shift towards longer latencies in the conditions with distractors, the inhibition of short latency saccades appears to be much more pronounced for onsets than for offsets. This observation is confirmed by an analysis of the Vincentiles (Ratcliff 1979), which were computed for each participant separately and then averaged. When the Vincentiles for the no-distractor and distractor conditions are compared (figure 3c), a clear shift towards higher values is found for distractor onsets, exceeding the size of the 95% confidence intervals (horizontal and vertical lines around the data points). For offsets, no such shift is observed.

3 Discussion

The present results demonstrate that when the saccade target location is known in advance, an RDE for stimulus *onsets* occurs, resulting in a slower initiation of eye movements to the target in the presence of a distractor, an effect that mainly affected the short latency saccades (Buonocore and McIntosh 2008; Walker et al 1997). By contrast, peripheral *offsets* did not increase or decrease latencies compared with the single target situation. Furthermore, single distractor onsets were equally disruptive to target-directed saccades as were multiple distractors. Our results agree with earlier findings by Boot et al (2005), but are in contrast to those of Ludwig et al (2008), Todd and van Gelder (1979), and Rolfs and Vitu (2007), who showed that distractor offsets can influence saccadic latencies. They are also inconsistent with the results by McSorley and Findlay (2003), who did find an effect of the number of
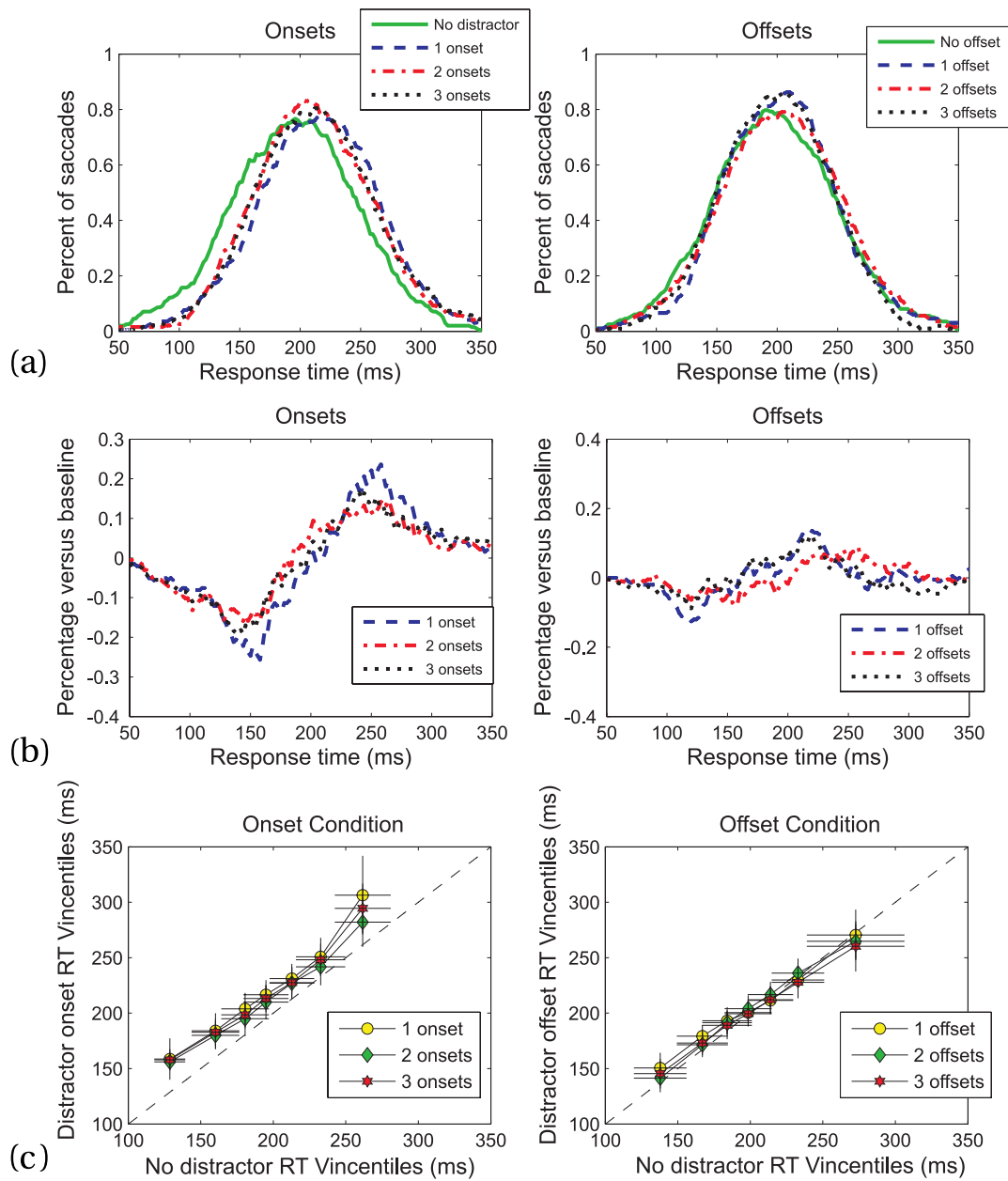
Figure 3. (a) Response-time distributions for the distractor onset (left) and distractor offset conditions (right). (b) Difference of the response-time distributions for the conditions with distractors and those without distractors. To align the distributions across participants, the individual mean response time for each condition was subtracted from each of the response times in that condition for that participant. The data were then pooled across participants, and the overall mean across participants was added to restore the original mean response time for each of the conditions. The response time distributions were obtained by sliding a window (100 ms wide) across the time line and by counting the number of saccade latencies within the window. (c) Comparison of Vincentiles [computed using the Matlab script kindly provided by Trisha van Zandt at http://maigret.psy.ohio-state.edu/~trish/ Downloads/matlab/index.html (Ratcliff 1979)] for the no-distractor onset (left) or no-distractor offset (right) conditions, with the conditions in which distractor onsets or offsets occurred. The horizontal and vertical bars surrounding the symbols indicate the width of the 95% confidence interval. The dashed line represents the values for which there are no differences in the positions of the with and without distractor Vincentiles.

