Eye abduction reduces but does not eliminate competition in the oculomotor system

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Although it is well established that there is a tight coupling between covert attention and the eye movement system there is an ongoing controversy whether this relationship is functional. Previous studies demonstrated that disrupting the ability to execute an eye movement interferes with the allocation of covert attention. One technique that prevents the execution of an eye movement involves the abduction of the eye in the orbit while presenting the stimuli outside of the effective oculomotor range (Craighero, Nascimben, & Fadiga, 2004). Although eye abduction is supposed to disrupt activation of the oculomotor program responsible for the shift of covert attention, this crucial assumption has never been tested experimentally. In the present study we used saccadic curvature to examine whether eye abduction eliminates the target-distractor competition in the oculomotor system. We experimentally reduced the ability to execute saccades by abducting the eye by 30° (monocular vision). This way the peripheral part of the temporal hemifield was located outside the oculomotor range. Participants made a vertical eye movement while on some trials a distractor was shown either inside or outside of the oculomotor range. The curvature away from distractors located outside the oculomotor range was reduced, but not completely eliminated. This confirms that eye abduction influences the activation of the oculomotor program, but points to the fact that other forms of motor planning, such as head movements are also represented in the oculomotor system. The results are in line with the idea that covert attention is an emerging property of movement planning, but is not restricted to saccade planning.

Introduction

The premotor theory of attention states that spatial attention is generated in the same neural circuits used to plan and execute motor actions (Klein, 1980; Rizzolatti, Riggio, Dascola, & Umiltá, 1987). According to this influential idea the preparation of an eye movement is a required step for any shift of attention (Belopolsky & Theeuwes, 2009, 2012). The eye movement can subsequently be executed (overt attention) or not (covert attention). Although there is ample evidence for an anatomical overlap between the neural circuits controlling saccade planning and the deployment of attention (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000; Perry & Zeki, 2000), it remains unclear whether the relationship between saccade planning and attention is functional. A critical question is whether saccade generation and covert attention can operate independently.

To address this question, a number of studies have focused on patients suffering from different forms of opthalmoplegia. This disorder is characterized by a weakness or paralysis of one or more extraocular muscles, which leads to the inability to execute eye movements to certain locations in the visual field. Patients with opthalmoplegia showed no cueing effects for the affected locations in the Posner cueing task, suggesting that they were unable to shift covert attention to these locations (Craighero, Carta, & Fadiga, 2001; Gabay, Henik, & Gradstein, 2010; Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988; Smith, Rorden, & Jackson, 2004). Craighero and colleagues (Craighero et al., 2004) developed a method to impair the ability to execute eye movements in healthy
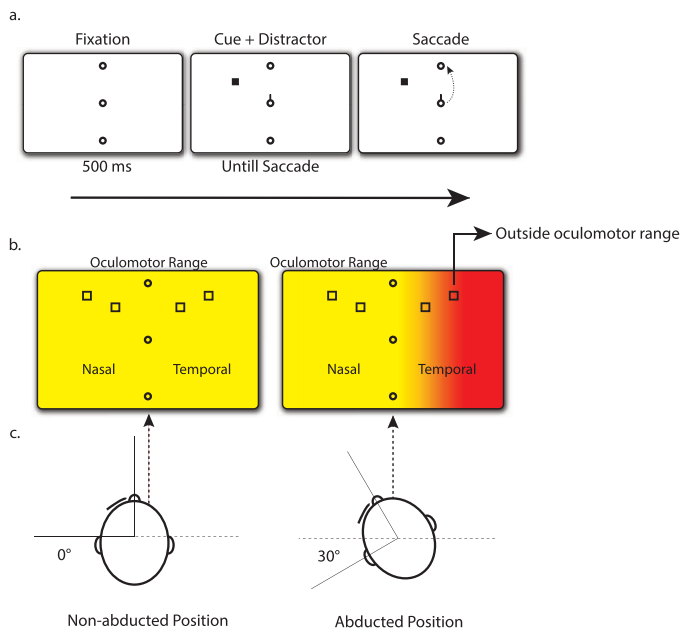
Figure 1. Experimental paradigm. (a) The fixation dot was located at the center of the screen. Two other fixation dots were placed 10° above and below fixation. The saccade cue was a small white line located either at the top or bottom of the central fixation dot. The distractor was presented simultaneously with the saccade cue. (b) Possible distractor locations for a trial with an upwards saccade. A close distractor was located at 5.75° of horizontal distance and 5.75° of vertical distance from the fixation point. A remote distractor was located at 10.75° of horizontal distance and 7.75° of vertical distance from the fixation point. (c) In the nonabducted part of the experiment the participant was looking straight ahead at the screen. In the abducted part the head was rotated 30° of arc, forcing the participant to look sideways at the screen.

