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Stimulus-salience and the time-course of saccade trajectory deviations

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The deviation of a saccade trajectory is a measure of the oculomotor competition evoked by a distractor. The aim of the present study was to investigate the impact of stimulus-salience on the time-course of saccade trajectory deviations to get a better insight into how stimulus-salience influences oculomotor competition over time. Two experiments were performed in which participants were required to make a vertical saccade to a target presented in an array of nontarget line elements and one additional distractor. The distractor varied in salience, where salience was defined by an orientation contrast relative to the surrounding nontargets. In Experiment 2, target-distractor similarity was additionally manipulated. In both Experiments 1 and 2, the results revealed that the eyes deviated towards the irrelevant distractor and did so more when the distractor was salient compared to when it was not salient. Critically, salience influenced performance only when people were fast to elicit an eye movement and had no effect when saccade latencies were long. Target-distractor similarity did not influence this pattern. These results show that the impact of salience in the visual system is transient.

Keywords: saccade deviation, time-course, stimulus-salience, distractors, eye movements

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Introduction

The presence of visual distractors may cause the saccade to deviate either towards or away from the distractor (for a recent review, see Van der Stigchel, 2010). When looking at the role of saccade latency in this process, it turns out that the time-course of saccade deviations develops in a specific way. Deviation towards the location of an irrelevant distractor is generally found when saccade latencies are short (less than 200 ms), whereas deviation away from the distractor location is observed when saccadic latencies are longer (e.g., Laidlaw & Kingstone, 2010; McSorley, Haggard, & Walker, 2005, 2006, 2009; Mulckhuyse, Van der Stigchel, & Theeuwes, 2009; Walker, McSorlev, & Haggard, 2006). Comparable to the time-course of saccade deviations, the time-course in oculomotor selection of location reveals a similar regularity in performance; that is, patterns in selection behavior are idiosyncratic to early or late execution of an eye movement (e.g., Donk & van Zoest, 2008, 2011; Hunt, von Mühlenen, & Kingstone, 2007; van Zoest & Donk, 2010; van Zoest, Donk, & Theeuwes, 2004). Specifically, these studies show that the impact of stimulussalience on visual selection is severely limited in time, such that salience affects selection only when saccadic latencies are short (<250 ms). Stimulus-salience here refers to the conspicuousness of an element relative to the surrounding elements. Top-down influences appear to come online later and primarily affect selection when saccadic latencies are long (>250 ms) (e.g., Siebold, van Zoest, & Donk, 2011; van Zoest & Donk, 2008). Given the characteristic time-courses of saccade deviations and of stimulus-driven visual selection, the aim of the present study was to investigate the impact of stimulussalience on the time-course of saccade deviations.

The deviations of saccade trajectories are typically explained in terms of competitive interactions between large populations of neurons that code specific movement vectors on a motor map (McPeek, Han, & Keller, 2003; Tipper, Howard, & Houghton, 2000; Tipper, Howard, & Jackson, 1997). The trajectory is ultimately determined by the weighted average of activity in this motor map, which incorporates both facilitation and inhibition at target and distractor locations (e.g., Godijn & Theeuwes, 2002; Kopecz, 1995; McPeek & Keller, 2001; Munoz & Corneil, 1995; Munoz & Wurtz, 1995; Trappenberg, Dorris, Munoz, & Klein, 2001). When the competition between the target and the distractor is unresolved, the residual activity at the distractor location may cause the weighted average to be directed in the direction of the distractor (e.g., McPeek, 2006). In this situation, the saccade will deviate towards the distractor location. This is the case, for example, when saccade latencies are short and top-down inhibition has not yet been established at the time the eye movement was programmed (McSorley et al., 2006; Walker et al., 2006). In contrast, later in time top-down control prevails and oculomotor inhibition is fully online to suppress the irrelevant distractor location; inhibition may result in distractor related activity dropping below baseline. The integration of distractor inhibition into the calculation of saccade program to the target then causes the saccade vector to be directed *away* from the inhibited distractor location. The strength of saccade deviations away is therefore thought to reflect the strength of the oculomotor inhibition applied to the distractor location (Godijn & Theeuwes, 2004). By looking at the impact of salience on saccadic trajectories deviations as a function of time, the present study aims to get a better insight into how stimulus-salience influences the oculomotor system over time.

One previous study has shown that stimulus-salience modulates eye movement trajectories. Godijn and Theeuwes (2004) found that the degree of saccade deviation away depends on the relative salience of the tobe-ignored element. In this experiment participants made an eye movement to a saccadic goal that was located straight up above or down below from the fixation point. A cue that was presented to the left or right of the saccadic goal location signaled to the participants whether the saccade was to be programmed up or down. This cue could either be an abrupt onset or a color singleton. The results showed that saccade trajectories to the target deviated away from the location of the cue. Furthermore, these deviations were greater when the cue was presented as an abrupt onset compared to when it was presented as a color singleton (Godijn & Theeuwes, 2004). Godijn and Theeuwes' (2004) findings were explained by the idea that the abrupt onset is more salient than the color singleton and that the more salient element results in more activation in a motor map than a less salient singleton. The salient singleton therefore requires more inhibition to be successfully rejected, hence explaining the greater deviation away from the abrupt onset compared to the color singleton. Variations in deviation away may thus be explained in terms of relative activation levels as a function of stimulus-salience (Trappenberg et al., 2001).