(onset) distractors. Our observations confirm the different roles of onsets and offsets and of irrelevant stimuli at fixation and those in the periphery for oculomotor preparation.

The present findings have implications for models of saccade target selection (eg Findlay and Walker 1999; Trappenberg et al 2001). Most models assume that possible saccade goals are represented in an oculomotor map, consisting of a layer of neurons each coding a possible saccade target location. When a stimulus is presented, the location in the map associated with a response to that location is activated, preparing the system for a saccade to the visual onset. The intention to shift gaze to a particular target results in top-down enhancement of target-related activity and the inhibition of nontarget activity. Moreover, when multiple stimuli are present, lateral inhibition operates between populations of neurons coding for competing saccade goals to ensure that only one saccade goal is represented at the moment the decision is made to initiate a saccade. Although all models assume some sort of oculomotor map, there are differences. For example, models differ in their assumptions on the dimensionality of the map,[1] either using a 2D map (Arai and Keller 2005; Meeter et al 2010), an array of neurons (Trappenberg et al 2001; Ludwig et al 2007), or single neurons coding for target and distractors, as in rise-to-threshold models (eg Carpenter and Williams 1995). They also differ in their assumption on what triggers the saccade, being either the saccade target neuron reaching threshold (Carpenter and Williams 1995; Godijn and Theeuwes 2002, 2004; Ludwig et al 2007; Trappenberg et al 2001), or fixation-related activity dropping below threshold (Findlay and Walker 1999). Other differences include the extent of lateral inhibition between neurons (short-range or long-range), whether saccades are made to the maximum peak of activation or a weighted average, and whether a winner-take-all criterion is applied.