participants. In their eye abduction paradigm the screen was placed to the right of participants' sagittal plane, forcing them to rotate the eye 40° into the temporal hemifield. Looking at the screen from this angle prevented them from making eye movements further into the temporal hemifield, while the visual acuity was unaffected. Similar to the opthalmoplegic patients, the authors found that cueing effects were abolished at locations to which no eye movement could be executed. Smith and colleagues (Smith, Ball, & Ellison, 2014; Smith, Ball, Ellison, & Schenk, 2010; Smith, Schenk, & Rorden, 2012) replicated these results in a variety of cueing and visual search tasks.

The reported absence of cueing effects at locations where the eye cannot move is attributed to disrupted activation of the oculomotor program responsible for the shift of covert attention. However, it is merely an assumption that abduction of the eye leads to the inability to represent these locations in the oculomotor system. The degree of attentional allocation is inferred based on the cueing effect (the difference between the

reaction time on valid versus invalid cued trials), which has been shown to be influenced by preceding trials, or by strategic top-down modulation (e.g., Macaluso & Doricchi, 2013). To establish a direct link between covert attention and eye movement preparation, it is crucial to determine whether the attentional deficits observed in eye abduction tasks stemmed from the inability to prepare an action toward it.

We designed a task in which saccadic curvature was used to examine whether eye abduction reduces the amount of activity visual distractors evoke in the oculomotor system. Crucially, participants were not required to perform an attentional task; the distractor was always completely irrelevant. This allowed us to directly measure the effect of allocation of attention on oculomotor activity. Saccade curvature has been attributed to competition between potential saccade targets in the oculomotor map, supposedly occurring within the intermediate layers of superior colliculus (Doyle & Walker, 2001; McPeek, 2006; McPeek, Han, & Keller, 2003; Van der Stigchel, Meeter, & Theeuwes, 2006; Walker & McSorley, 2008). Curvature toward distractor locations has been suggested to arise from failure to suppress competing distractor representations (McPeek, 2006), whereas successful suppression of the competing distractor representations results in curvature away from the distractor location (Belopolsky & Theeuwes, 2011). If the attentional deficits observed in previous studies stemmed from the inability to prepare an action, saccades should not curve away from distractors presented outside of the oculomotor range. This would point toward a strong functional coupling between oculomotor preparation and the allocation of attention. Alternatively, if oculomotor activity is unaffected by eye abduction, this would indicate that previously reported attentional deficits are independent of action preparation.

Experiment 1

We experimentally reduced the ability to execute saccades by abducting the eye 30° into the temporal hemifield (monocular vision), which placed the peripheral part of the temporal hemifield outside of the oculomotor range (Figure 1). A salient distractor could be shown either within or beyond the oculomotor range. Traditionally, the effects of abduction are compared across visual hemifields. One problem with this analysis is that the nose is blocking the visual stimulation presented in the nasal hemifield in the nonabducted, but not in the abducted condition. To that end we also manipulated distractor location. Participants made a vertical eye movement while on some trials a salient distractor could be presented either

at a close or remote location in one of the hemifields. This meant that in the temporal hemifield, the close distractor was presented inside of the oculomotor range, whereas the far distractor was presented outside of it. Crucially, this distractor was completely irrelevant for the task as participants were never required to attend or respond to this stimulus. If the inability to execute a saccade eliminates the target-distractor competition in the oculomotor system we expected to observe no curvature away from the distractors presented outside of the oculomotor range.

Methods

Fourteen participants, ages 19 to 27 (mean: 23 years, eight females), received either money or study credit to participate in two 30-minute experimental blocks with a 15-minute break in between, consisting of 720 trials in total. To assess eye dominance each participant sat 2 m away from the experimenter while extending their arms and bringing their hands together in front of the eyes, leaving only a small gap. They were told to look at the experimenter through this gap. The eye visible to the experimenter was recorded as dominant. Only participants with a right dominant eye were allowed to participate in Experiment 1. The present and all following experiments, including the consent procedure, were approved by the local ethics committee of the VU University Amsterdam. Participants received information about the study and their rights and gave a written informed consent. Participants were naïve with respect to the aim of the study and had normal or corrected-to-normal visual acuity.