Nonetheless, it has been demonstrated in a number of different studies that the impact of stimulus-salience in visual selection is limited in time (Donk & Soesman, 2010, 2011; Donk & van Zoest, 2008, 2011; Siebold et al.,

2011; van Zoest & Donk, 2005, 2006, 2010; van Zoest et al., 2004). For example, in one study participants were instructed to make a saccadic eve movement to the target item that was presented among a group of homogeneous nontargets and one additional distractor (van Zoest et al., 2004). The salience of an additional singleton distractor was varied such that the irrelevant singleton could be less, equal, or more salient than the target. The results showed that stimulus-salience guided selection only when participants were quick to elicit eye movements after the display appeared (see also Donk & van Zoest, 2008). As saccadic latency increased, the impact of stimulus-salience decreased, with no effect of stimulussalience at the longest saccadic latencies. The slower saccades were primarily goal-driven. Motivated by the finding that stimulus-salience modulates eye movement trajectories (Godijn & Theeuwes, 2004; Trappenberg et al., 2001) and that the effect of stimulus-salience has a characteristic time-course, the question of the present study is how stimulus-salience affects the dynamics of saccade deviations.

There are at least two ways in which stimulus-salience could modulate the time-course of saccade deviations. On the one hand, the modulation may depend on topdown inhibition and the moment in time at which the inhibition becomes available. In this case, because inhibition takes time to develop, the effects of irrelevant stimulus-salience will only be observed for the longer saccadic latencies. A more salient distractor would then result in more saccadic deviation away than a less salient distractor, a difference that should come about relatively late in time. On the other hand, based on the idea that the effects of stimulus-salience are transient and completely degrade with time (Donk & van Zoest, 2008) one predicts that stimulus-salience will modulate deviations only early in time, when saccade latencies are short. Indeed, this modulation may occur at a stage of processing that is completely independent from top-down inhibition (van Zoest & Donk, 2005, 2008). Specifically, one would predict that a more salient distractor would result in more saccadic deviation toward than a less salient distractor and that this effect comes about only when saccadic latencies are short. Alternatively, both early and late modulation may be observed. In this case the two functions for the salient and nonsalient distractor would be expected to cross over as a function of time. Initially, one would find more deviation towards the salient distractor than the nonsalient distractor, while later in time one would find more deviation away from the salient than from the nonsalient distractor.

In the present study stimulus-salience was carefully manipulated by varying orientations of small distractor line elements relative to the background. These stimuli have proven to provide a subtle yet effective way to manipulate stimulus-salience (Donk & van Zoest, 2008; van Zoest & Donk, 2006, 2008; van Zoest et al., 2004).

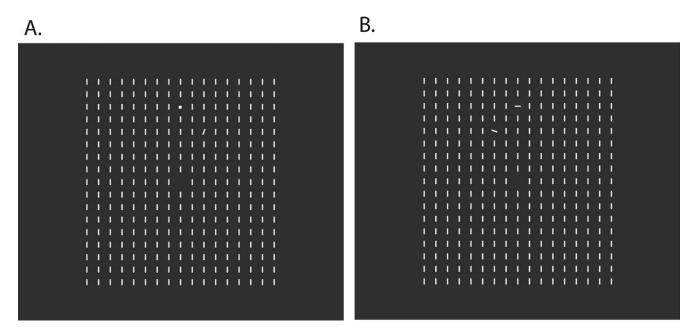


Figure 1. An example of the search displays in Experiments 1 and 2. The saccade target was a small circle in Experiment 1 (A) and a vertical orientation singleton in Experiment 2 (B) that was presented above or below fixation. An irrelevant distractor, i.e., orientation singleton, was presented that was oriented at 22.5° (A) or oriented at 67.5° (B).

Experiment 1

Participants were required to make a vertical saccade to a target that was presented above or below the central fixation point. The target was a small circle that was presented among a matrix of vertical line elements (see Figure 1A).

In addition to the presentation of the homogenous group of vertical line elements, one line element was presented that was different from the vertical line elements. This orientation singleton could be a salient distractor, i.e., with a high orientation contrast relative to the vertical line elements, or a nonsalient distractor, i.e., with a low orientation contrast relative to the vertical line elements. Note that this distractor line element bore no similarity relation the target—i.e., circle—to exclude potential confounds of target-distractor similarity. It was predicted that the amount of deviation of the saccades directed to the saccade target is modulated by the salience of the distractor.

Methods

Participants

Twelve observers ranged in ages 19–26 (average 20.5) participated in the experiment. All reported having normal or corrected-to-normal vision.

Apparatus

All subjects were tested in a sound-attenuated, dimlylit room with their heads resting on a chinrest. The monitor was located at eye level 75 cm from the chinrest.

A Pentium IV computer with a processor speed of 2.3 GHz controlled the timing of the events. Displays were presented on an Iiyama 21" SVGA monitor with a resolution of 1024×768 pixels and a 100-Hz refresh rate. Eye movements were recorded by means of an Eyelink II tracker (SR Research Ltd., Canada) with a 500-Hz temporal resolution and a 0.2° of visual angle spatial resolution. The system uses an infrared video-based tracking technology to compute the pupil centre and pupil size of both eyes.