It has been proposed that distractor onsets can exert an influence on saccade initiation in two ways (Cruickshank and McSorley 2009; Walker et al 1997). The first involves a direct interaction between target-related and distractor-related activity operating via long-range (intercollicular) interactions (Trappenberg et al 2001). The second possibility is that distractors indirectly influence saccade initiation by influencing fixation activity, which then influences target activity, for which shorter range connections would suffice (Findlay and Walker 1999). For distractor onsets, evidence was obtained that the second process (involving fixation activity) dominates the influence of distractors on saccade latencies (Cruickshank and McSorley 2009; Walker et al 1997). Our results suggest that such processes are not evoked by stimulus offsets and are therefore unique to newly appearing stimuli.

The lack of an effect of remote distractor offsets can be understood as follows. The initial onset of the stimulus array (containing distractors and a fixation point) results in the automatic activation of neurons in the oculomotor map. However, activity at the distractor sites may be suppressed because of the instruction to maintain fixation rather than to saccade towards one of the distractors. In this respect, remote offset distractors differ from those presented at fixation, as in the gap effect, for which activation can be assumed to have remained (in order to maintain fixation). When the target appears following the fixation foreperiod, activity at the distractor sites has been suppressed to baseline, and therefore a reduction of activity, as in the gap effect, is no longer possible. As a consequence, saccade latencies will not be influenced by the offset of the remote distractors.

An alternative explanation involving top-down effects is also possible. Remote offsets may result in a slower initiation of saccades towards the target only when the target is also defined by an offset.[2] Such a prediction would be consistent with the contingent capture hypothesis, which states that capture of attention is contingent on the top-down settings of

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[1] The choice of a lower dimensionality of the map is mostly for practical purposes, ie to reduce the computational complexity of the simulations.

[2] The authors thank Casimir Ludwig for suggesting this alternative explanation.

the observer [eg when the observer is looking for a red target, only red distractors will have an effect (for a review of such effects see Theeuwes et al 2010)]. Following this hypothesis, onset distractors in our study had an effect because the target was defined as a stimulus onset. If it could be demonstrated that remote offset distractors affect saccades to target offsets, while remote onsets do not influence such saccades, this would provide further support for the role of top-down information in oculomotor programming (Born and Kerzel 2009).

The question remains why discrepancies have been found among the effects of distractor offsets in the different studies. The findings from the present RDE study and the oculomotor capture study of Boot et al (2005) are similar in that offsets had no effect on saccade latencies. By contrast, Ludwig et al (2008) reported similar effects of onsets and offsets. This difference in results between studies could relate to differences in the relative strengths of the target-related and distractor-related activity (see also Born and Kerzel 2008). In the current study, targets were defined by a sudden onset, which might have provided a relatively strong signal in the oculomotor map. Moreover, target position was known in advance, which could have led to some advance activation at the site where the target was expected to appear. Similarly, Boot et al used a colour change to indicate the saccade target, which might have resulted in a stronger activation in the oculomotor map than the contrast changes used by Ludwig et al (2008), where distractor offsets mainly affected saccade planning when the target contrast change was small. The relatively strong target signals in the present study and Boot et al might have been immune to offsets, assuming that they have weaker effects than onsets. In contrast, for weak contrast changes, the target signals in Ludwig et al could be influenced by the offset signals. This explanation would also account for Boot et al's finding that partial onsets did not result in slower saccade latencies, possibly because the weak signals from the partial distractor onset were not able to compete with the strong signal from the target. Note, however, that this does not explain why Ludwig et al (2008) did not find any quantitative differences between the effects of distractor onset and offsets.