The experiment was conducted in a darkened room. Stimuli were presented on a 21-inch monitor (Samsung 2233RZ, Samsung, Seoul, South Korea) with a spatial resolution of 1680×1050 pixels and a refresh rate of 120 Hz. Participants performed the task monocularly, with the left eye patched. Participants viewed the screen from a distance of 70 cm, and eye movements were recorded with the Eyelink 1000 (SR Research, Mississauga, Ontario, Canada), sampling at 1000 Hz. The fixation dot and saccade targets were white open circles with a radius of 0.37° and a luminance of 105 cd/m^2 placed on a black background. The saccade cue was a small white line of 0.56° located either on top or at the bottom of the central fixation dot (Figure 1).

In the nonabducted block the eye was positioned in the center of the orbit with the participants looking straight ahead with their head fixed in a table mounted headrest. In the abducted block the headrest was rotated 30° to the left, bringing the eye in an abducted position when looking at the screen. The angle of 30° was chosen because participants were still able to maintain a stable fixation and make accurate vertical

eye movements in this position, but were unable to execute large eye movements into the temporal hemifield. The order of the blocks was counterbalanced across participants.

Participants had to look at the fixation dot placed at the center of the screen and press spacebar to start a trial. The potential saccade targets were placed on top and at the bottom of the screen, at a distance of 10° from fixation. After 500 ms the saccade cue appeared. The saccade cue was a small white line located either on top or at the bottom of the central fixation dot. In two-thirds of the trials the distractor was presented simultaneously with the saccade cue. This distractor was located in the upper hemifield if an upward saccade had to be made and in the lower hemifield if a downward saccade had to be made. A close distractor was located at 5.75° of horizontal distance and 5.75° of vertical distance from the fixation point, in any of the two hemifields (nasal or temporal). A remote distractor was located at 10.75° of horizontal distance and 7.75° of vertical distance from the fixation point (nasal or temporal hemifield). In one-third of the trials no distractor was presented. These trials were used to assess the baseline saccade trajectory for every participant. The saccade target remained on the screen until a saccade was detected. If the direction of the detected saccade was more than 30° of arc off from the saccade target, a beep was heard and the trial was discarded.

For each saccade we calculated the angular deviation of the saccade path for each 1-ms sample point that was further than 0.5° from the central fixation and further than 0.5° from the endpoint of the saccade, relative to a straight line from the starting point of the saccade to the saccade endpoint. A median of these deviations was calculated for each saccade. For each participant and each condition this curvature was averaged across saccade direction and normalized to distractors in the top left hemifield. The effect of the distractor was determined by calculating the difference with curvature in the no distractor baseline condition. This was done separately for the nonabducted and abducted position (for a similar method see Belopolsky & Theeuwes, [2011] and Van der Stigchel et al., [2006]).

To determine the average saccade trajectories, eye position samples of each saccade were rotated so that all trials matched an upward saccade. Because every saccade had a different amplitude we normalized the eye positions samples. For each sample point its position relative to the total saccade amplitude was calculated. These normalized sample points were divided in ten amplitude bins. For each amplitude bin the average distance of the sample points away from the straight line connecting start and endpoint of the saccade was calculated. Subsequently, these values were averaged across trials and participants. Trajectories were plotted by connecting the values in each amplitude

bin. This was done separately for each hemifield (temporal/nasal), eye position (nonabducted/abducted), and distractor eccentricity (close/far). Note that every person has its own idiosyncratic baseline saccade trajectory. To correct for this we used the no-distractor trials as a baseline condition. This was done separately for the abducted and nonabducted position. Next, we subtracted out this baseline for each distractor location.

Results

Trials in which a saccade was detected before target onset were discarded. If the saccade was more than 3° shorter or longer than the 10° separating the fixation point and saccade target, had a latency shorter than 80 ms or longer than 600 ms, or did not start within 2° from fixation and end within 3° from the target, the trial was discarded. This resulted in an average loss of 25% of all trials.