Stimuli

The stimulus display consisted of multiple vertical line segments presented in a 17×17 square matrix with a raster width of $17.4^{\circ} \times 17.4^{\circ}$ of visual angle. Elements had an approximate length of 0.76° and width of 0.15° . The saccadic goal was a small circle (diameter 0.44° of visual angle) presented above or below the central fixation-point at a retinal eccentricity of 7.6° of visual angle. In 80% of all trials an orientation singleton was presented that was either oriented $\pm 22.5^{\circ}$ or $\pm 67.5^{\circ}$ relative to the vertical background lines. This singleton was considered a nonsalient distractor if the absolute difference in orientation between this element and the

vertical background elements was 22.5°, and was considered a salient distractor if this difference was 67.5°. The distractor was presented 3.8° away from the fixation in the horizontal direction and 5.1° away in the vertical direction (i.e., angular deviation from the target of 37°). Half of the distractors were located to the left of the saccade goal and half were located to the right. If a distractor was presented, it always appeared in the vertical half containing the saccade goal.

Procedure and design

Each block started with a nine-point grid calibration procedure. In addition, simultaneously fixating the center fixation point and pressing the space bar recalibrated the system by zeroing the offset of the measuring device at the start of each trial. A fixation point was presented for 500 ms following which the fixation point was removed at five different stimulus onset asynchronies (SOAs) of -150, -50, 0, 50, and 150 ms relative to the appearance of the display. The display was presented for 1500 ms. Note that negative values indicate a gap condition in which the fixation point offset occurred before the appearance of the display, whereas the positive values indicate an overlap condition. The SOA manipulation was used to generate a larger variability in saccadic latencies (Saslow, 1967). Participants were instructed to fixate the center fixation point and to make a saccade towards the small circle that could appear directly above or below fixation as soon as the display was presented.

The experiment consisted of a training session of 24 trials and an experimental session of 600 trials. The experimental session was divided into four blocks of 150 trials. Participants received feedback regarding the latency of their saccades every 25 trials. Feedback was given throughout the experiment to keep participants motivated to respond quickly following target onset. Participants heard a short tone when their saccade latency on a given trial was longer than 600 ms or shorter than 80 ms. The sequence of trials was randomized for each participant, in terms of both target location (upper or lower field) and distractor condition (distractor left, right, or absent). Participants were instructed prior to the experiment block and were allowed to take breaks in between blocks.

Data analysis

An eye movement was considered a saccade when either eye velocity exceeded 35° /s or eye acceleration exceeded 9500° /s². Saccade latency was defined as the interval between the presentation of the saccade target and the initiation of a saccade eye movement. If saccade latency was shorter than 60 ms, longer than 600 ms, or if the duration of the saccade was longer than 80 ms, the trial was removed from further analyses. If the eyes were not within 2° of the fixation point when the saccade was elicited, or if the saccade missed the target in case the endpoint of the first saccade had an angular deviation of more than 18.5° from the center of the target, the saccade was classified as an error and also not further analyzed. If after trimming of the data according to these criteria less than 2/3 of the data for a single participant remained, the participant was removed from further analyses.

Because of the variation in the duration of individual saccades (and therefore in the number of recorded raw samples), saccadic deviation was calculated on the basis of a linear interpolation of each eye movement. For each saccade, 50 evenly-spaced location values were extrapolated from the given raw samples. Deviation was then defined as the difference in mean angle of the extrapolated saccade path and the shortest path (i.e., straight line) measured from the saccade starting position and the target location. The mean angle of the saccade path in a single trial was calculated by averaging the angles of the straight line between the saccade starting position and the different sample points (for a more detailed overview of saccade trajectory computation, see Van der Stigchel, Meeter, & Theeuwes, 2006). Because our measure of deviation takes the complete trajectory into account (including saccade endpoint), saccade endpoint is an important factor in determining the saccade deviation. Indeed, saccade endpoint and saccade deviation are known to be strongly correlated (Van der Stigchel, Meeter, & Theeuwes, 2007). Therefore, any effect on saccade deviation is likely to be reflected in a similar effect in saccade endpoint.

In order to investigate the time-course of saccadic deviation, for each of the two conditions corresponding to the two levels of distractor type, the overall distribution of each participant's latencies of the saccade was rank ordered from shortest to longest latency and subsequently partitioned into four equal saccadic latency bins. For each participant, the average saccadic deviation per condition and per latency bin was then calculated. The quartiles of deviation and latency were then averaged across participants to obtain the group distribution (Ratcliff, 1979; Vincent, 1912). Note that for all ANOVAs that included factors with three or more levels the *p*-values are Greenhouse-Geisser corrected.

