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✉ For correspondence:

a.m.van.harmelen@vu.nl

freek.van.ede@vu.nl

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China

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Microsaccades track shifting but not necessarily maintaining covert visual-spatial attention

Anna M van Harmelen ✉, Freek van Ede ✉

Institute for Brain and Behaviour Amsterdam, Department of Experimental and Applied Psychology, Vrije Universiteit Amsterdam, Amsterdam, Netherlands

eLife Assessment

This **useful** study demonstrates that microsaccade direction primarily indexes shifts rather than the maintenance of covert spatial attention, offering a focused interpretation that may help reconcile inconsistencies in the prior literature. However, the evidence remains **incomplete** due to limited engagement with the broader body of existing work and the absence of independent measures, single-trial analyses, and neutral-condition controls needed to substantiate the central claims. The work will be of broad interest to researchers investigating attention, eye movements, and visuomotor mechanisms.

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Abstract

Covert attention enables the brain to prioritise relevant visual information without directly looking at it. Ample studies have linked covert visual-spatial attention to the direction of small fixational eye movements called microsaccades, offering researchers and clinicians a potential non-invasive tool to track internal states of covert attention. However, other studies have reported only a weak link or no link at all. We now show that the link between covert visual-spatial attention and microsaccades critically depends on the stage of attentional deployment. Across two experiments—each employing a distinct but widely adopted approach to fixational control—we show that spatial microsaccade biases were more pronounced (Experiment 1) or even exclusively present (Experiment 2) during the initial stage of shifting covert spatial attention, even when covert attention was subsequently maintained as testified by enhanced visual discrimination. This shows that the involvement of the brain's oculomotor system in covert visual-spatial attention qualitatively changes over the course of attentional deployment, and how its peripheral fingerprint in the form of microsaccades reliably indexes shifting but not necessarily maintaining covert visual-spatial attention.

Significance statement

Covert attention is essential for efficient processing of information from our surroundings. Several studies have linked covert attention to the direction of miniscule eye-movements known as microsaccades. Other recent studies have questioned this link. We now explain this discrepancy by treating 'attention' not as a single static construct but as a dynamic process. We show that the link between microsaccades and covert attention critically depends on the stage of attention—with microsaccades robustly tracking shifting but not maintaining covert attention. This reveals how the contribution of the brain's oculomotor system to attention changes dynamically over time. These findings have implications for the use of microsaccades as an accessible marker of attentional (mal)function across psychological and neurological conditions.

Introduction

Visual-spatial attention refers to the dynamic process by which the human brain selects and prioritises the processing of currently relevant visual information (1–3). Visual-spatial attention can operate in two modes: overtly, by physically directing gaze towards relevant stimuli, and covertly, by attending to peripheral visual information outside of the current fixation. Extensive research has established that the neural circuitry that mediates shifts of overt visual-spatial attention, namely the oculomotor system, also contributes to covert visual-spatial attention (4–8). A canonical behavioural manifestation of this overlap in neural circuitry comes from the study of microsaccades—small eye movements that occur even during attempted fixation (9–13). In particular, many studies have reported an association between spatial biases in microsaccade direction and the allocation of covert visual-spatial attention.

This link between microsaccades and covert visual-spatial attention has been demonstrated repeatedly: both in humans (14–25) and non-human primates (26, 27), and both during externally directed perceptual attention (15–17, 20, 21, 24–27) and internally directed attention within visual working memory (14, 18, 19, 22, 23). At the same time, the link between covert visual-spatial attention and microsaccades is not always found (28–30), leading to mixed results in the literature. Notably, in a recent article, Willett & Mayo (30) reported no bias in microsaccade directions, despite clear behavioural and neural demonstrations that covert attention was allocated to the relevant visual stimulus.

One possible source underlying the mixed results that pervade the literature may be that ‘attention’ has been treated as a unitary and static construct. This is problematic under the hypothesis that the link between microsaccades and covert attention may only be reliable for specific stages associated with the deployment of spatial attention, such as when shifting between locations, but not when subsequently maintaining attention at the new location (31). Indeed, while most studies that reported a link used tasks that required *shifting* covert visual-spatial attention, the recent study by Willett & Mayo (30) that questioned this link used a task that required *maintaining* covert visual-spatial attention after it had already been shifted. Thus, whether—and how reliably—microsaccades track covert visual-spatial attention may fundamentally depend on whether one considers the period of shifting attention, or the ensuing period of maintaining attention after the shift (31).

