

There is no attentional global effect: Attentional shifts are independent of the saccade endpoint

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Many studies have found a strong coupling between selective attention and eye movements. The premotor theory of attention suggests that saccade preparation is directly responsible for such attentional shifts. While it has already been shown that the attentional shift is not directly coupled to the final stages of motor execution, it is currently unknown to what aspect of the earlier stages of saccade preparation the attentional shift is coupled. An important step in this preparation process is resolving the landing point when multiple elements compete for the saccade. Here we ask how such a competition influences the presaccadic attentional locus and whether the presaccadic shift of attention is coupled to the saccade landing position or the possible saccade goals. To this end, we adopt a global effect paradigm where a target is accompanied by a salient distractor resulting in the majority of eye movements landing in between target and distractor. To determine the allocation of attention, participants are presented with a discrimination task shortly before the execution of the saccade. Despite a strong global effect obtained for saccade endpoints, we find little evidence for attentional facilitation at the location between target and distractor, but strong attentional facilitation at the location of the target and distractor. We argue that attention is coupled to active oculomotor programs, but not part of the resolution of these programs towards the execution of the saccade.

Introduction

Many theorists have argued for an obligatory coupling between eye movements and attention. An important example is the premotor theory of attention, which states that the mechanisms involved in both the programming of an eye movement and the shifts of spatial attention are the same (Rizzolatti, Riggio, &

Sheliga, 1994). Indeed, there have been numerous studies showing that the execution of an eye movement is accompanied by an attentional shift towards the saccade target location (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Shepherd, Findlay, & Hockey, 1986; Van der Stigchel & Theeuwes, 2005). In these dual-task studies, the primary task is to execute an eye movement to a peripheral saccade goal as indicated by a central cue or a peripheral onset. While preparing the eye movement, participants have to perform a discrimination task on a probe stimulus presented either at the location of the saccade goal or at a different location in the visual field. The rationale for this type of paradigm is that the accuracy on the discrimination task should be dependent on *where* visual attention is allocated during saccade. Providing evidence for the idea that attention and eye movements are tightly coupled, performance on the discrimination task is best at the location of the saccade goal shortly before the execution of the eye movement and impaired at any other location in the display (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Khan, Blohm, Pisella, & Munoz, 2015; Kowler, Anderson, Doshier, & Blaser, 1995; Van der Stigchel & Theeuwes, 2005). Besides this behavioral evidence, the coupling between eye movements and attention has also been confirmed by electrophysiology as well as electrical stimulation (Bisley & Goldberg, 2003; Kustov & Robinson, 1996; Moore & Armstrong, 2003; but for a dissociation, see Juan, Shorter-Jacobi, & Schall, 2004).

While executing saccadic eye movements, there is a frequent discrepancy between the intended saccade goal and executed saccade program. For instance, it has repeatedly been observed that saccades undershoot their targets by about 10% (Adeli, Vitu, & Zelinsky, 2015; Kapoula & Robinson, 1986). Moreover, there is continuous variation of landing point over repeated

Citation: Van der Stigchel, S., & de Vries, J. P. (2015). There is no attentional global effect: Attentional shifts are independent of the saccade endpoint. *Journal of Vision*, 15(15):17, 1–12, doi:10.1167/15.15.17.

doi: 10.1167/15.15.17

Received July 7, 2015; published November 25, 2015

ISSN 1534-7362 © 2015 ARVO

instances (Becker, 1989). Given that the intended action is rarely consistent with the executed action, the question arises whether the attentional shift is coupled to the intended saccade goal or to the saccade endpoint. In a similar dual-task experiment as described previously, Deubel and Schneider (1996) observed that performance on the discrimination task was highest when the probe was presented at the same position as the saccade goal, independent of where the eyes landed. This indicates that the attentional shift is coupled to the intended saccade target rather than the actual landing position. Similar results were obtained in a paradigm with no obligatory saccade target in which subjects were allowed to aim freely within the spatially extended target (see also, Doré-Mazars, Pouget, & Beauvillain, 2004). These results seem to imply that target selection by means of an attentional selection process is precise, but the executed saccade is not. There is therefore no precise transformation of the spatial coordinates provided by the attentional mechanism into the spatial coordinates used for saccade execution.

Aside from these naturally occurring landing point variations, systematic landing point deviations can also be induced artificially. By shifting the target position systematically during the saccade over a number of trials it has been found that this adaptation process can be studied in a laboratory setting. Findings on the attentional allocation during saccadic adaptation have been mixed. One study found results in line with the idea that attention is allocated towards the goal of the adapted saccade rather than its endpoint (Ditterich, Eggert, & Straube, 2000), whereas Doré-Mazars and Collins (2005) observed that the orientation of attention followed the adaptive shift of saccadic endpoints. These inconsistent results could potentially be explained by the differences in the type of saccade that had to be executed, as the study by Doré-Mazars and colleagues required voluntary saccades in contrast to the study by Ditterich and colleagues (2000) in which reactive saccades were used. It could be that attention is only allocated towards the endpoint of adapted saccades when voluntary saccades are performed (for a discussion, see Doré-Mazars & Collins, 2005).

Dissociations between the intended and actual saccade landing positions in previous studies were evoked by deviations in the motor execution, either by the noisy motor system (Deubel & Schneider, 1996) or by saccadic adaptation (Ditterich et al., 2000; Doré-Mazars & Collins, 2005). It is currently unknown to what aspect of the saccade the attentional shift is coupled when the landing position differs from the intended landing position when there are multiple elements competing for the saccade. In the current study, our aim was to investigate the coupling between attention and eye movements using a paradigm in which the intended and actual saccade landing posi-

tions are dissociated due to the strong competition evoked by the presentation of competing stimuli, resulting in frequent involuntary saccades to a location other than the intended target location.