Results

Two participants did not provide enough data (loss of more than 1/3 of trials in each individual dataset) and were removed from further analyses. The data of a total of 10 participants is reported below. Trials on

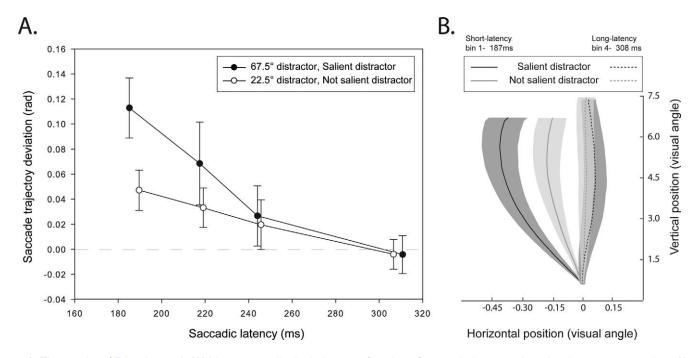


Figure 2. The results of Experiment 1. (A) Mean saccadic deviation as a function of saccadic latency when the distractor was salient (67.5° distractor) and the when the distractor was not salient (22.5° distractor). Error bars represent standard errors of the mean. (B) Averaged across all participants the actual saccade trajectories in the first and last bin for the salient and not salient distractor. These plots are in reference to a target in the upper hemifield and distractor in the left upper quadrant. The solid line represent short-latency saccadic eye movement in the first bin, the dotted lines depict long-latency saccadic movements in the fourth bin. The shaded areas represent standard error of the mean.

which saccade latency was shorter than 80 ms (5.6 % trials), longer than 600 ms (0.3%), or saccade duration was longer than 80 ms (2.0%) were discarded from further analyses. An additional 2.7% of the trials were discarded because the eyes were not within 2° of the fixation point when the first saccade was elicited and 10.3% of trials were removed because the first saccade missed the target.

Saccadic latency

To check whether the SOA manipulation helped to generate variation in the saccade latencies, a repeatedmeasures analysis of variance (ANOVA) was performed with distractor condition (salient, nonsalient, and no distractor) and SOA (-150, -50, 0, 50, 150) as within-subject factors. The main effect of distractor condition was not significant (F < 1). The main effect of SOA was significant [F(4, 44) = 15.96, p = 0.001, $\eta_p^2 = 0.64$] and revealed that saccadic latencies increased with an increasing overlap between fixation point and display onset. Saccadic latencies ranged from 231.6 ms in the -150 ms gap condition to 252.7 ms in the 150 ms overlap condition. The interaction between distractor condition and SOA was not significant [F(8, 72) = 1.02, p = 0.40, $\eta_p^2 = 0.10$].

To test whether the overall distribution of saccadic latency collapsed over SOA condition was affected by distractor saliency, an ANOVA was performed with distractor condition (salient, nonsalient distractor) and bin (four) as within-subject factors. The main effect of distractor condition was not significant (F < 1). The main effect of bin was significant [F(5, 45) = 115.43, p < 0.0001, $\eta_p^2 = 0.93$]. The interaction between distractor condition and bin was not significant [F(5, 45) = 3.29, p = 0.077, $\eta_p^2 = 0.27$].

Saccadic deviation

Figure 2 depicts the measure of distractor-induced deviation for the salient and nonsalient distractor as a function of saccade latency divided in four equal bins, averaged over participants. Three important observations can be made from Figure 2. First, the deviation towards the distractor was greater in the presence of a salient distractor than the presence of a nonsalient distractor. Second, the deviation decreased as a function of saccade latency. Third, the decrease in deviation as a function of saccade latency was greater in the salient than in the nonsalient distractor condition. These observations were tested in a repeated-measures ANOVA with distractor condition (salient and nonsalient) and bins (four) as within-subject factors. The main effect of distractor [F(1, 9) = 8.91, $p = 0.015, \eta_p^2 = 0.50$], of bin [F(3, 27) = 12.60, p < 0.0001, $\eta_p^{2^{1P}} = 0.58$], and the interaction between

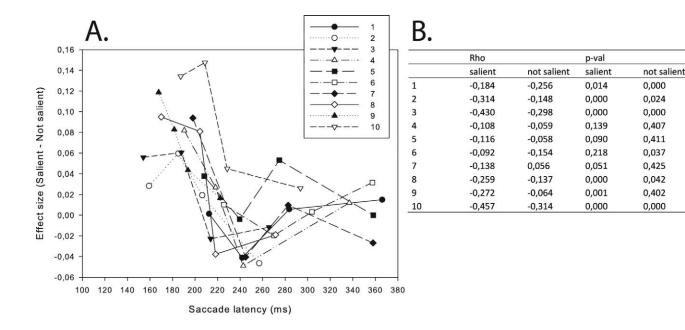


Figure 3. Individual participants' analyses for Experiment 1 (A) The difference in saccade deviation between the salient and not salient distractor as a function of bin for each participant for Experiment 1. (B) Individual correlations between saccade latency and deviation and their associated *p*-values.

distractor and bins $[F(3, 27) = 5.96, p = 0.009, \eta_p^2 = 0.40]$ were all significant. Fisher LSD post-hoc comparisons revealed a significant difference between the salient and nonsalient distractor in the first two bins (first bin p < 0.0001; and second bin p = 0.01) but no significant difference was found between these conditions in the third and fourth bin.

To test whether the distractor induced a significant saccadic deviation for the different bins, the mean deviation in each bin was tested against zero using a one-sample *t*-test (no deviation). Note that *p*-values were Benjamini-Hochberg corrected for multiple comparisons. The results showed that in the salient distractor condition, saccades deviated significantly towards the distractor in the first bins [bin 1, t(9) =5.28, p = 0.002] and significant in the second bin [bin 2, t(9) = 2.84, p = 0.025]. Significant deviation towards was also found in the nonsalient distractor condition for the first bin [bin 1, t(9) = 3.19, p = 0.0048] and second bin [bin 2, t(9) = 2.48, p = 0.047]; all further comparisons were not significant from zero (all p >0.05). Figure 3 depicts individual analyses for each of the participants. The individual results are in accordance with the overall results presented above.