This differentiation by stage of attention also naturally follows from the putative function of the brain’s oculomotor system in attention. Consider the case of overt attention: when aiming to attend to an object by looking at it, the oculomotor system is initially engaged once to shift the eyes. Once the eyes have landed on the attended location, no further eye-movements are necessary, yet overt attention can remain at this location. We pose that the same may apply for covert attention: shifting covert attention may engage the oculomotor system particularly to relocate the focus of covert attention, leading to a bias in microsaccade direction particularly while the shift occurs. Once shifted, visual-spatial attention may effectively remain at the covertly attended location, but with a distinct contribution from the oculomotor system that does not necessarily result in a bias of microsaccade direction.

To address the hypothesis (31) that microsaccades may particularly track *shifting* covert visual-spatial attention—in comparison to *maintaining* attention at this location after the initial shift—we conducted two complementary experiments that each employed a distinct but widely adopted approach to gaze control during the task. Consistent with our hypothesis, microsaccades predominantly (Experiment 1) or exclusively (Experiment 2) tracked shifting compared to maintaining covert visual-spatial attention, even though covert attention was maintained at the attended location after the initial shift, as evidenced by visual discrimination performance.

Results

Forty-eight healthy human volunteers performed a covert visual-spatial attention task in which a central colour cue indicated which of two laterally presented stimuli (positioned on the left and right below central fixation) would be most likely to show the target event: a slight orientation change that had to be judged as being clockwise or anticlockwise (Fig. 1A). To be able to study covert attention across both shifting and subsequent maintaining phases, we varied the interval between cue and target from 500 to 3200 ms. This necessitated shifting attention immediately in response to the cue (as the target event could already occur 500 ms after cue onset) as well as maintaining it on the cued stimulus (since the target event would often occur after longer cue-target intervals). We conducted two versions of this task, differing only in the approach to fixational control during the task. In Experiment 1, central fixation was instructed and monitored by the experimenter. Experiment 2 included gaze-contingent trial termination whenever gaze deviated more than 2° from central fixation, as controlled by custom software. Adopting both approaches enabled us to relate our findings to a broader set of prior studies given that both are widely used in the vast literature on covert visual-spatial attention.

Attention was successfully shifted and maintained

We first verified that our task was successful in inducing early shifts of visual-spatial attention that were maintained even for target events occurring several seconds after the cue that prompted the initial attention shift. As shown in Figure 1B, responses were faster and more accurate for target events occurring at the cued (valid) versus the other (invalid) stimulus, with cue benefits extending across all cue-target intervals. Cue-validity effects are summarised in the bar graphs in Figure 1B, and were robust in both experiments, for both reaction times (E1: $t(23)=4.673$, $p=1.052e-04$, $d=0.540$; E2: $t(23)=4.098$, $p=4.407e-04$, $d=0.894$) and accuracy (E1: $t(23)=3.281$, $p=0.003$, $d=0.383$; E2: $t(23)=3.062$, $p=0.006$, $d=0.745$). (For cue-validity effects at each of the tested cue-target intervals, see Supplementary Table S1.)

Attention was accompanied by a bias in microsaccade direction

Building on prior demonstrations of a bias in microsaccade direction accompanying the spatial allocation of covert visual attention (see introduction), we assessed whether microsaccades are also biased towards the cued stimulus in our orientation change detection task. We were specifically interested in the *temporal dynamics* of such a microsaccade bias in our task, which invoked both shifting covert attention to the cued visual stimulus, as well as maintaining it there until the target event (the orientation change) would occur.

We exclusively analysed directional microsaccade biases prior to the orientation change, to ensure our results are uncontaminated from potential responses related to the target event itself. To ensure sufficient trials for analysing microsaccades, we included all trials where the orientation change occurred later than 1400 ms after cue onset. This provided a good trade-off between having sufficient trials, while also having sufficient time to capture microsaccade biases during the initial shifting phase and the ensuing phase in which attention was maintained on the cued stimulus after this shift. Importantly, our conclusions remain unaffected when investigating the entire time course through a complementary analysis (see Supplementary Figure S1).