The difference between the present results and those by Todd and van Gelder (1979) and Rolfs and Vitu (2007), who reported faster response times with distractor offsets, could be related to the choice aspect involved in the latter two studies. Because participants had to decide at the moment the target was presented where to look (eg to the near or the far target), distractor offsets might have aided the choice, because they removed stimuli that could have been possible targets and therefore might have interfered with the selection process. Moreover, the choice aspect in these studies resulted in relatively long response times, compared with those in the present study. A possibility is, therefore, that latency facilitation effects were not produced by offsets in the present study, simply because participants were already making very fast responses, which could have excluded the possibility to respond even faster (ie a floor effect may have occurred). Furthermore, a warning effect from the distractor offsets might have been absent because target and distractors were presented simultaneously, leaving insufficient time to process the distractor offsets for them to act as a temporal cue. Note, however, that such explanations are difficult to reconcile with the results by Ludwig et al (2008), who showed a general *increase* in response times due to distractor offsets.

In the present study the number of distractor onsets had no effect, in contrast with findings from an earlier study by McSorley and Findlay (2003), who noted such an effect. This difference suggests that the origin of the effect of number of distractors in McSorley and Findlay (2003) resides in the search task that participants performed, which required a decision process to determine where the target was located. The present results suggest that the automatic activation of the oculomotor map following the sudden appearance of multiple distractors influences activity coding for the target to the same extent as for a single

distractor. The implication that the distractor effects are relatively immune to the distribution and strength of activity in the oculomotor map remote from the target and from fixation agrees with findings showing relatively weak effects of distractor contrast [Born and Kerzel (2008); however, see Bompas and Sumner (2009)] on the remote distractor effect as well as weak effects of the size and contrast of a distractor (Hermens and Walker forthcoming) on saccade trajectories towards a peripheral target.

The effects of remote distractors on goal-directed saccade initiation may be related to another inhibitory effect observed on saccade latency termed saccadic inhibition (Reingold and Stampe 2002, 2004). Studies of saccadic inhibition have shown that the onset of a visual distractor results in the temporary suppression of saccades around 70–100 ms after distractor onset (Buonocore and McIntosh 2008; Edelman and Xu 2009; Reingold and Stampe 2002). Moreover, the inhibitory influence of remote distractors and the saccadic inhibition effect have both been related to inhibitory processes operating in oculomotor structures such as the intermediate layers of the superior colliculus (Reingold and Stampe 2002; Walker et al 1997). An examination of latency distributions for our data shows a similar reduction in the number of short latency saccades, although maximum inhibition of saccadic latencies seems to occur slightly later than in earlier studies (however, see Walker et al 1995). This reduction in the number of faster saccades appears to be present both for onsets and offsets, but is much more pronounced for onset distractors. Future work should establish whether the observed reduction of fast saccadic latencies with offsets is genuine by testing offset and no-offset conditions across many trials for each participant.

Because the influence of distractor onsets and offsets was only tested for a simultaneous presentation of target and distractors, the possibility cannot be excluded that distractor offsets affect saccadic latencies at a different temporal interval than that optimal for distractor onsets (Walker et al 1997). Possibly, offsets need more time to be processed and therefore only affect saccade target selection at a longer stimulus onset asynchrony (SOA) between target and distractor. Moreover, the SOA with strongest interference from the distractor(s) on the target could vary across participants (Bompas and Sumner 2009). Similarly, increases in the number of distractor onsets could possibly have an effect if, simultaneously with the increase in their number, the interval between the target and the distractor is increased. Therefore, to exclude the possibility that distractor offsets, and the number of onsets, have no influence on saccade initiation at any target-distractor onset asynchrony, a range of SOAs should be tested. However, our results do show that peripheral onsets and offsets differ, either in their timing, or in their strength of interference, and that the effects of peripheral offsets are different from those of offsets that occur at central fixation.