Discussion

The results of Experiment 1 revealed that stimulussalience had a significant influence on saccadic deviations. Saccades deviated towards the irrelevant distractor and this deviation was stronger for the salient distractor than for the nonsalient distractor. Moreover, the modulatory effect of stimulus-salience was only evident for the shortest saccadic latencies and no evidence was found of modulation when saccade latencies were long. This finding is in line with previous work that has shown that the effect of stimulus-salience is transient (e.g., Donk & van Zoest, 2008). Similar to the study of Donk and van Zoest, stimulus-salience was seen to influence performance only when saccadic latencies were short. The present results suggest that salience has a transient effect on oculomotor programming.

The results of Experiment 1 did not show modulation of saccade deviation away; in fact, there was no evidence for saccade deviation away at all, even for the longest saccade latencies. The present results are unlike the study of Godijn and Theeuwes (2004) who showed modulation of saccade deviation away as a function of the salience of the irrelevant singleton. Saccadic deviation away was also found in the studies that investigate how goal-driven influences affect the time-course of saccade deviation (Ludwig & Gilchrist, 2003; Mulckhuyse et al., 2009). In these studies, goal-driven influences were investigated by manipulating target-distractor similarity, the idea being that a similar distractor bears more relevance and is therefore stronger activated and in turn requires more inhibition to be rejected. Observers were instructed to saccade towards a green or red circle (the target) that was positioned above or below the fixation point. Simultaneous to the presentation of the target, a distractor was presented that either matched the color of the target or did not. The results showed that target-distractor similarity influenced deviations depending on saccade

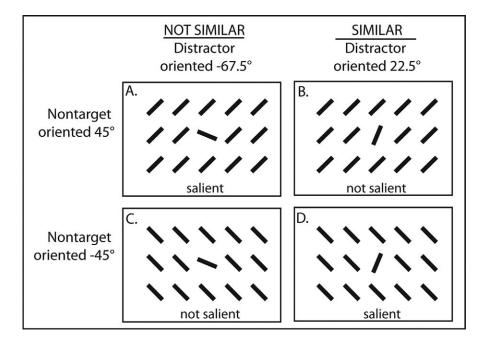


Figure 4. The combination of distractors and nontargets presented in Experiment 2. The target was a vertical line element. Distractors presented were either rotated -67.5° (target-distractor similarity low) or 22.5° (target-distractor similarity high). Nontargets were rotated at $-45^{\circ}/+45^{\circ}$. Depending on the surrounding nontargets, distractors appear as salient (cases A and D) or not (cases B and C).

latency. When saccade latencies were short, more deviation away was found for dissimilar distractors than for similar distractors (i.e., distractors matching the color of the target), suggesting that the similar distractor was inhibited less than the dissimilar distractor early in time. In contrast, when saccade latencies were long, more deviation away was found when the distractor was similar than when it was dissimilar, suggesting that the similar distractor was inhibited more than the dissimilar distractor later in time. Deviation away may thus critically depend on the similarity of the irrelevant distractor to the target. In Experiment 1, the irrelevant distractors bore absolutely no relevance and were not in any way related to the target: The target was a small circle while the irrelevant distractor was an orientation singleton. As such, there was no similarity relation between the target and distractors.

A second experiment was performed to more closely examine how salience affects the time-course of saccade deviation under conditions in which distractor and target were similar as compared to different from each other. The major question here was whether the effects of salience on saccadic deviation are modulated by the similarity between the target and distractor.

Experiment 2

The aim of Experiment 2 was to investigate to what extent salience and target-distractor similarity influence

saccadic deviations in multiple element displays. In order to answer this question, the saccadic target was changed into a vertical orientation singleton (0°) and two types of nontargets were used ($+45^{\circ}$ or -45°). The distractor (-67.5° or $+22.5^{\circ}$) could be more or less salient dependent on the type of nontargets presented (see van Zoest & Donk, 2006). In addition, the distractor could be more or less similar to the saccadic target as determined by the absolute orientation difference between the distractor and the target (see Figure 4).

Methods

Participants

Fourteen observers ranged in age 19–38 (average 24) participated in the experiment. All reported having normal or corrected-to-normal vision.

Apparatus and data analysis

The apparatus was identical to the apparatus used in Experiment 1. The data analysis was identical to the analysis in the previous experiment.

Stimuli, design, and procedure

Experiment 2 was similar to Experiment 1 except for the following changes. Displays consisted of one target (0° of arc relative to the vertical), a series of nontargets (oriented +45° or -45° of arc relative to the vertical), and one distractor ($+22.5^{\circ}$ and -67.5° of arc relative to the vertical). The combination of target, two types of nontargets, and two types of distractors led to four different combinations of distractor saliency and target-distractor similarity (see Figure 4). Note that the absolute difference in orientation between the target and the nontargets was always 45°, and the absolute difference in orientation between the two types of distractors and the nontargets was either 22.5° or 67.5°. The distractor was considered to be a salient item when the absolute difference in orientation between the distractor and its surrounding nontargets was 67.5° (see Figures 4A and 4D) and a nonsalient item when this difference was 22.5° (see Figures 4B and 4C). Target distractor similarity was considered high when the distractor was oriented at +22.5° (see Figures 4B and 4D) and low when the distractor was oriented at -67.5° (see Figures 4A and 4C). A target and distractor were presented in every trial. Participants completed 800 trials in one session of 90 minutes and took breaks every 200 trials.