We adopted the global effect paradigm in which competing elements are presented simultaneously in close proximity (Findlay, 1982; Van der Stigchel & Nijboer, 2011). Even though the appearance of the target is known to the participant, many eye movements land in between the target and the distractor, or even on the distractor itself. This phenomenon can best be viewed as competition in oculomotor selection, where both elements trigger saccade preparation, which has to be resolved by top-down activation of the target and inhibition of the distractor. When saccades are initiated shortly after these elements are presented, both elements are still associated with strong activity, resulting in an “averaged” saccade directed to the intermediate location in between these two elements, or even to the distractor in case the distractor is visually more salient than the target (Deubel, Wolf, & Hauske, 1984). For longer latencies, top-down information can influence the selection process (van Zoest, Donk, & Theeuwes, 2004; van Zoest, Donk, & Van der Stigchel, 2012), resulting in a higher proportion of saccades towards the target. The global effect is therefore the strongest for saccades with a short latency (Findlay, 1982).

Here we will investigate the dynamics of the presaccadic attentional allocation during the preparation of a saccadic eye movement towards a target when accompanied by a distractor, resulting in deviations of the saccade landing position. This allows us to investigate whether the presaccadic shift of attention is coupled to the saccade landing position or the possible saccade goals. Therefore, in our experiment, participants were presented with a single target ring on half of the trials (single target condition), whereas a distractor ring was presented in close proximity to the target ring on the other half (target-distractor condition). To measure presaccadic attentional shifts for the resulting deviating landing points, a probe discrimination task was introduced: Within each ring a mask-line sequence was presented alternating every two frames (~23.5 ms). At some point prior to saccade initiation the line in one ring flipped from vertical to diagonal (for the duration of two frames) and back. The assumption here is that if attention is allocated to a particular location, discrimination accuracy should be higher at this location than at surrounding locations.

In this paradigm contrasting predictions emerge for the saccades that land near the center in the target-distractor condition. An eye movement executed to a location in between the target and the distractor does not reflect the selection of this intermediate location, but is the result of an incomplete selection process.

Both the target and distractor locations are still selected on the moment an averaged saccade is executed. If the presaccadic attentional shift is tightly coupled to the saccade landing point we expect high performance on the central location (coupling hypothesis). A contrasting prediction comes from the notion that both the target and distractor are still selected as possible saccade goals, but the irrelevant middle location is not. It could therefore be that attention follows the possible saccade goals and that performance is high at the location of both the target and the distractor (selection hypothesis). Finally if presaccadic attentional shifts follow only the intention of the participant, as indicated by the task instruction, we would expect to see only facilitation at the location of the target (intention hypothesis).

Experiment

Methods

Participants

Ten participants (six females) participated in the experiment. All participants had normal or corrected-to-normal vision and ranged in age from 20 to 34 years (mean: 25.4 years; *SD*: 4.5 years). All except author JV were naive to the purpose of the experiment. Naive participants were recruited using a public website and were paid 7 euros per hour (typically amounting to 21 euros).

The research reported in this article involved healthy human participants, and did not utilize any invasive techniques, substance administration or psychological manipulations. Therefore, compliant with Dutch law, this study only required, and received, approval from our internal faculty board (Faculty's Advisory Committee under the Medical Research [Human Subjects] Act [WMO Advisory Committee] at Utrecht University). Furthermore, this research was conducted, and informed consent of each participant obtained, according to the principles expressed in the Declaration of Helsinki.

Stimulus chronology

Upon trial initiation the stimulus consisted of 10 light gray rings (1.6° radius; 0.23° thickness; 64.2 cd/m²), five left and five right of a white central fixation dot (0.2°) placed on an imaginary circle with an eccentricity of 7.9° on a midgray background (32.1 cd/m²; Figure 1A). The center of the five rings was always deviated either slightly up or down from the horizontal axis (by 6.8° or 20.3° between the centers of each ring). This was done to prevent any ring from standing

exactly on the horizontal midline as this might provide an unfair advantage in the probe discrimination task (described later). The angular separation (with the fixation dot as reference) between the centers of neighboring rings was 13.5°. Within each ring a mask and a green vertical line (1.2° × 0.2°) were alternated every two frames (~23.5 ms; Figure 1B), starting with the mask. The mask was noise in the form of red (46.9 cd/m²) and green (86.5 cd/m²) squares (0.1° × 0.1°) randomly making up the circular shaped mask.

On half of the trials (single target condition) one of the light-gray rings changed to dark gray (target; 10.1 cd/m²) and on the other half of the trials (target-distractor condition) one light gray ring turned dark gray and one turned black (distractor; 0.6 cd/m²). The target was placed either left or right of fixation and its location within the five rings was randomly chosen from the location above or below the central ring. Therefore, the target eccentricity regarding the fixation point was always the same. In the target-distractor condition the distractor was placed above or below the target, separated by the central ring, putting it at an angular separation of 27°. Recent studies have shown that saccade averaging can still occur for separations up to 35° (e.g., Van der Stigchel & Nijboer, 2013).

One of the lines tilted left or right 23.5–235 ms after the onset of the target and potentially distractor. This happened either at the location of the target (target probe condition), the location opposite to the target (distractor probe condition, where in half of the trials the distractor was present) or at the central location in between the target and distractor (center probe condition). The tilted probe was present for two frames with the other vertical lines. On the next line presentation the probe reverted to vertical. The angle of the probe was determined for each participant individually to ensure performance was similar over participants and was measured repeatedly to compensate learning effects.