Figure 2A shows the time-resolved rates of downwards saccades made either towards the cued stimulus or towards the other stimulus, for both experiments. To zoom in on the ‘attentional modulation’, Figure 2B shows the spatial saccade bias, as the difference in saccade rates toward the cued versus the other stimulus. In both experiments, a significant saccade bias is present towards the cued item, starting around 200 ms after cue onset (E1: cluster $p < 0.001$; E2: cluster $p=0.036$). While in Experiment 1 saccade directions remain significantly biased towards the cued stimulus throughout the entire investigated period, in Experiment 2—where fixation demands were more strict, as trials were terminated upon breaking fixation—this bias became short lived, occurring only within the typical window associated with attentional shifting (see 14, 15, 18, 20, 23, 32–34).

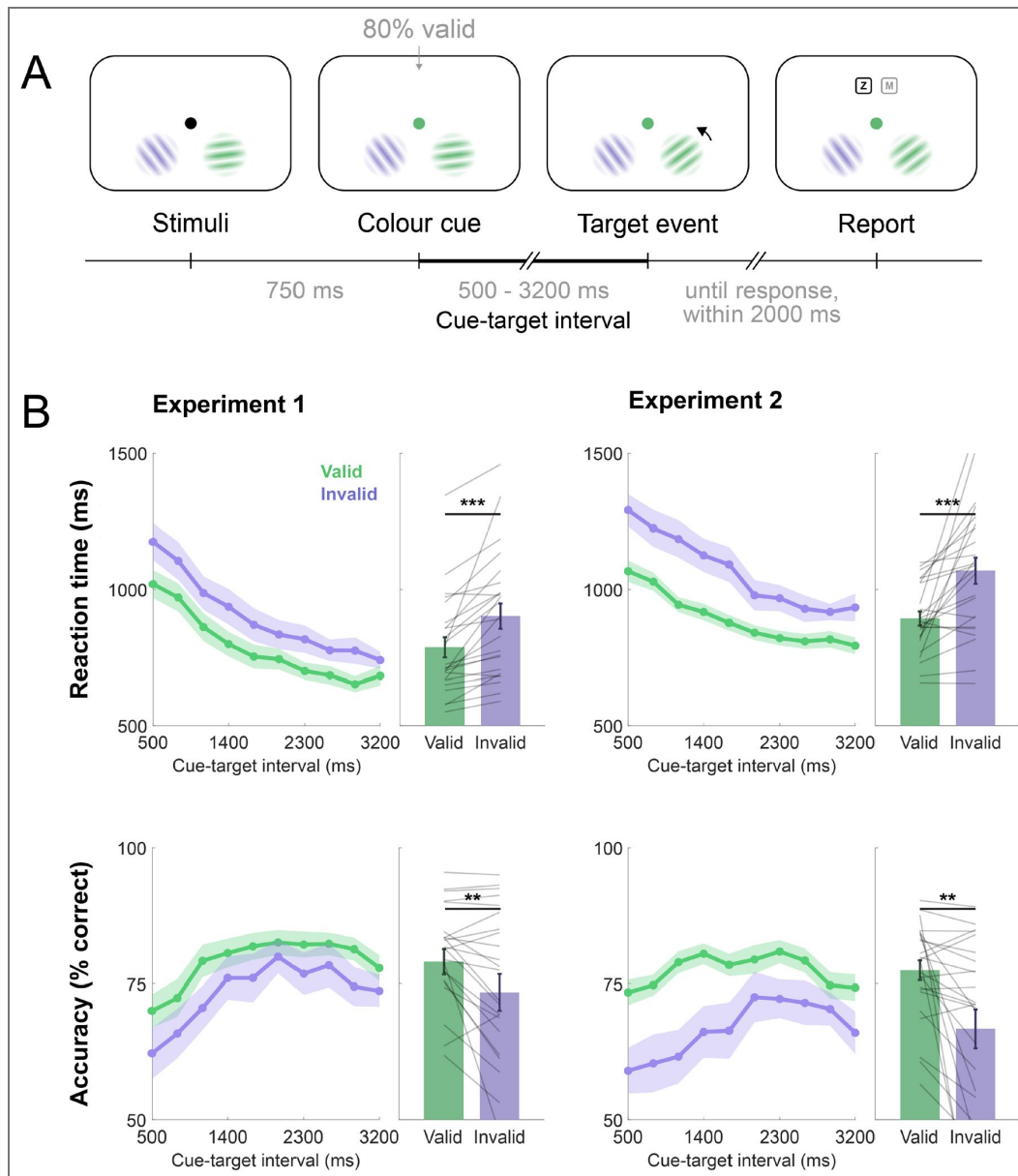


Figure 1. Attention was successfully shifted and maintained.