Results

Two participants did not provide enough data (loss of more than 1/3 of trials in each individual dataset) and were removed from further analyses. The data of a total of 12 participants are reported below. Trials on which saccade latency was shorter than 80 ms (4.58%trials) or longer than 600 ms (0.27%) or saccade duration was longer than 80 ms (0.86%) were discarded from further analyses. An additional 3.35% of the trials were discarded because the eyes were not within 2° of the fixation point when the first saccade was elicited; 4.52% of trials were removed because the first saccade missed the target.

Saccadic latency

To check whether the SOA manipulation helped to generate short and long saccade latencies, a repeatedmeasures ANOVA was performed with target-distractor similarity (low and high), distractor saliency (low and high), and SOA (-150, -50, 0, 50, 150) as withinsubject factors. There were no main effects of targetdistractor similarity or distractor salience, both F < 1. The main effect of SOA was significant [F(4, 44)] = 23.75, p < 0.0001, $\eta_p^2 = 0.68$] and revealed that saccadic latencies increased with an increasing overlap between fixation point and display onset. Saccadic latencies ranged from 211.8 ms in the -150 ms gap condition to 232.8 ms in the 150 ms overlap condition. None of the interactions between target-distractor similarity, distractor saliency, and SOA reached significance. To test whether the overall distribution of saccadic latency collapsed over SOA condition was affected by distractor condition, an ANOVA was performed with target-distractor similarity (low and high), distractor saliency (low and high), and bin (four) as within-subject factors. The main effect of target-distractor similarity was not significant, F < 1; the main effect distractor salience was not significant [F(1, 11) = 3.77, p = 0.078, $\eta_p^2 = 0.26$] and none of the interactions between targetdistractor similarity, distractor salience, and bin reached significance. The main effect of bin was significant [F(3, 33) = 155.24, p < 0.0001, $\eta_p^2 = 0.93$].

Saccadic deviation

Figure 5 depicts the measure of distractor-induced deviation for the four different conditions as a function of saccade latency divided in four equal bins and vincentized over participants. The results were tested in a repeated-measures ANOVA with target-distractor similarity (low and high), distractor saliency (low and high), and bin (four) as within-subject factors. There was a main effect of target-distractor similarity [F(1,11) = 6.94, p = 0.023, $\eta_p^2 = 0.39$], a main effect of distractor salience $[F(1, 11) = 6.82, p = 0.024, \eta_p^2 = 0.38]$, and a main effect of bin [F(3, 33) = 3.74, p =0.020, $\eta_p^2 = 0.35$]. The results showed that saccades deviated more towards the similar distractor (0.018 rad) than the dissimilar distractor (0.012 rad) and more towards a salient distractor (0.028 rad) than a nonsalient distractor (0.002 rad). Further, there was a significant interaction between distractor salience and bin $[F(3, 33) = 3.74, p = 0.035, \eta_p^2 = 0.25]$. Fisher LSD post-hoc comparisons revealed a significant difference between the salient and nonsalient distractor in the first three bins [first bin p < 0.0034; second bin p < 0.0001, third bin, p < 0.021]. No significant difference was found between these conditions in the last fourth bin. There were no other interactions.

One-sample *t* tests tested against zero showed that, independent of target-distractor similarity, only when the distractor was salient did saccades deviate significantly toward the distractor in bins one and two [target-distractor similarity high: bin 1, t(11) = 3.35, p = 0.0256, bin 2, t(11) = 3.49, p = 0.0067; target-distractor similarity low: bin 1, t(11) = 4.03, p = 0.008; bin 2, t(11) = 3.09, p = 0.013]. No other contrast deviated significantly from zero (all p > 0.05). *P*-values are Benjamini-Hochberg corrected. Figure 6 depicts individual analyses for each of the participants.

To compare the results of Experiment 2 to those of Experiment 1, an ANOVA was conducted on saccade deviation with Experiment as the between-subject variable and distractor saliency (low and high) and bin (four) as within-subject variables. The results of Experiment 2 were collapsed over similarity condition. Experiment did not have a main effect [F(1, 20) = 1.76,

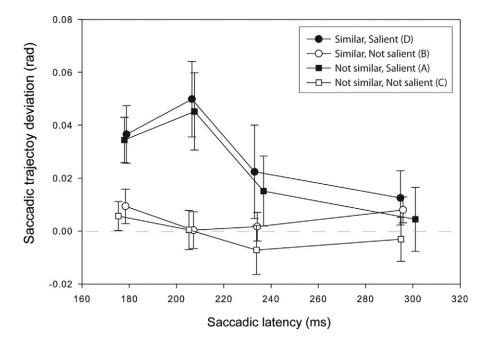


Figure 5. The results of Experiment 2. Mean saccadic deviation as a function of saccadic latency when the distractor was similar oriented at 22.5° and salient, similar oriented at 22.5° and not salient, not similar oriented at -67.5° and salient, and not similar oriented at -67.5° and salient. Error bars represent standard errors of the mean. The letters in the legend refer to the different conditions as depicted in Figure 4.

p = 0.20] but did significantly interact with bin [F(3, 60) = 7.03, p < 0.0005], showing that overall change in deviation over time was larger in Experiment 1 than in Experiment 2. No other two-way or three-way interaction was significant (all p > 0.05).