Procedure

Participants were instructed to keep their eye on the fixation dot during the appearance of the 10 place-holders with within each of them an alternating mask-line sequence. After a target onset asynchrony (600–900 ms) the gray target appeared, either by itself (single target condition) or with a black distractor (target-distractor condition). Participants were instructed to make an eye movement towards the target as soon as possible. They were informed that the dark gray ring could be accompanied by a black ring. She/he was also made aware of the fact that this ring could be distracting, but it was emphasized that while they had to try to make an eye movement towards the gray ring they should not delay this saccade in favor of avoiding

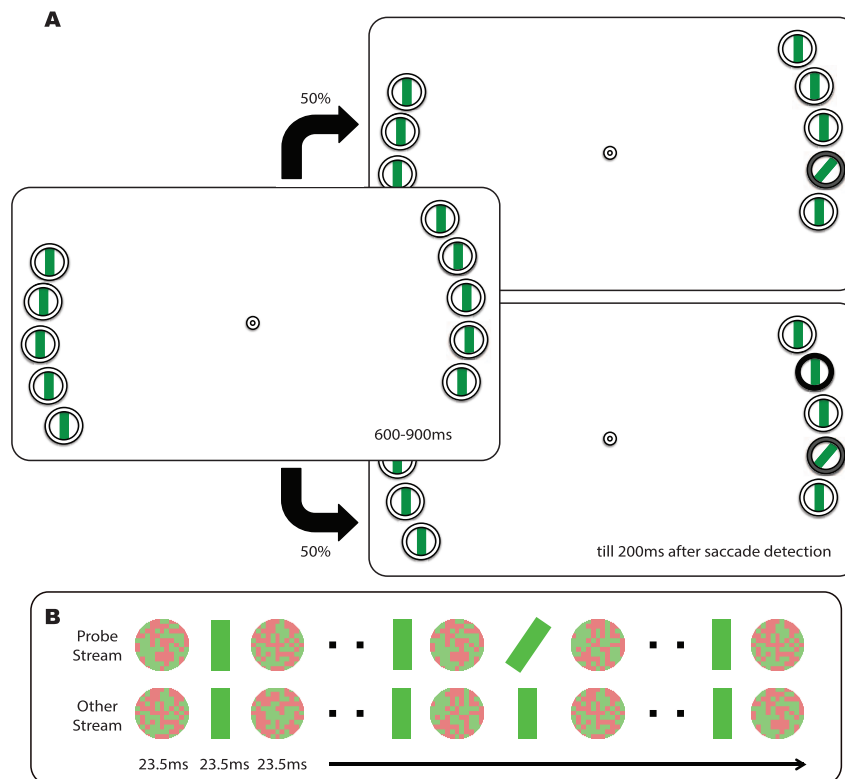


Figure 1. (A) Schematic trial sequence. Each trial starts with 10 placeholders on a gray background (here white): five left and five right of fixation, oriented slightly from the horizontal axis (up or down either 6.75 or 20.25°). After a target onset asynchrony of 600–900 ms, one of the placeholders turns dark-gray (target) and (in case of the distractor condition) another turns black (distractor). Here the tilted probe is drawn within the target ring. However, it could appear equally likely at either the target position, central position or distractor position on the side of the target shortly after target onset (23.5–235 ms). (B) Within each ring a continuous sequence of mask and line alternation takes place. In all except one ring the alternation is always that of mask and vertical line (other stream). However, at either the target location, central location or the location opposite to the target, the line tilts left or right for ~ 23.5 ms (probe stream). The onset of the tilt occurs in the period 23.5 to 235 ms from target onset.

the distractor. Trials were ended 200 ms after a saccade was detected or when the maximum trial time of 1000 ms was exceeded. At the end of the trial participants were prompted to respond whether they saw the probe tilt left or right. They did this by pressing the left or right arrow key on the keyboard; the next trial was initiated when both the response was given and the eye was detected to have returned to the central fixation dot.

Participants performed four sessions, each comprised of a staircase procedure followed by the search trials where a saccade towards the target was required. Each search trial block contained 528 trials. These were equally divided over the two main conditions (single target/target-distractor) as well as over the three subconditions (target/center/distractor probe). This resulted in a total of 2,112 trials per participant.

Staircase procedure

To determine the tilt angle of the probe during the experiment, before each block of trials, interleaved

quest staircases were run (Watson & Pelli, 1983). Staircase displays always contained three rings on an imaginary circle (again 7.9° radius) with the central ring either left or right of fixation on the horizontal axis. Participants made an eye movement to the central ring where the probe tilted from 71 ms to 94 ms (well before the eye movement was initiated). Participants had to discriminate using the left and right arrow keys whether they saw the probe tilted left or right.

To balance for the different compositional effects, we ran three interleaved staircases each estimating the 90%¹ correct threshold for a different composition: one staircase was performed on a light gray placeholder element flanked by two black rings, the other two staircases consisted of a dark-gray target ring or black distractor ring (respectively) flanked by two (light-gray) placeholder rings. This resulted in three interleaved quest staircases of 40 trials each. After the three staircases were completed, QuestMean was used on each staircase to determine the probe angle corresponding to the 90% correct threshold. The average

threshold of the three staircases was used as the probe angle in the regular trials.

Apparatus and eye movement analysis

Stimuli were presented on a 19-inch LaCie monitor (Electron Blue IV, LaCie, Tigard, France) at a resolution of 1600×1200 and a frame rate of 85 Hz. Stimuli were generated using the Psychtoolbox (Brainard, 1997), including the EyeLink toolbox (Cornelissen, Peters, & Palmer, 2002). Eye movements were recorded using an SR-Research EyeLink II system (SR-Research, Mississauga, Ontario, Canada) at a sampling frequency of 500 Hz. The participant's head was placed in a chinrest so that the eyes were at a distance of 57 cm from the screen. Images were viewed binocularly, but eye movements were recorded from the left eye only. A nine-point calibration procedure was executed prior to each staircase procedure and each search trial block, individually. Eye movement data were used both for online and offline analysis.

Online analysis was limited to detecting the initial saccade. A saccade was detected when the eye position moved outside of a range of 3° from the central fixation dot. For offline saccade detection a velocity threshold of $20^\circ/s$ was used, after which start and endpoint of the saccade were approximated by searching back and forth until the velocity was two standard deviations higher than the velocity during fixation (as in, Smeets & Hooge, 2003). Saccades with amplitudes smaller than 0.5° were removed from the analysis. When a small saccade was removed, the fixations before and after this saccade were added together. Fixations shorter than 50 ms were removed from further analysis. For the analyses below only the landing point of the first saccade and the latency were required. We calculated the latency by subtracting the onset time of the target from the onset time of the first saccade after target onset. The landing point of the saccade was based on the subsequent fixation: We averaged the vertical and horizontal eye position over the fixation directly preceding the first saccade. Finally, a radial landing point is calculated by finding the angle between the fixation dot and the landing point of the saccade.