Figure 2 shows the mean curvature away from the distractor and the averaged saccade trajectories for all conditions. As can be seen from this figure saccades always curved away from the distractor, even when it was presented beyond the oculomotor range (t test, $t(13) = 4.36$, $p < 0.001$). The critical question is whether in the abducted position the magnitude of this curvature was decreased for remote distractors in the temporal hemifield. In order to test this, the data were subjected to a repeated-measures analyses of variance (ANOVA) with hemifield (temporal/nasal), eye position (nonabducted/abducted), and distractor eccentricity (close/far) as factors. This conventional eye abduction paradigm analysis (Craighero et al., 2004; Smith et al., 2010, 2012, 2014) revealed a main effect of eye position, $F(1, 13) = 4.92$, $p < 0.05$, $\eta_p^2 = 0.27$, but not of hemifield, $F(1, 13) < 0.0001$, $p = 0.99$, or distractor eccentricity, $F(1, 13) = 3.42$, $p = 0.09$. There was a significant three-way interaction between hemifield, eye position, and distractor eccentricity, $F(1, 13) = 4.84$, $p < 0.05$, $\eta_p^2 = 0.27$, indicating that presenting a distractor outside of the oculomotor range led to a decrease of oculomotor competition in the temporal, but not in the nasal hemifield. Given potential problems with comparison across visual hemifields outlined already, we conducted separate Eye position × Distractor eccentricity repeated-measures ANOVAs for each hemifield. As expected, there were no significant main effects or interactions for distractors in the nasal hemifield. For the temporal hemifield there was a marginally significant interaction between eye position and distractor eccentricity, $F(1, 13) = 3.83$, $p = 0.07$, $\eta_p^2 = 0.23$. Post-hoc comparisons revealed a decrease in curvature between close and remote distractor locations in the temporal hemifield in the abducted position (paired-samples t test, $t(13) = 2.40$, $p < 0.05$), but not in

any of the other conditions (paired-samples t tests, all nonsignificant), suggesting that remote distractors evoked less curvature than close distractors, but only when presented outside of the oculomotor range.

Discussion

The results of Experiment 1 show that a visual distractor always elicits oculomotor competition. Nonetheless, we found a decrease of distractor-related activity for locations outside of the oculomotor range using a conventional analysis. However, the analysis focused on the temporal hemifield revealed only marginal effects. One possible explanation for the absence of a significant interaction for this hemifield is the quality of the eye tracking data in the abducted position. Examination of the normalized saccade trajectories revealed that these were noisier in the abducted condition than in the nonabducted condition. We suspected that this was caused by pupil being partially occluded in the abducted condition by the corners of the eye (see Figure 3). In Experiment 2 we undertook two measures to decrease the influence of this distortion.
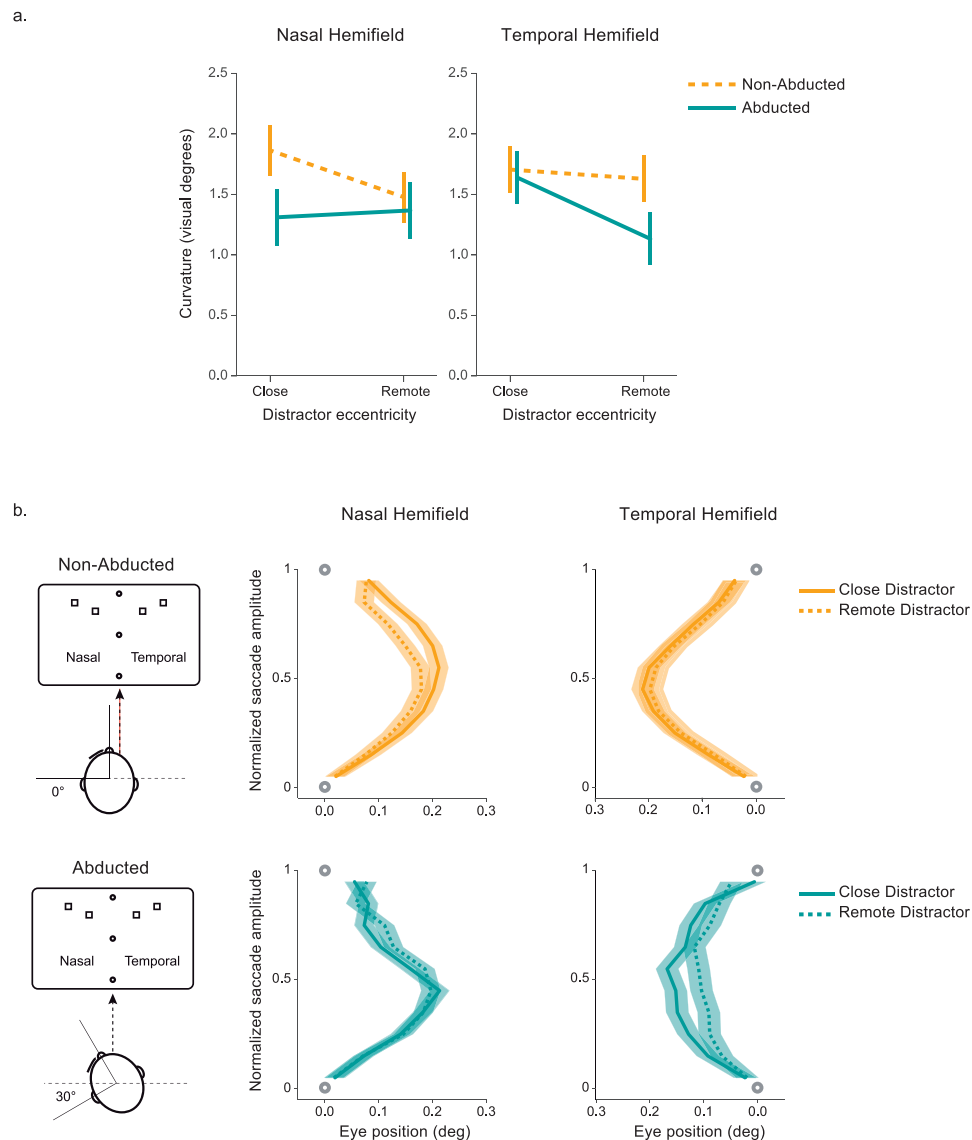
Experiment 2