(A) Schematic showing the progression of a single example trial. A colour change of the central fixation dot cued which of two visual stimuli was most likely to change orientation (the visual target). After a variable delay, the target event (the orientation change) occurred in either the cued (80% of trials, valid) or other (20%, invalid) stimulus and participants reported whether it was clockwise or anticlockwise. Colours shown serve only as an example, for the experimental colours, see the methods section. Supplementary Figure S2 shows the stimulus screen and stimulus sizes and distances to scale. (B) Behavioural performance (reaction times above, accuracy scores below) as function of cue-target interval for validly vs. invalidly cued targets. Circular markers indicate mean values, with shaded areas indicating the standard error of the mean. Bars reflect the mean behavioural performance, with whiskers indicating the standard error of the mean. Grey lines indicate individual participants' data.

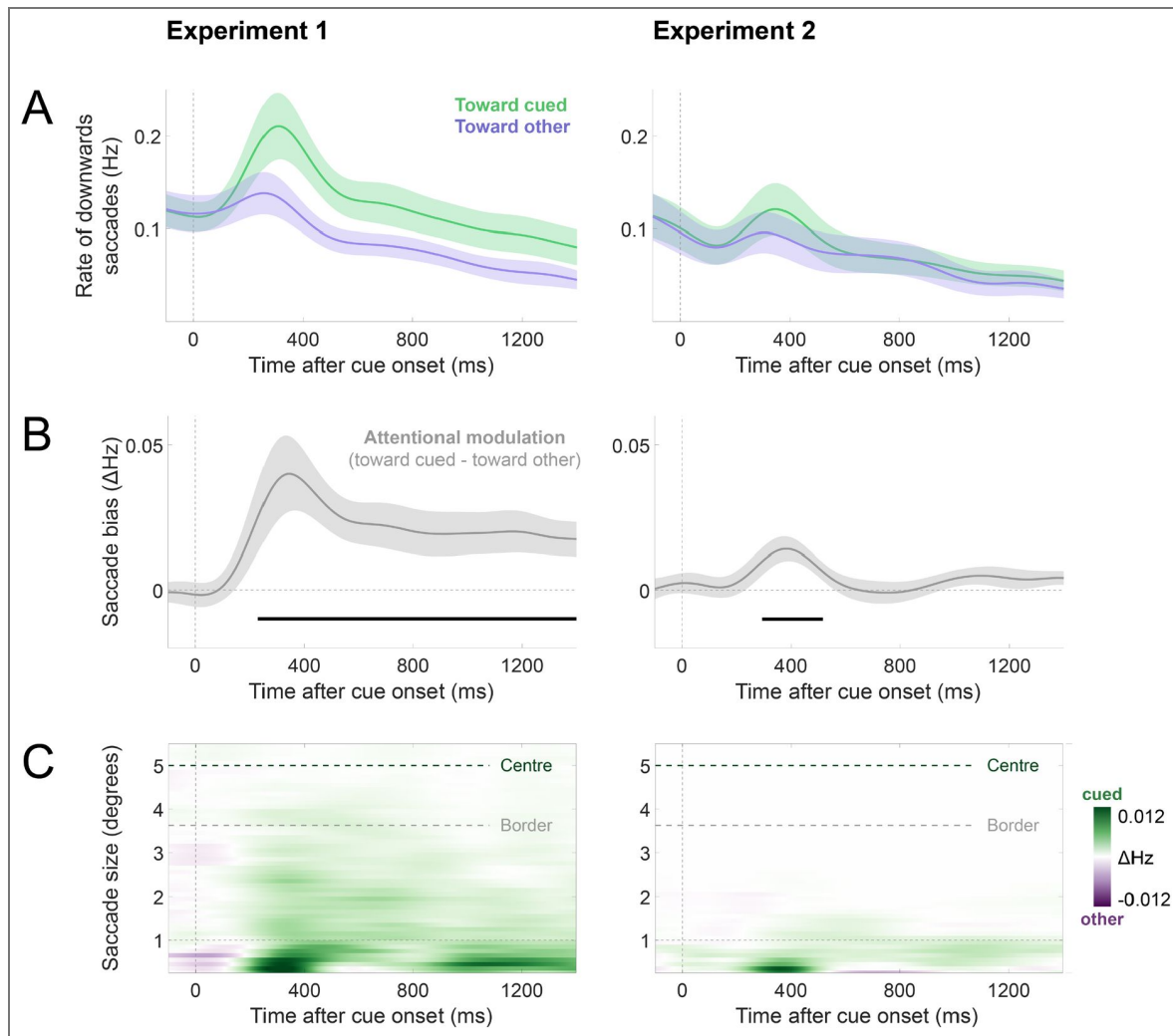


Figure 2. Attention was accompanied by a bias in microsaccade direction.

(A) Time courses of saccade rates for saccades towards the cued and the other item. This analysis only includes downward saccades, as stimuli were positioned at a 45° angle below fixation, allowing us to distinguish saccades towards the item from those returning to central fixation. The time courses indicate mean values, with shaded areas indicating the standard error of the mean. (B) Time courses of the attentional modulation of saccade direction (toward cued – toward other). The time courses indicate mean values, with shaded areas indicating the standard error of the mean. Black horizontal lines indicate significant temporal clusters (as determined by a cluster-based permutation test). (C) Time courses of attentional modulation (as shown in B) as a function of saccade size. For reference, dashed horizontal lines indicate 1 degree visual angle, as well as the original locations of the centre and closest border of the visual stimulus.