To exclude erroneous trials, the resulting saccade characteristics were used to determine whether a trial is included in the final analysis. (The average percentage of trials on which a specific error occurs is given behind each criterion). First, the eye had to be within a range of 1.5° of the central fixation dot upon the onset of target and potentially distractor (2.4%). Secondly, saccades with latencies shorter than 60 ms and longer than 500 ms were excluded from further analysis (3.1%). Thirdly, saccades were required to have a minimum amplitude of 70% and a maximum of 130% of the target eccentricity (3.5%) and to have a landing

with an angular separation from the center ring of no more than 33.8° (2.0%). In very rare occasions frame presentations missed the required timing and the probe was onscreen for more than two frames (0.1%). Finally, saccades initiated earlier than 12 ms after the onset of the probe were excluded from further analysis (33.8%), as the probe can no longer be discriminated from saccade onset. The combination of the criteria led to an exclusion of 38.1% of the trials. Note that this high percentage is mainly the result of the timing of the probe with respect to the latency: Purely evaluating whether participants properly executed their eye movements, less than 7% of the trials would have been excluded.

Results

Global effect

To investigate how the deviation of saccade landing positions from the (intended saccade) target influences presaccadic attentional shifts it is essential that our distractor manipulation resulted in a broad distribution of landing points. Not only do we require eye movements to be captured by the distractor, but also eye movements should land at positions in between the target and distractor. In Figure 2 we plot a histogram of all eye movements (collapsed data from all participants) as a function of radial landing position. To account for different stimulus orientations, all eye movement landing positions were first oriented as if the central ring stood directly right of fixation (π radians on the x -axis). In blue we see the number of saccades for the single target condition. This distribution shows that the presentation of the placeholders did not result in a bias in saccade endpoints as there is no shift in the direction of the majority of the placeholders (which would be leftward in this figure). In red the broader distribution is the result of the additional distractor (target-distractor condition). Clearly, we find a broad landing point distribution, slightly skewed in the direction of the distractor. As it is important that the broad distribution is found not only in collapsed data, but also for individual participants, distributions for individual participants are plotted in Figure 3. We find the distractor manipulation was successful in establishing a global effect.

Typically the global effect is also expressed in shorter latencies for saccades landing near the center/salient distractor. To evaluate this we sorted the trials based on the radial landing position (angle between fixation point and endpoint of the first saccade) for each participant, separately. The data were divided over five bins and for each bin we calculated the median radial landing position and the median latency. In Figure 4 we plot latencies as a function of median landing position averaged over the 10 participants. While the results from Figure 4 reveal an

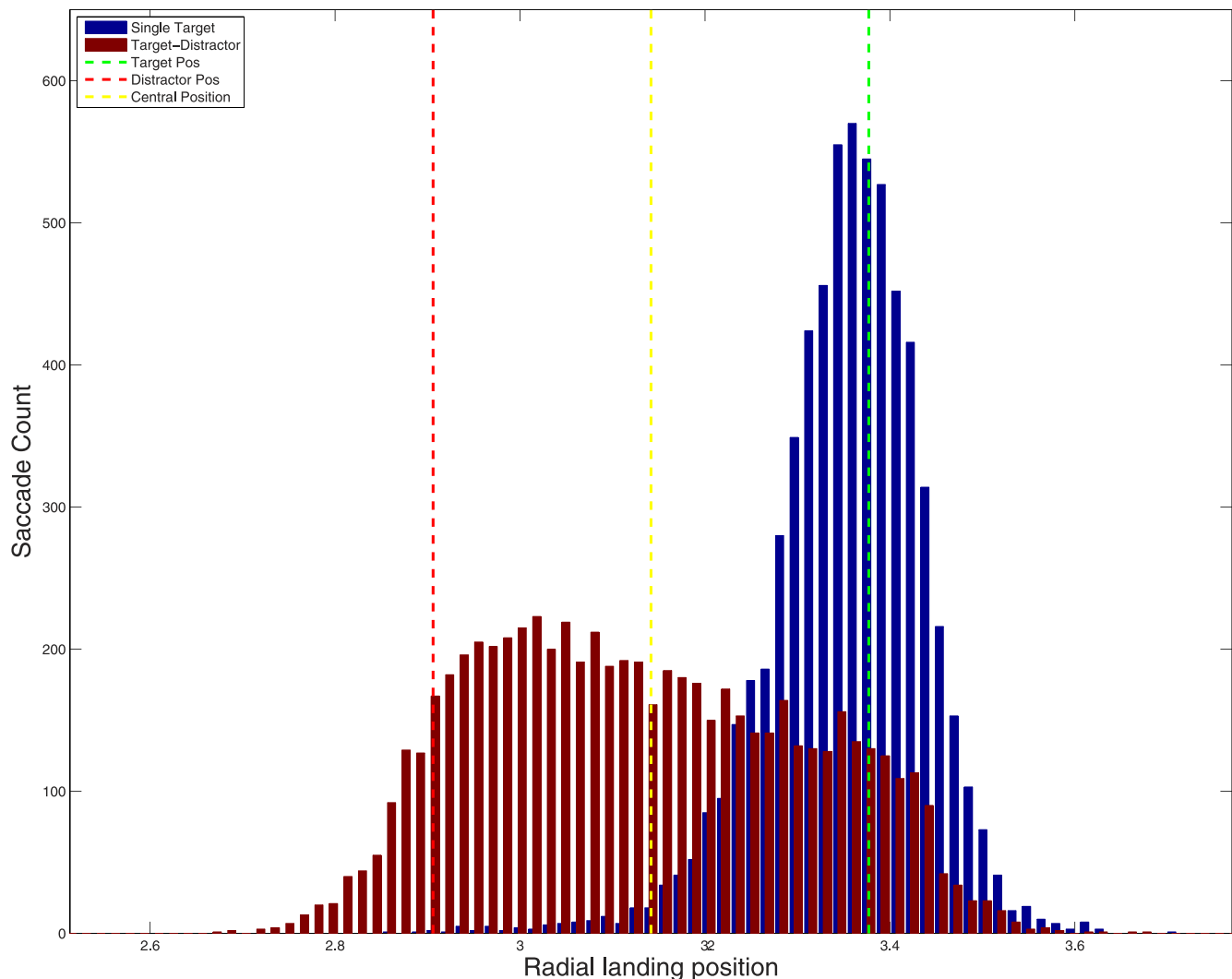


Figure 2. Histogram of landing point positions in radians collapsed over participants. Both the distribution of landing points for the single target condition (in blue) and the target-distractor condition are plotted in the same Figure. The vertical yellow dashed line refers to the location of the element in between the target and the distractor, whereas the green and red line refer to the target and the distractor, respectively.