References

Arai K, Keller E L, 2005 "A model of the saccade-generating system that accounts for trajectory variations produced by competing visual stimuli" *Biological Cybernetics* **92** 21–37 doi:10.1007/s00422-004-0526-y ◄

Bompas A, Sumner P, 2009 "Temporal dynamics of saccadic distraction" *Journal of Vision* **9** 1–14 doi:10.1167/9.9.17 ◄

Boot W R, Kramer A F, Peterson M S, 2005 "Oculomotor consequences of abrupt object onsets and offsets: Onsets dominate oculomotor capture" *Perception and Psychophysics* **67** 910–928 ◄

Born S, Kerzel D, 2008 "Influence of target and distractor contrast on the remote distractor effect" *Vision Research* **48** 2805–2816 doi:10.1016/j.visres.2008.09.008 ◄

Born S, Kerzel D, 2009 "Congruency effects in the remote distractor paradigm: Evidence for top-down modulation" *Journal of Vision* **9** 1–13 doi:10.1167/9.9.3 ◄

Braun D, Breitmeyer B G, 1988 "Relationship between directed visual attention and saccadic reaction times" *Experimental Brain Research* **73** 546–552 doi:10.1007/BF00406613 ◄

Buonocore A, McIntosh R D, 2008 "Saccadic inhibition underlies the remote distractor effect" *Experimental Brain Research* **191** 117–122 doi:10.1007/s00221-008-1558-7 ◄

Carpenter R H S, Williams M L L, 1995 "Neural computation of log likelihood in the control of saccadic eye movements" *Nature* **377** 59–62 doi:10.1038/377059a0 ◄

Cruickshank A G, McSorley E, 2009 "Involuntary inhibition of movement initiation alters oculomotor competition resolution" *Experimental Brain Research* **493** 467–476 doi:10.1007/s00221-008-1645-9 ◄

Dorris M C, Olivier E, Munoz D P, 2007 "Competitive integration of visual and preparatory signals in the superior colliculus during saccadic programming" *Journal of Neuroscience* **27** 5053–5062 doi:10.1523/JNEUROSCI.4212-06.2007 ◄

Edelman J A, Xu K Z, 2009 "The inhibition of voluntary saccadic eye movement commands by abrupt visual onsets" *Journal of Neurophysiology* **101** 1222–1234 doi:10.1152/jn.90708.2008 ◄

Findlay J M, Walker R, 1999 "A model of saccade generation based on parallel processing and competitive inhibition" *Behavioral and Brain Sciences* **22** 661–721 ◄

Fischer B, Boch R, 1983 "Saccadic eye movements after extremely short reaction times in the monkey" *Brain Research* **260** 21–26 doi:10.1016/0006-8993(83)90760-6 ◄

Fischer B, Weber H, 1993 "Express Saccades and Visual Attention" *Behavioral and Brain Sciences* **16** 553–567 doi:10.1017/S0140525X00031575 ◄

Gandhi N J, Keller E L, 1999 "Comparison of saccades perturbed by stimulation of the rostral superior colliculus, the caudal superior colliculus, and the omnipause region" *Journal of Neurophysiology* **82** 3236–3253 ◄

Godijn R, Theeuwes J, 2002 "Programming of exogenous and endogenous saccades: Evidence for a competitive integration model" *Journal of Experimental Psychology Human Perception & Performance* **28** 1039–1054 doi:10.1037/0096-1523.28.5.1039 ◄

Godijn R, Theeuwes J, 2004 "The relationship between inhibition of return and saccade trajectory deviations" *Journal of Experimental Psychology Human Perception & Performance* **30** 538–554 doi:10.1037/0096-1523.30.3.538 ◄

Hermens F, Walker R, forthcoming "Gaze and arrow distractors influence saccade trajectories similarly" *Quarterly Journal of Experimental Psychology* ◄

Ludwig C J H, Mildinhall J W, Gilchrist I D, 2007 "A population coding account for systematic variation in saccadic dead time" *Journal of Neurophysiology* **97** 795–805 doi:10.1152/jn.00652.2006 ◄

Ludwig C J H, Ranson A, Gilchrist I D, 2008 "Oculomotor capture by transient events: A comparison of abrupt onsets, offsets, motion, and flicker" *Journal of Vision* **8** 11–11 doi:10.1167/8.14.11 ◄