Rather than classifying saccades as ‘micro’ or ‘macro’ based on an inherently arbitrary threshold, [Figure 2C](#) shows the attentional modulation (saccade bias) as a function of the size of the saccades that contributed to it. Consistent with our instructions to deploy attention covertly, the reported bias was not driven by participants looking directly at the cued stimulus at 5 degree visual angle from central fixation, but rather by smaller saccades that were *biased* in the direction of the cued stimulus. Indeed, the saccade bias was driven predominantly (Experiment 1) or exclusively (Experiment 2) by saccades in the classic microsaccade range, i.e. below 1 degree.

Microsaccade directions are biased predominantly during attentional shifting

To summarise our findings, we finally quantified the observed spatial bias separately in two time windows that were chosen a-priori to capture either the period of ‘shifting’ or the ensuing period of ‘maintaining’ covert attention at the cued stimulus, after the initial shift. Specifically, we defined the shift period as the time period from 200 to 600 ms after cue onset, consistent with prior microsaccade studies (e.g., 14, 15, 18, 20, 23) as well as with complementary behavioural studies showing that voluntary attentional deployment unfolds between 200–600 ms after an endogenous attention cue (e.g., 32–34). Following the logic that participants were required to shift attention to the cued stimulus and retain it there, we defined the maintenance period simply as the interval immediately following the period of shifting: from 600 to 1400 ms after cue onset.

[Figure 3](#) shows a quantification of the directional bias in both timeframes. This confirmed a significant directional bias during the ‘shift period’ in both experiments (E1: $t(23)=3.117$, $p=0.005$, $d=0.615$; E2: $t(23)=2.543$, $p=0.018$, $d=0.502$), while the bias in the ‘maintain period’ was significantly only in Experiment 1 ($t(23)=2.838$, $p=0.009$, $d=0.560$) and no longer present in Experiment 2 ($t(23)=0.889$, $p=0.383$, $d=0.175$). To clarify this result, we found moderate Bayesian evidence for the absence of a bias during the maintenance period in Experiment 2 ($BF_{01}=3.26$). This corresponds with the absence of a significant cluster in Experiment 2 in [Figure 2](#). Finally, complementing the findings for Experiment 1 shown in [Figure 2](#)—where we found a single cluster spanning both shift and maintenance periods—an additional targeted quantification revealed that in Experiment 1, the bias was still significantly larger during the shift than during the post-shift maintain period ($t(23)=2.300$, $p=0.031$, $d=0.329$).