increase in average latencies as saccades land closer towards the target, a one-way repeated measures ANOVA with landing position as a factor and latency as the measure revealed only a trend of landing position in the target-distractor condition, $F(1.939, 17.451) = 3.119$, $p = 0.071$, with Greenhouse-Geisser correction because the sphericity assumption was violated.

Performance

As there is the possibility that some of these effects unfold differently over time, we plot performance for each condition as a function of the time from the probe onset to the onset of the saccade. We do this by again binning saccades: First sorting was done based on the time to the saccade from probe onset (subtracting saccade onset time from probe onset time), following sorted saccades were

divided over five bins and for each bin the median time to saccade and proportion correct was calculated. In Figure 5A the performance for the single target condition is shown and in Figure 5B the performance for the target-distractor condition is shown. As expected for the single target condition, probe performance was much higher at the target location than the center and distractor location. A two-way repeated measures ANOVA with time to saccade and probe condition as factors and proportion correct as a measure showed a significant main effect of probe location, $F(2, 18) = 102.533$, $p < 0.001$. Pairwise comparisons showed that the probe was discriminated significantly more frequent when displayed in the target than in the middle ($p < 0.001$) or opposite location ($p < 0.001$). While it appears the probe is also selected slightly more frequent than the opposite location, we should note that separate t tests demonstrated that while the

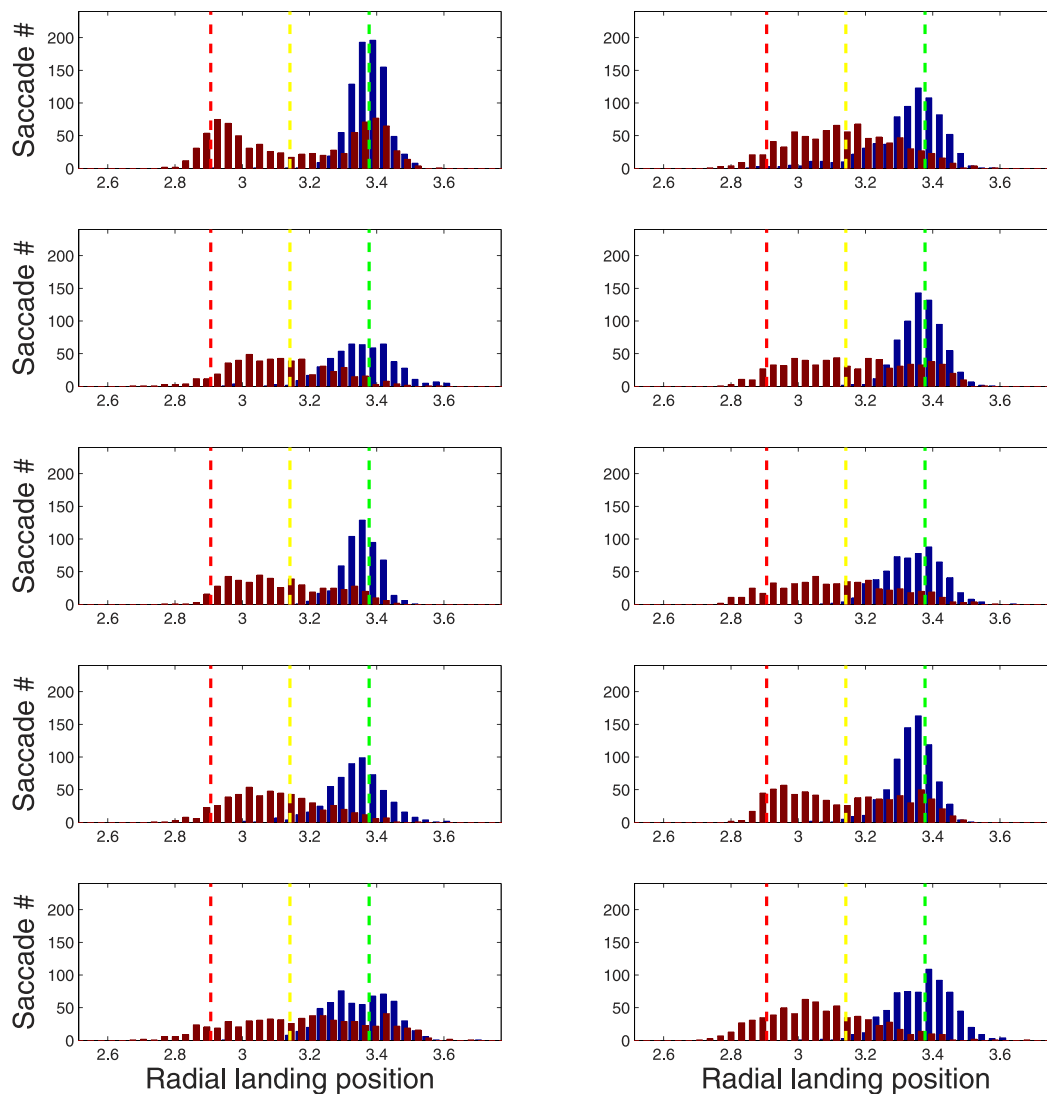


Figure 3. Histogram of landing point positions in radians for individual participants. Both the distribution of landing points for the single target condition (in blue) and the target-distractor condition are plotted in the same Figure.

proportion correct for the target location differed significantly from chance at a Bonferroni corrected alpha level of 0.0167, $t(9) = 9.460$, $p < 0.001$, the proportion correct for the center position did not significantly differ from chance, $t(9) = 2.271$, $p = 0.049$.