The goal of Experiment 2 was to replicate and extend the findings of Experiment 1. We slightly adjusted the paradigm to decrease the distortion in the eye-tracking signal caused by eye abduction. First, the overall luminance of the screen was increased. This should cause the pupil to constrict and make it less likely that the pupil is occluded by the edges of the eye. Second, we removed the trials on which no distractor was present in order to increase the number of trials.

Methods

Fourteen new participants, aged between 19 and 43 (mean: 26 years, 11 female) received money or study credit to participate in two 30-minute experimental blocks with a 15-minute break in between, consisting of 720 trials in total. The order of the blocks was counterbalanced across participants. Before the experiment eye dominance was assessed. In contrast to Experiment 1, both participants with a left (seven participants) and a right (seven participants) ocular dominance participated. Participants performed the task monocularly, with the nondominant eye patched.

Although the task was very similar to that of Experiment 1, there were two important changes. First, to reduce the pupil size, we increased the overall

Figure 2. Results of Experiment 1. (a) The curvature away from distractors in the nasal (left), and temporal (right) hemifield. Orange dashed lines indicate curvature in the nonabducted condition; blue solid lines indicate curvature in the abducted condition. For every participant curvature is calculated relative to the no distractor baseline separately for abducted and nonabducted condition. The error bars represent 95% within-subject confidence intervals on the close versus remote distractor eccentricity comparisons. (b) Normalized saccade trajectories for distractors in the nasal (left), and temporal (right) hemifield. Orange lines indicate trajectories in the nonabducted condition; blue lines indicate trajectories in the abducted condition. Solid lines indicate trajectories for distractors close to fixation, dashed lines indicate trajectories for distractors far from fixation. Trajectories were averaged across saccade directions. Note the different scales used for the horizontal and vertical axis. The pattern of results is different across visual hemifields: The effect of remote distractor is reduced under abduction in the temporal, but not in the nasal hemifield.

luminance of the screen by presenting black stimuli on a light gray background (luminance of 22 cd/m^2). Second, to increase the number of trials we removed the baseline condition. Instead, for both the nonabducted and the abducted position we calculated a baseline trajectory by averaging saccade trajectories across all distractor locations (nasal-close, nasal-remote, temporal-close, and temporal-remote). By leaving out the no-distractor condition the number of trials in the other conditions was increased by 50%.

Results

Trials in which a saccade was detected before target onset were discarded. If the saccade was more than 3° shorter or longer than the 10° separating the fixation point and saccade target, had a latency shorter than 80 ms or longer than 600 ms, or did not start within 2° from fixation and end within 3° from the target, the trial was discarded. This resulted in an average loss of 27% of all trials. Increasing the background luminance
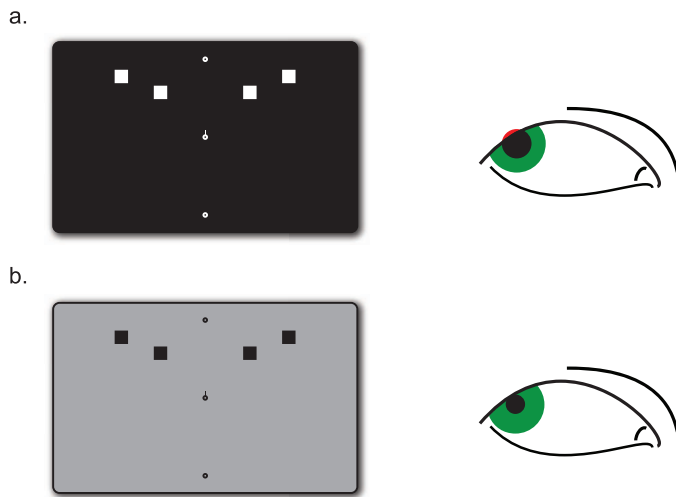
a.