Discussion

By investigating attention as a dynamic process, we reveal how the relationship between microsaccades and covert visual-spatial attention critically depends on the stage of attentional deployment. Specifically, our results show that microsaccade directions are predominantly (Experiment 1) or even exclusively (Experiment 2) biased during the initial process of shifting covert attention to a relevant visual stimulus, as opposed to the subsequent stage of maintaining attention on this stimulus after the initial shift. We observed this even though visual discrimination performance confirmed the allocation of attention well beyond the initial shift window. The insight that the relation between microsaccade direction and covert visual-spatial attention depends on the stage of attention provides a critical nuance in our general understanding of the relationship between the oculomotor system and covert attention. This insight may not only clarify apparent inconsistencies in the literature (31), but also has important theoretical and practical implications, as we elaborate below.

When considering microsaccades as a peripheral marker of the oculomotor system (35, 36), our data suggest that role of the oculomotor system is likely distinct during different stages of covert attentional deployment. While the role of the wider oculomotor system in attention is well documented (4–8), the notion that this role may fundamentally differ across stages of attentional deployment (37) remains underappreciated. Yet, this dynamic stage-dependent participation is highly plausible when we consider that the same system is responsible for both covert and overt shifts of attention. In the case of overt attention, we make an eye movement to bring a new object into view once, and then simply keep this object foveated. By studying microsaccades, we provide

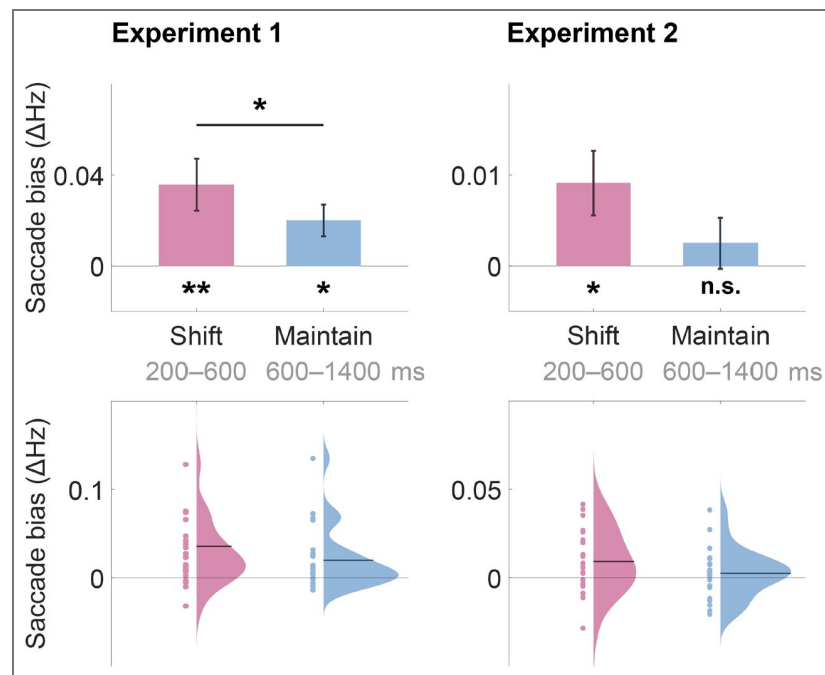


Figure 3. Microsaccade directions are biased predominantly during attentional shifting.

Bars represent the mean saccade towardness rate in the denoted timeframes, with whiskers indicating the standard error of the mean. Distribution and scatter plots show individual participants' data, with dark lines indicating the mean. Note that the y-axes have different scales between Experiment 1 and Experiment 2 and between bar graphs and distribution plots, for visualisation purposes.

evidence that a similar dynamic participation of the oculomotor system likely holds for covert visual-spatial attention. This does not necessarily imply that the oculomotor system contributes *more* during attentional shifts—it simply contributes differently. For example, shifting covert attention may principally recruit populations of motor and visual-motor neurons within the oculomotor system, while after attention has been shifted, covert attention may be held in place primarily by visually selective neurons in the same system that do not bias microsaccade directions (for the widely studied distinction between visual, motor, and visual-motor tuning, see e.g., 38, 39). Future work using direct neurophysiological recordings are required to assess this possibility.