Turning to the target-distractor condition we see a decrease in performance at the target location, however, a two-way repeated measures ANOVA again revealed a significant main effect of probe, $F(2, 18) = 10.332$, $p < 0.005$. As in the single target condition the probe at the target location was discriminated significantly more frequent than at the center location ($p < 0.005$). Also at the distractor location the probe was discriminated significantly more frequent than at the central location ($p < 0.05$). Discrimination proportion exceeded chance level for all probe conditions for a corrected alpha of 0.0167 [$t(9) = 7.102$, $p < 0.001$; $t(9) = 5.327$, $p < 0.001$; $t(9) = 3.629$, $p < 0.01$, respectively for

the target, distractor and center probe location] indicating that performance of all locations was facilitated in the target-distractor condition.

The fact that both performance on the target and distractor location exceeded that of the center probe location is counter to the notion that there is a tight coupling between the saccade endpoint and attention. In this light, it is important to note that there are other potential reasons why performance on the central location falls short of the higher performance on the target and distractor location. For instance, it is possible that the probe was more difficult to discriminate in the central ring.

Staircase performance

If masking was indeed stronger on the central location we should be able to see this difference in the threshold

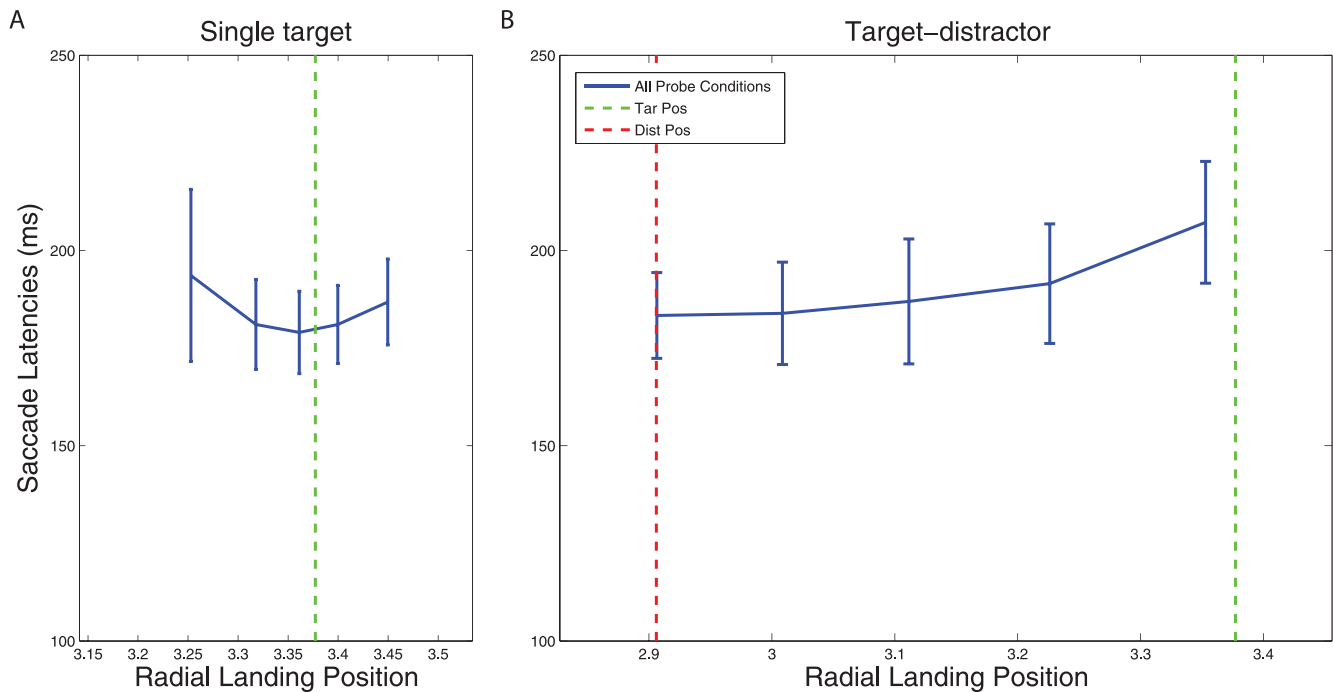


Figure 4. Mean of the median latencies of initial saccades as a function of landing position. Error bars denote standard error of the mean.

angle resulting from the quest staircases. Using the QuestMean procedure and averaging over the four staircases and the 10 participants (in that order) resulted in a threshold angle of 32.9 for the target (*SE*: 4.4), 35.0 (*SE*: 4.2) for the distractor, and 24.3 (*SE*: 2.7) for the central probe. Separate *t* tests showed that the threshold for the center probe was significantly lower than both

the threshold for the target probe and the distractor probe at a Bonferroni corrected alpha level of 0.0167, $t(9) = 3.900, p < 0.005$; $t(9) = 5.4813, p < 0.0005$, respectively. The fact that the threshold for the central probe resulted in the lowest threshold makes it highly unlikely that probe discrimination at the central location was facilitated compared with other locations.