b.

Figure 3. Experimental stimuli of Experiment 1 and 2. (a) In Experiment 1 white stimuli were presented on a black background. The low overall luminance resulted in a relatively large pupil size. This led to the pupil being partially occluded by the edges of the eye in the abducted block. (b) In Experiment 1 black stimuli were presented on a light gray background, increasing the overall luminance of the screen. This resulted in more pupil constriction making it less likely that it was occluded by the edges of the eye.

and number of trials had the desired effect; the quality of the data was considerably better than in Experiment 1 (see Figure 4b).

The overall pattern of results was very similar to Experiment 1 (see Figure 4). Saccades always curved away from the distractor location, even when it was presented beyond the oculomotor range, t test, $t(13) = 3.60$, $p < 0.01$. Statistical analysis revealed a main effect of distractor eccentricity, $F(1, 13) = 22.71$, $p < 0.001$, $\eta_p^2 = 0.64$, but not of hemifield, $F(1, 13) = 1.28$, $p = 0.28$, or eye position, $F(1, 13) = 2.13$, $p = 0.17$. The three-way interaction was marginally significant, $F(1, 13) = 3.58$, $p = 0.08$, $\eta_p^2 = 0.22$. Critically, separate Eye position × Distractor eccentricity ANOVAs for each hemifield revealed a significant two-way interaction for distractors in the temporal hemifield, $F(1, 13) = 5.23$, $p < 0.05$, $\eta_p^2 = 0.29$, but not for distractors in the nasal hemifield, $F(1, 13) = 0.81$, $p = 0.28$. Post-hoc tests showed a significant decrease of curvature in the temporal hemifield for the abducted position, $t(13) = 4.36$, $p < 0.001$, but not for the nonabducted position, $t(13) = 1.13$, $p = 0.28$. Just like in Experiment 1, post-hoc comparisons between close and remote distractor conditions showed a decrease in curvature in the temporal hemifield in the abducted position (paired-samples t test, $t(13) = 4.36$, $p < 0.001$, but not in any of the other conditions (paired-samples t tests, all nonsignificant). Remote distractors evoked less curvature than close distractors, but only when they were presented outside of the oculomotor range.

Given a close resemblance between the data patterns of the two experiments, an analysis of the pooled data was run with hemifield (temporal/nasal), eye position (nonabducted/abducted), and distractor eccentricity (close/far) as within-subject factors and Experiment (1/2) as a between-subject factor. As there was neither a main effect of experiment, $F(1, 26) = 1.35$, $p = 0.26$, nor a significant four-way interaction, $F(1, 26) = 0.00006$, $p = 0.99$, the factor Experiment was dropped from the model. The resulting $2 \times 2 \times 2$ ANOVA revealed a significant three-way interaction, $F(1, 26) = 8.59$, $p < 0.01$, $\eta_p^2 = 0.24$. Separate Eye position × Distractor eccentricity ANOVAs for each hemifield revealed a significant interaction between eye position and distractor eccentricity for distractors in the temporal hemifield, $F(1, 26) = 9.33$, $p < 0.01$, $\eta_p^2 = 0.26$, suggesting that remote distractors evoked less curvature than close distractors, but only when presented outside of the oculomotor range. Nonetheless saccades did still curve away from distractors presented at these locations (mean curvature: $1.56°$, t test, $t(27) = 4.86$, $p < 0.001$). For distractors in the nasal hemifield there was a small trend in the opposite direction, $F(1, 26) = 3.01$, $p = 0.09$, which was probably an effect of the nose blocking the lower part of the nasal hemifield in the nonabducted position, but not in the abducted position (see Supplementary Material for a separate analysis of upward and downward saccades, supporting this hypothesis).