Our findings also have practical implications. When using microsaccades as a marker to study covert attention, our data demonstrate that this marker is predominantly useful for tracking attentional shifts, but less so for tracking subsequent maintaining of visual-spatial attention. This does not necessarily negate its use to also track more sustained forms of attention (24, 40), but our data make clear how this is less reliable and may break down, especially when employing stricter fixational control (as was shown in Experiment 2). Furthermore, while our data confirm a robust link between microsaccade direction and shifts of covert visual-spatial attention on a trial average, it is important to note that microsaccades are not necessarily a reliable marker of attention shifts at the single-trial level. In fact, previous research has shown that microsaccades and attention shifts can decouple at the single-trial level (18, 28, 41), and that attention shifts only influence the likelihood of microsaccades following the same direction as attention, without directly triggering any new microsaccades (19).

In this current work, we assessed the relationship between microsaccades and covert attention in two experimental settings with different approaches to fixation control: instructed fixation with monitoring by the experimenter (Experiment 1) or with gaze-contingent trial termination controlled by custom software (Experiment 2). Because both approaches are commonly employed in the field, this set-up allows our data to be comparable with a broader literature on covert attention. In both cases, microsaccades were more reliably associated with the initial shifting of attention. Moreover, during the stricter fixation demands of Experiment 2, the link between microsaccades and attention could exclusively be established during the initial shifting period. This was the case even though we observed clear performance benefits at intervals far beyond the initial shift period. Together, these complementary experiments reinforce our central conclusion that the link between microsaccades and covert visual-spatial attention critically depends on the attention stage under investigation. In addition, they show how the exact mode of fixation control can shape the observed nature of this link.

The present study specifically examined microsaccade biases in relation to shifting and the ensuing period of maintaining covert visual-spatial attention in a task where the target event could occur anywhere between 500 and 3200 ms after cue onset. In future work, it will be valuable to extend our findings to situations where covert visual-spatial attention must be sustained over much longer timescales. Such situations may also naturally invoke lapses of attention that then require a re-establishing or re-shifting of covert visual-spatial attention. Whether such refocusing resembles the cue-induced shifts studied here—and is therefore similarly tracked by microsaccades—remains an interesting question for future research.

By considering attention not as a unitary and static construct but as a dynamic process, our data highlight how the involvement of the oculomotor system in covert visual-spatial attention fundamentally depends on the stage of attentional deployment, as reflected peripherally by microsaccades. This provides new insight into the intricate dynamics of covert visual-spatial attention and its oculomotor underpinnings and carries implications for the utility of microsaccades as an accessible peripheral marker of attention and its dysfunction in various neurological and psychiatric conditions.

Method

All experimental procedures were reviewed and approved by the ethics committee of the Vrije Universiteit Amsterdam. Each participant provided written informed consent prior to participation and was reimbursed with 10 euros/hour or participation credits.

Participants

We performed two experiments that only differed in the approach to fixation control (detailed below under ‘*Experiment 1 vs. Experiment 2: Gaze-contingent trial termination*’). A sample size of twenty-four per experiment was set a-priori, as based on previous publications from our lab with similar experimental designs and outcome measures.

All participants were recruited from the Vrije Universiteit Amsterdam. Twenty-five healthy human volunteers participated in experiment one, one of which was excluded post-hoc due to the inability to keep stable fixation. This resulted in the a-priori determined sample size of twenty-four participants (age range: 18-37; 19 women, 4 men and 1 non-binary; 21 right-handed). Twenty-nine healthy human volunteers participated in experiment two, five of which were unable to finish the experiment due to the inability to keep stable fixation. This resulted in the a-priori determined sample size of twenty-four participants (age range: 18-28; 20 women, 4 men; 23 right-handed). Recruitment for both experiments was done independently, with the constraint that participants were not allowed to participate in both experiments.

Task and procedure

Experiment 1 and Experiment 2 used the same task that we depict in [Figure 1A](#). This consisted of a covert visual-spatial attention task requiring participants to detect and discriminate a sudden orientation change in one of two presented Gabor patches. Prior to the orientation change, a colour cue was shown indicating with 80% reliability which Gabor patch would contain the target event (i.e., the orientation change).

Both experiments contained 20 blocks of 40 trials each. Before starting the experiment, participants practiced both the required response and entire trials until they felt acquainted with the task.