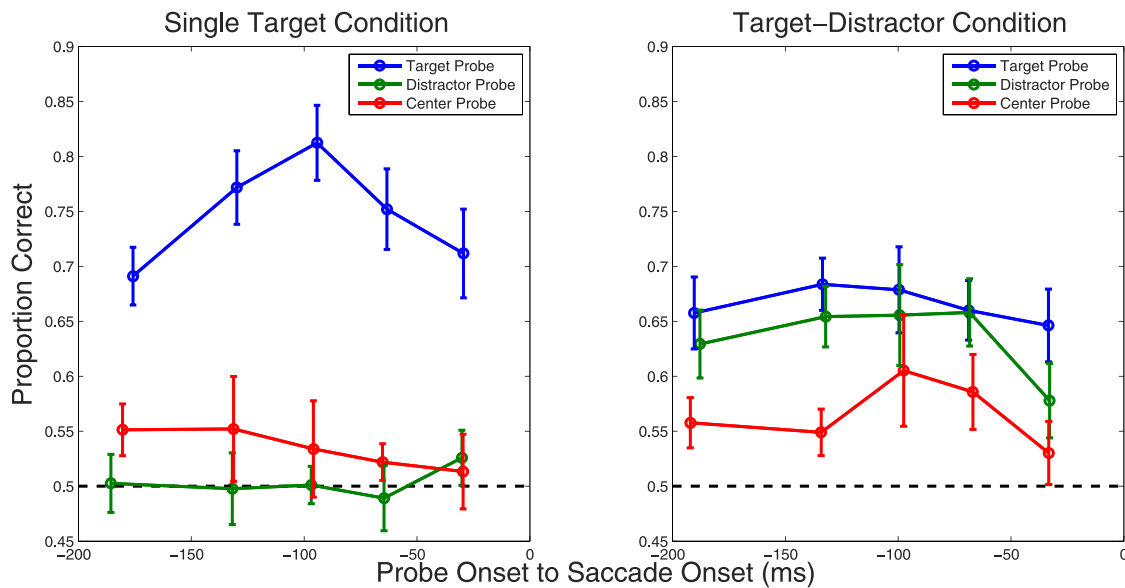


Figure 5. Performance on the probe detection task as a function of the time between saccade onset and probe onset. (A) Performance for the probe on the target location (blue), distractor location (green), and central location (red). (B) As A only now for the target-distractor condition. Error bars represent standard error of the mean.

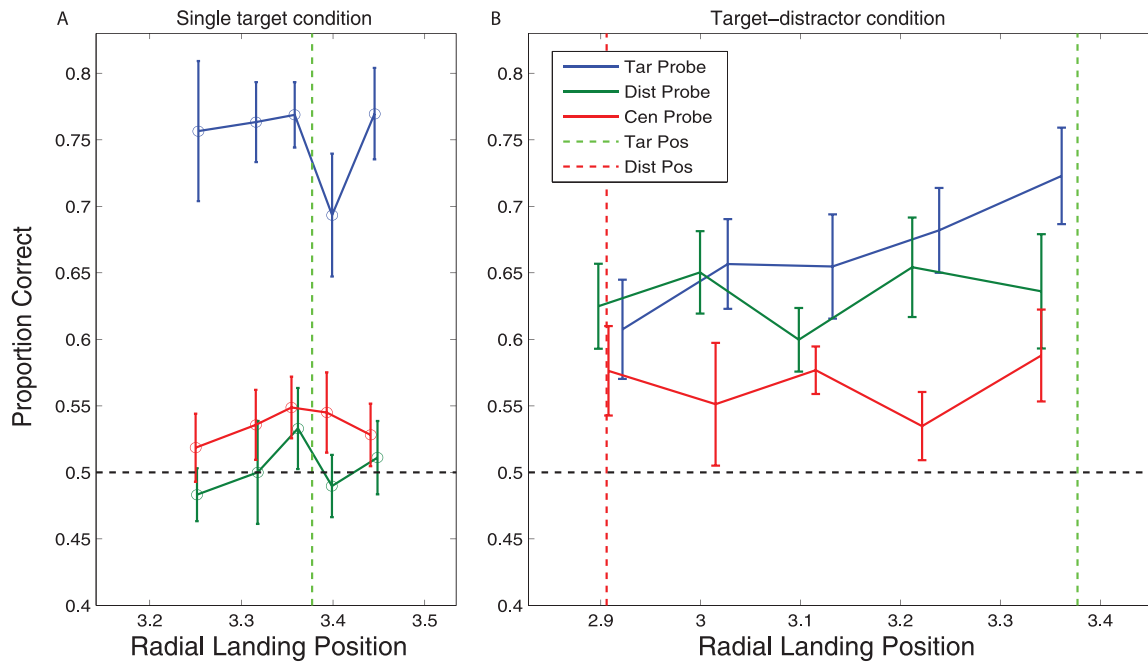


Figure 6. Performance on the probe detection task as a function of the time between saccade onset and probe onset. (A) Performance for the probe on the target location (blue), distractor location (green), and central location (red). (B) As A only now for the target-distractor condition. Error bars represent standard error of the mean.

Landing position

Even though performance at the central probe location was close to chance level, inspection of Figure 5B shows a slight boost in performance towards the initiation of the saccade. Thus, technically there is still a possibility that the saccade landing point does lead to a performance increase when saccades fall closer to the center than the outside. If performance is indeed coupled to the landing point we should find the strongest facilitation for eye movements that land closest to the central ring. To evaluate, we again sorted saccades on the basis of their landing position and divided the sorted saccades over five equal bins. For each bin we calculated both median landing position and proportion correct, resulting in Figure 6 where performance as a function of radial landing position is presented for each probed location averaged over all participants. If there is a coupling between presaccadic attention and landing point we expect performance to be highest at the landing points corresponding to the probe location. That is, for the red line reflecting the eye movements to the center probe condition, we would expect performance to be highest for eye movements falling closest to the central location. This pattern did not emerge, however, for the eye movements in both the center probe and the distractor probe condition. Only in the target probe condition did we see facilitation towards the target. Nevertheless, a two-way repeated measures ANOVA with landing point and probe condition as factor and proportion correct as

measure revealed no main effect for landing position, $F(4, 36) = 1.474$, $p = 0.230$. Also the interaction between probe condition and landing bin was not significant, $F(8, 72) = 1.250$, $p = 0.283$.