Discussion

In Experiment 2, distractor salience was manipulated independently from target-distractor similarity. The findings revealed, similar to those in Experiment 1, a

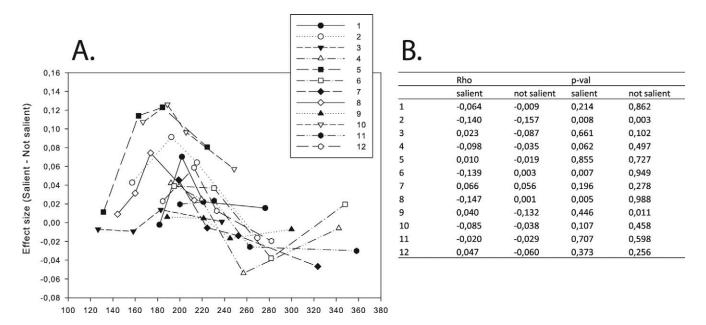


Figure 6. Individual analyses for Experiment 2 collapsed over target-distractor similarity. (A) The difference in saccade deviation between the salient and not salient distractor as a function of bin for each participant in Experiment 2. (B) Individual correlations between saccade latency and deviation and their associated *p*-values.

significant interaction between the effects of stimulussalience and latency. Saccades deviated towards the irrelevant distractor and this deviation was stronger for the salient distractor than for the nonsalient distractor. This effect was primarily evident for the shortest saccadic latencies; no evidence suggested that salience modulated saccadic deviation when saccade latencies were long. Importantly, this interaction was not in any way affected by similarities between the target and distractor. While there was a significant main effect of target-distractor similarity, this variable did not interact with distractor salience or the time-course of performance.

Target-distractor similarity in our study did not alter the effects of salience, suggesting that similarity and salience are independent (van Zoest et al., 2004). Similarity did have a small but reliable overall effect in the present study. Earlier work has demonstrated that target-distractor similarity specifically affects the time-course of saccade deviation (Ludwig & Gilchrist, 2003; Mulckhuyse et al., 2009). This discrepancy between previous work and the present study might be explained by the different interpretation or definition of target-distractor similarity. In the high-similarity condition in Ludwig and Gilchrist (2003) and Mulckhuyse et al. (2009) the target and distractor had the same identity (e.g., both green squares) whereas in the low similarity condition, the target and distractor had different identities (e.g., a red and a green square). Similarity accordingly was expressed as an all-or-none characteristic. In the present study, similarity between target and distractor was manipulated in a continuous manner; the target and distractor could be more or less similar, but were never identical. Although our manipulation was potent enough to evoke a consistent influence of similarity on saccade deviation toward the distractor, the representation of similarity may not have been strong enough to warrant the need for active top-down inhibition beyond the baseline of zero.

Previous studies that have investigated the role of target-distractor similarity in visual search using the same manipulation as the present study have demonstrated robust similarity effects. For example, similarity in orientation influenced the average detection performance in covert attention (van Zoest & Donk, 2004) and influenced the time-course of performance in saccadic selection (van Zoest & Donk, 2006). In a saccadic selection visual search task, the results showed that target-distractor similarity did not affect the shortlatency saccadic movements to the target, but did influence saccadic targeting when latencies were high (van Zoest & Donk, 2006). The predictability of the target location may explain why this time-dependent contingency was found in the visual search study but not in the present saccade selection task. In a visual search task the location of the target is much more uncertain than in the simple *prosaccade* distractor task of the present study, where the target always appeared either above or below the fixation point. With fewer target locations, top-down control for target-selection may be much more readily established, thereby reducing the potential influence of other variables that could modulate the relative contribution of top-down control.

General discussion

The aim of the present study was to investigate the impact of stimulus-salience on the time-course of saccade trajectory deviations to get a better insight into how stimulus-salience influences the oculomotor system over time. The experimental results reveal four main findings. First, relative salience affects saccadic deviations in that saccades deviate more towards a salient as compared to a nonsalient distractor. Second, the effect of stimulus-salience is limited to early processing as evident from the finding that only short-latency saccades are affected by salience. Third, similarity as manipulated in Experiment 2 does not alter the effects of salience. Finally, similarity appears to have a small but reliable overall effect, as saccades deviate more towards similar than dissimilar distractors; however, this effect was not influenced by time.