Mayfrank L, Mobashery M, Kimmig H, Fischer B, 1986 "The role of fixation and visual attention in the occurrence of express saccades in man" *European Archives of Psychiatry and Neurological Sciences* **235** 269–275 doi:10.1007/BF00515913 ◄

McSorley E, Findlay J M, 2003 "Saccade target selection in visual search. Accuracy improves when more distractors are present" *Journal of Vision* **3** 877–892 doi:10.1167/3.11.20 ◄

Meeter M, van der Stigchel S, Theeuwes J, 2010 "A competitive integration model of exogenous and endogenous eye movements" *Biological Cybernetics* **102** 271–291 doi:10.1007/s00422-010-0365-y ◄

Munoz D P, Wurtz R H, 1993a "Fixation cells in superior colliculus. I. Characteristics of cell discharge" *Journal of Neurophysiology* **70** 559–575 ◄

Munoz D P, Wurtz R H, 1993b "Fixation cells in superior colliculus. II. Reversible activation and deactivation" *Journal of Neurophysiology* **70** 576–589 ◄

Ratcliff R, 1979 "Group reaction time distributions and an analysis of distribution statistics" *Psychological Bulletin* **86** 446–461 doi:10.1037/0033-2909.86.3.446 ◄

Reingold E M, Stampe D M, 2002 "Saccadic inhibition in voluntary and reflexive saccades" *Journal of Cognitive Neuroscience* **14** 371–388 doi:10.1162/089892902317361903 ◄

Reingold E M, Stampe D M, 2004 "Saccadic inhibition in reading" *Journal of Experimental Psychology Human Perception & Performance* **30** 194–211 doi:10.1037/0096-1523.30.1.194 ◄

Reuter-Lorenz P A, Oonk H M, Barnes L L, Hughes H C, 1995 "Effects of warning signals and fixation point offsets on the latencies of pro- versus antisaccades: implications for an interpretation of the gap effect" *Experimental Brain Research* **103** 287–293 doi:10.1007/BF00231715 ◄

Rolfs M, Vitu F, 2007 "On the limited role of target onset in the gap task: Support for the motor-preparation hypothesis" *Journal of Vision* **7** 1–20 doi:10.1167/7.10.7 ◄

Ross L E, Ross S M, 1980 "Saccade latency and warning signals: stimulus onset, offset, and change as warning events" *Perception and Psychophysics* **27** 251–257 ◄

Saslow M G, 1967 "Effects of components of displacement-step stimuli upon latency for saccadic eye movement" *Journal of the Optical Society of America* **57** 1024–1029 doi:10.1364/JOSA.57.001024 ◄

Theeuwes J, Olivers C N L, Belopolsky A, 2010 "Stimulus-driven capture and contingent capture" *Wiley Interdisciplinary Reviews Cognitive Science* **1** 872–881 ◄

Todd J T, van Gelder P, 1979 "Implications of a transient-sustained dichotomy for the measurement of human performance" *Journal of Experimental Psychology Human Perception & Performance* **5** 625–638 doi:10.1037/0096-1523.5.4.625 ◄

Trappenberg T P, Dorris M C, Munoz D P, Klein R M, 2001 "A model of saccade initiation based on the competitive integration of exogenous signals in the superior colliculus" *Journal of Cognitive Neuroscience* **13** 256–271 doi:10.1162/089892901564306 ◄

Walker R, Deubel H, Schneider W X, 1997 "Effect of remote distractors on saccade programming: evidence for an extended fixation zone" *Journal of Neurophysiology* **78** 1108–1119 ◄

Walker R, Kentridge R W, Findlay J M, 1995 "Independent contributions of the orienting of attention, fixation offset and bilateral stimulation on human saccadic latencies" *Experimental Brain Research* **103** 294–310 doi:10.1007/BF00231716 ◄