Discussion

The results of Experiment 2 closely resemble those of Experiment 1. As in Experiment 1 we found a decrease, but no abolishment of distractor-related activity for locations outside of the oculomotor range. In contrast to Experiment 1, the analysis focused on the temporal hemifield revealed significant effects. Although the traditional comparison between hemifields revealed only a marginally significant effect, the analysis of the data pooled across the two experiments showed significant effects for the across hemifield analysis, as well as for the analysis within the temporal hemifield. Taken together, the results clearly demonstrate that target-distractor competition is reduced for the distractors that are located at positions where the eye cannot move.

General discussion

The present results demonstrate that saccade curvature is reduced but not completely abolished for distractors presented outside of the oculomotor range. A distractor is known to evoke activity in the oculomotor system, which interferes with saccades to
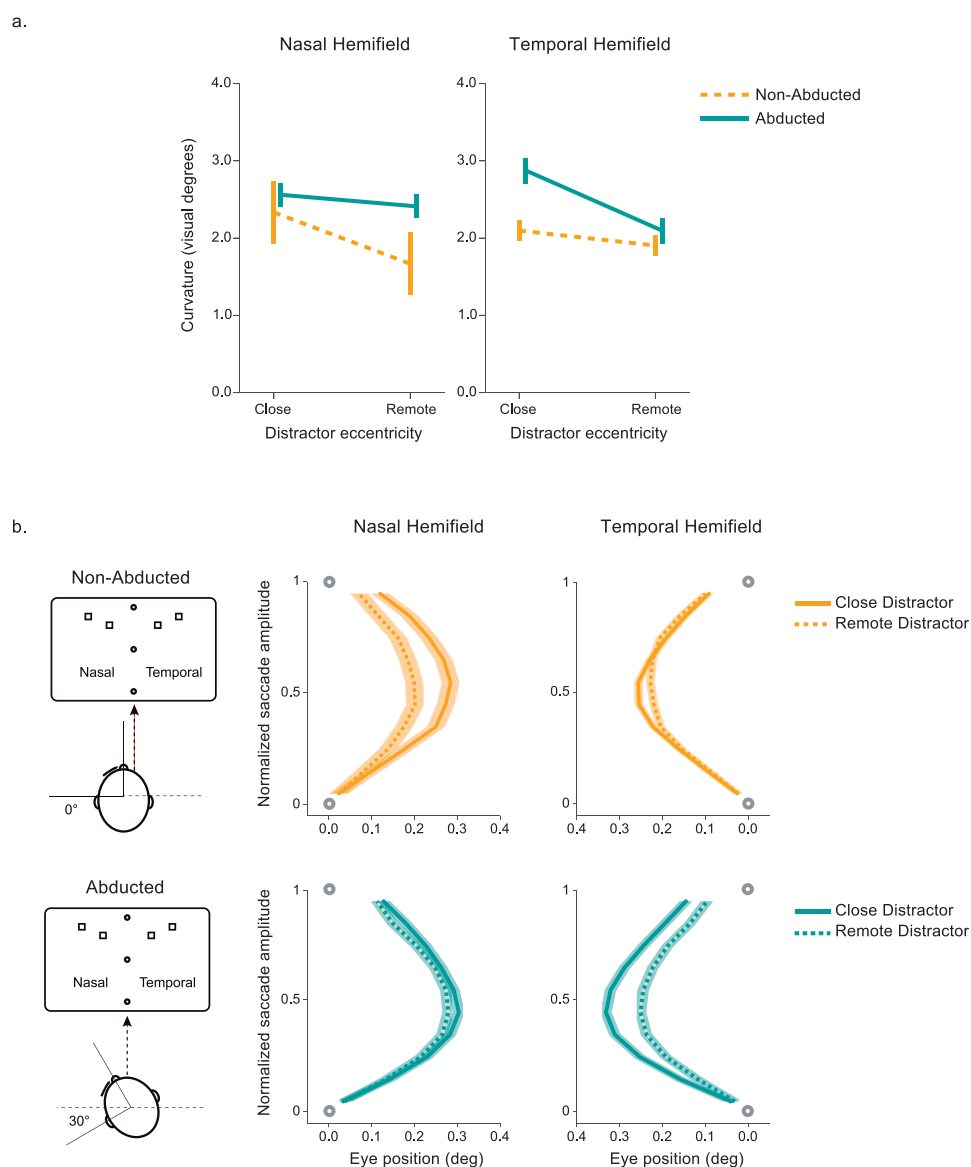
Figure 4. Results of Experiment 2. (a) Curvature away from distractors in the temporal (left), and nasal (right) hemifield. Orange dashed lines indicate curvature in the nonabducted condition; blue solid lines indicate curvature in the abducted condition. The error bars represent 95% within-subject confidence intervals on the close versus remote distractor eccentricity comparisons. (b) Normalized saccade trajectories for distractors in the nasal (left) and temporal (right) hemifield. Orange lines indicate trajectories in the nonabducted condition; blue lines indicate trajectories in the Abducted condition. Solid lines indicate trajectories for distractors close to fixation, dashed lines indicate trajectories for distractors far from fixation. Trajectories were averaged across saccade directions. Note the different scales used for the horizontal and vertical axis. Remote distractors evoked less curvature than close distractors, but only when they were presented outside of the oculomotor range.