The observed pattern of results is consistent with the idea that salience only briefly influences our visual system (Donk & van Zoest, 2008). It is generally accepted that saccade deviations towards a distractor are caused by the unresolved competition between target and distractor (e.g., McPeek, 2006). The stronger deviation towards a salient distractor compared to a nonsalient distractor thus implies that the activation of the salient distractor was stronger than the nonsalient distractor. Critically, finding that this difference was only observed when saccade latencies are short suggests that for longer latencies the relative activations of the salient and nonsalient distractor level reached equilibrium such that both irrelevant distractors resulted in an equal amount of deviation. Specifically in the end, deviation to distractors showed neither deviation towards or away but remained around the baseline of zero. Previous studies in visual selection have similarly demonstrated that irrelevant salient distractors influences saccadic target selection only when saccade latencies are short (Coeffe & O'Regan, 1987; Hunt et al., 2007; Mulckhuyse, van Zoest, & Theeuwes, 2008; Ottes, Van Gisbergen, & Eggermont, 1985; Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). In these cases, salience typically affected the course of the eye movements in such a way that the eyes were captured by the salient object, resulting in an eye movement to a location that was completely different than the intended target location. These capture saccades represent very dramatic errors in oculomotor programming and are quite distinct from the subtle deviations observed in saccadic programming in the present study. In the present study, all analyzed eye movements were essentially goaldriven in that they ended up near the correct target location. Nevertheless, the modulations in the trajectory revealed the influence of the salience of the irrelevant distractor and its impact over time.

Theories of saccade deviations assume that saccades with longer latencies are more strongly influenced by top-down processes than saccades with shorter latencies (Godijn & Theeuwes, 2002; Trappenberg et al., 2001). These top-down processes inhibit the distractor location and activate the target location, generally resulting in stronger deviations away from a distractor for longer latencies than for shorter latencies (Ludwig & Gilchrist, 2003; Mulckhuyse et al., 2009). However, the findings of the present study demonstrate that stimulus-salience did not influence saccade deviations when latencies were long. This suggests that the later top-down processes were unaffected by the relative difference in salience in the present display. A related finding was that there was no evidence for saccadic deviation away from the irrelevant distractor, irrespective of the saliency or the similarity of the distractor. These results are seemingly in contrast with the general idea that the amount of inhibition is related to the strength of activation of the distractor (McSorley et al., 2006; Walker et al., 2006) and that saccades generally tend to deviate away from irrelevant salient distractors when saccade latency is long (e.g., Godijn & Theeuwes, 2004; Laidlaw & Kingstone, 2010; Walker et al., 2006). Finding no evidence in the present study for saccadic deviation away suggests that the distractors presented in the present displays did not necessitate top-down inhibition beyond the baseline of zero. This finding is in line with the idea that the impact of stimulus-salience passively decays and that active top-down inhibition is not a requisite to discount the potential effects of salience (Coeffe & O'Regan, 1987; Donk & van Zoest, 2008; Ottes et al., 1985; van Zoest & Donk, 2005). However, though no explicit inhibition in terms of deviation away was found that is beyond the baseline of zero, a contribution for top-down inhibition cannot be completely discounted. Specifically, the observed decrease in deviation towards implies that the relative activations at the distractor locations diminished over time. Active top-down inhibition may have contributed to decline this activation in saccadic deviation towards. Though the present data do not distinguish between a passive decay and active inhibition mechanism, the present results suggest in any case that stimulussalience only transiently influences the motor map in the oculomotor system.

The divergence with previous work in finding saccadic deviation away may be further explained by methodological dissimilarities between the present study and previous work. The present study is the first to investigate saccade trajectory deviations in a cluttered visual display, where salience is defined by the conspicuousness of a tilted orientation singleton relative to the surrounding orientation nontargets. In previous work, the target and distractor were typically presented as abrupt onsets on an empty background (e.g., Mulckhuyse et al., 2009). In the present study, target and distractor were surrounded by multiple other elements resulting in the presentation of an equal number of elements to the left and right of fixation. This difference between previous work and the present might explain why no saccadic deviation away from the distractor was found in the current study. Evidence for this idea is provided by McSorley, Haggard, and Walker (2004), who found that the presence of a second distractor in the opposite hemifield straightened saccades (i.e., they no longer deviated away from the task irrelevant distractor). In that study it was concluded that the inhibition of the distractors was coarse and balanced out as a result of the presentation of elements on both sides of the saccade trajectory. This same line of reasoning may explain the absence of inhibition and deviation away in the present study.

Various studies have provided evidence for the idea that saccadic deviations result from distractor-related activity in the frontal eye fields (FEF) and superior colliculus (SC) at the moment of saccade initiation (e.g., McPeek, 2006; McPeek et al., 2003; McPeek & Keller, 2001; Walker, Techawachirakul, & Haggard, 2009). McPeek (2006) demonstrated that FEF activity at the location corresponding to a distractor is related to the size and direction of saccadic deviation: Higher activity at the distractor site causes deviation towards whereas lower activity cause deviation away from the distractor location. Recently, Walker et al. (2009) showed that transcranial magnetic stimulation (TMS) of the right FEF increases saccadic deviation away. These results showed that the distractor had a larger effect on saccade deviation following stimulation. This modulation was only found when TMS was applied at 150 ms after cue onset, but not at 250 ms. Walker et al. (2009) have proposed that the FEF modulation transiently altered the relative salience between the target and the distractor. Following stimulation, the distractor was relatively more active and this required greater levels of inhibition, as indicated by the greater deviation away from its location. The present results further add to the idea of the FEF playing a critical role in representing relative levels of salience between competing objects, in that the present data demonstrate that relative raw stimulus-salience has a transient effect on oculomotor programming.

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