General discussion

The aim of the present study was to investigate the coupling between saccade preparation and the locus of presaccadic attentional shifts during oculomotor competition. To this end we introduced a global effect paradigm where the instructed saccade target could be accompanied by a neighboring salient distractor. To determine the allocation of attention, shortly before the execution of the saccade, participants were presented with a discrimination task. On trials in which the distractor was present, landing points were skewed in the direction of the distractor: A large proportion of saccades landed in between the target and the distractor or even on the distractor. This broad distribution of landing points allowed us to evaluate whether the coupling between attention and eye movements is associated with the instructed target, the elements competing for the saccade, or follows saccade preparation to the location in between the elements competing for the saccade.

As expected when only the target was present, probe performance was much higher at the target location than at the neighboring locations, verifying that in our

paradigm presaccadic attention is narrowly allocated to the intended saccade target when there is no competition for the saccade. Crucially, in trials in which a distractor was present (and the majority of saccades landed in between target and distractor), attention did not follow the executed saccade: The discrimination probability was higher for the target and distractor location compared to that of the intermediate location. This finding clearly contrasts to the coupling hypothesis presented in the Introduction that is based on the notion that the presaccadic attentional shift is directly linked to the saccade landing point. Furthermore, given that the performance at the distractor location was similar to the target location, presaccadic attentional shifts also do not strictly follow the participant's intention (intention hypothesis). Rather our data are best explained by the selection hypothesis, as attentional benefits were found at both the location of the target and distractor, but not to the landing point of the averaged saccade.

Given that our results do not follow the coupling hypothesis they seem to be in conflict with a strict interpretation of the original premotor theory of attention. It has already become evident that saccade preparation is not always the determining factor in attentional shifts as is proposed in the original premotor theory of attention (see also, Born, Mottet, & Kerzel, 2014; see also, Smith & Schenk, 2012). For instance, endogenous attention can be shifted without the need for saccade preparation, demonstrating that not every attentional shift requires saccade preparation (Smith, Rorden, & Schenk, 2012). On the other hand previous studies have shown that there is no precise transformation of the coordinates provided by the attentional mechanism into the coordinates used for saccade execution (e.g., Doré-Mazars et al., 2004). Thus the late stages of motor execution have been shown not to influence the attentional locus. Our study extends this finding by demonstrating that saccade landing point resolution, in light of multiple elements competing for the saccade, also does not influence the locus of attention.

While this limits the strict coupling of attention and eye movement preparation, it does not mean they have to be completely separate. The deviation in landing points in the direction of the distractor is typically strongest for the shorter latencies (while not significant for the current data, we also find effects at a trend level). This is in line with the idea that eye movements initiated shortly after the presentation of two competing stimuli are predominantly based on physical, bottom-up, information (van Zoest et al., 2004). In these situations, the executed eye movement can best be seen as the weighted average of the different saccade vectors present in the oculomotor system. An eye movement executed to a location in between the target and the

distractor does not therefore reflect the selection of this intermediate location, but is the result of an incomplete selection process. Thus, whereas the saccadic endpoint is determined by the averaging of the active oculomotor programs, it appears that the attentional shifts follow the locations of the active programs that are still part of the ongoing oculomotor competition.

In contrast to previous studies, we did not observe any effect of the timing of the probe before saccade onset on the discrimination task. Previous studies have observed that attentional facilitation at the saccade goal gradually builds up over the 150 ms prior to saccade onset, peaking right before saccade onset (Born, Ansorge, & Kerzel, 2013; Deubel, 2008; Doré-Mazars et al., 2004). We think this discrepancy might be explained by the abrupt onsets of the target and the distractor in the present study. To evoke a strong global effect, we made both elements conspicuous compared to the placeholders. For this reason, the onsets will have captured attention to both locations, followed by the presaccadic attentional shift due to the competition evoked by both elements. We therefore think that the lack of an effect of discrimination performance over time is due to a mixture of attentional capture and presaccadic attentional shifts, resulting in a more constant level of facilitation at both the locations of the target and the distractor.

It might be argued that the low performance at the central probe location is unrelated to presaccadic attentional shifts, but simply because discrimination is more impaired in the central location. This is unlikely for two reasons. First, the target and distractors form onsets resulting in forward masking at the target and distractor locations. Therefore, the discrimination of the probe should be more impaired at these locations compared to the central location where the placeholder ring luminance stays constant with the onset of target and distractor. Secondly, as we have shown in the result section the threshold estimated by the staircases is actually lowest for the central position even when such onsets are not present. Together this means that if anything, discrimination of the probe in the central ring should be facilitated rather than impaired compared to the other two locations.

With respect to saccade averaging, neurophysiological recordings have shown that both the target and the distractor are represented as peaks of activity in the superior colliculus (SC) (Edelman & Keller, 1998). The SC is a midbrain structure, which contains a retinotopically-organized map in which neural activity is correlated with target selection (Wurtz, Goldberg, & Robinson, 1980). Interestingly, the SC is also involved in the allocation of spatial attention (Krauzlis, Lovejoy, & Zenon, 2013). Our finding that attentional allocation was strongest at the possible saccade targets seems to be in line with the evidence that the largest neural

activity in the SC during averaging saccades remains at the sites of the two visual stimuli (Edelman & Keller, 1998). The coupling between the oculomotor system and attention might therefore still be present at the level of the SC, with lower-level oculomotor areas determining the actual saccade landing point. In this view, attentional allocation is linked to the peaks of activity in the SC.

In short, the results demonstrate that there is no “attentional global effect” as attention is not averaged at the location in between the elements competing for the saccade. Rather than following the saccade preparation process to its final destination, attention is distributed over competing saccade targets. Thus, we propose that the role of attention can best be viewed as following active oculomotor motor programs. At any point in time only one eye movement can be executed. Therefore, the competition between the oculomotor programs has to be resolved to determine the saccade endpoint. Nevertheless, this resolution is not required for attentional allocation: While a single landing point has to be determined, attention can remain linked to the active oculomotor programs and does not follow the saccade landing point in light of elements competing for this saccade.

Keywords: global effect, saccadic eye movements, premotor theory

Acknowledgments

This research was funded by grant 452-13-008 from NWO (Netherlands organization for Scientific Research) to SvdS.

Commercial relationships: none.

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Footnote

¹ One single initial participant performed the staircases with 82% correct threshold.

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