the target, causing the eyes to curve away from distractor's location (Sheliga, Riggio, & Rizzolatti, 1995). When the eye abduction procedure rendered the eye movements to the remote distractors impossible, the distractor evoked less activation in the oculomotor system and created less competition with saccades to the target.

According to the premotor theory of attention (Sheliga et al., 1995) oculomotor preparation is functionally equivalent to directing attention. Previous studies demonstrated that attentional effects were indeed abolished at locations outside of the oculomotor range (Craighero et al., 2004; Smith et al., 2012). Although these findings appear to be consistent with the premotor theory, it is unknown whether the manipulation really disrupted oculomotor preparation. In the current task participants were not required to perform an attentional task. Instead, we measured oculomotor activity elicited by a completely irrelevant distractor. This method allowed us to directly measure

the effect of eye abduction on distractor evoked oculomotor activity. We hypothesized that if previously reported attentional deficits are the consequence of disrupted activation of the oculomotor program, this should be evident in the absence of oculomotor activity when the distractor was presented outside of the oculomotor range. Interestingly, the results show that saccades always curve away from the distractor, even when it was presented beyond the effective oculomotor range. Nonetheless, oculomotor competition was significantly reduced for distractors that are located where the eye cannot move.

The fact that oculomotor activity was only slightly reduced for distractors presented beyond the oculomotor range is inconsistent with the complete abolishment of attentional effects reported in earlier studies (Craighero et al., 2004; Smith et al., 2012). Note, however, that the premotor theory states that the allocation of attention is not limited to the programming of eye movements, but can originate from the planning of any goal-directed movement (Jonikaitis & Deubel, 2011; Rizzolatti, Riggio, & Sheliga, 1994). During normal orienting behavior subjects seldom make only isolated eye movements. Instead, gaze shifts are usually accomplished by combined eye and head movements. Interestingly, both appear to be controlled by the same mechanism. There is a vast body of evidence demonstrating that the SC not only codes for eye movements but is also involved in the control of other forms of motor behavior such as head and arm movements (Freedman, Stanford, & Sparks, 1996; Guitton, Crommelinck, & Roucoux, 1980; Roucoux, Guitton, & Crommelinck, 1980; Stuphorn, Bauswein, & Hoffmann, 2000). For example, electrical stimulation of the monkey SC elicits combined eye head movements (Freedman et al., 1996; Segraves & Goldberg, 1992). In line with this it was shown that in patients suffering from acute opthalmoplegia eye movements are replaced by head movements showing all the characteristics of normal saccadic eye movements (Gaymard et al., 2000). In addition to the link between attention and eye movements, there also appears to be a strong relationship between attention and head movements preparation. Covert orienting leads to elevated electromyographic (EMG) activity from the neck muscles (Corneil, Munoz, Chapman, Admans, & Cushing, 2008), while the planning of a head movement results in attention shifting in the same direction just before the movement commences (Cicchini, Valsecchi, & De'Sperati, 2008), similar to the presaccadic shifts of attention shown earlier (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). Although in the current experiments the headrest limited participants from moving their head in the direction of the distractor, the preparation of such a movement might have resulted in

there still being oculomotor competition in the abducted field, despite the inability to program an eye movement. However, the fact that the strength of this competition is significantly decreased indicates that, at least in the current experimental setup, these forms of movement are not completely interchangeable.

To summarize, we show eye abduction affects the amount of activity visual distractors evoke in the oculomotor system. Although activity is reduced for distractors located beyond the oculomotor range, it is not abolished completely. This extends the previous work reporting deficits in orienting of attention to locations where the eye could not move. The results are in line with the idea that covert attention is an emerging property of movement planning and is not restricted to saccade planning.

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