The stimuli would always be on the screen for 750 ms before the central fixation marker would change to match the colour of either stimulus serving as the cue. Left and right cues were equally likely and counterbalanced across trials. The interval between cue onset and the target event (the orientation change of either stimulus) varied from 500 to 3200 ms in discrete steps of 300 ms, resulting in ten possible cue-target intervals. Cue-target intervals were randomly drawn and counterbalanced across trials. The inclusion of early target events ensured that participants had an incentive to shift attention upon cue onset, while the inclusion of later target events enabled us to also study the period of subsequently maintaining attention on the cued stimulus.

After the orientation change occurred, participants reported the direction of the orientation change (i.e. clockwise or anticlockwise) by pressing either the ‘z’ (anticlockwise) or ‘m’ key (clockwise). Clockwise and anticlockwise target events were equally likely and counterbalanced across trials.

The Gabor patches were each positioned at an angle of 45° below the central fixation dot (see [Supplementary Figure S2](#) for a to-scale representation of the stimulus screen), one to the left and the other to the right. Critically, this positioning prevents conflating saccades associated with returning to fixation after moving in the direction of one stimulus with saccades directed towards the other stimulus.

Experimental set-up

Both tasks were programmed in Python 3.8.17 using the PsychoPy library (42) to generate the stimuli. Participants were seated 70 cm in front of a 24-inch LCD monitor, with a 1920 × 1080 pixel resolution and a 239 Hz refresh rate.

Gabor patches presented on a dark grey background (rgb: 64, 64, 64) could be one of four colours: blue (rgb: 19, 146, 206), magenta (rgb: 217, 103, 241), green (rgb: 101, 148, 14), orange (rgb: 238, 104, 60). Colours were randomly intermixed across trials with the constraint that the two Gabors in each trial had a different colour. All four colours were calibrated prior to the experiment to ensure equiluminance on the monitors used in the lab. All Gabor patches were 2.75 degrees visual angle in diameter, presented at a 5 degree distance to the fixation dot (centre to centre) (all distances are shown to scale in [Supplementary Figure S2](#)). The fixation dot was 0.2 degrees in diameter and near-white (rgb: 234, 234, 234). The orientation change that occurred as the target event was always 2° clockwise or anticlockwise. Orientations of Gabor patches were randomly generated from a 160°-space, where orientations from -85 to -5 and 5 to 85 degrees were allowed, to avoid cardinal orientations.

Experiment 1 vs. Experiment 2: Gaze-contingent trial termination

We conducted two complementary versions of the above described experiment that each employed a distinct but widely adopted approach to gaze control during the task. In Experiment 1, participants were instructed to fixate on the central fixation dot at all times and this was monitored by the experimenter who would repeat fixation instructions when necessary.

In contrast, during Experiment 2, trials were terminated when fixation strayed more than 2 degrees visual angle from the centre pixel in any direction. This set-up was attained by custom code that checked the current gaze position every 15 ms. Every gaze sample was checked in real-time and the trial was terminated as soon as any single sample was out of the allowed bounds. Upon trial termination, instructions to return to fixation were shown for 1 second. After this, the fixation dot was shown on its own for half a second, so participants could get their fixation back in order before the task continued with the next trial. Terminated trials were not replaced.

Eye-tracking acquisition and preprocessing

Horizontal and vertical gaze positions of the participant's right eye were continuously sampled using an EyeLink 1000 Plus at a rate of 1000 Hz throughout the experiment. The eye-tracker was positioned 10 cm in front of the monitor, and 60 cm away from the eyes. Prior to recording, the eye tracker was calibrated and validated using the built-in HV9 calibration module. The eye tracker was always re-calibrated exactly halfway through the experiment (after 10 blocks), and could additionally be re-calibrated in each break, if the signal was deemed of too poor quality.

Following acquisition, eye-tracker datafiles were converted from their original Eyelink Data Format (.edf) to an ASCII text file (.asc), and analysed in MATLAB R2024b using a combination of the Fieldtrip analysis toolbox (43) and custom code. Custom code was used to detect blinks and remove them from the signal for 100 ms before and after each blink (by replacing these data with NaNs). After blink removal, data were epoched relative to cue onset. Finally, all trials with a premature keyboard response were removed from the saccade data analyses. In Experiment 2, we additionally removed all trials that were terminated by a break in fixation before the target event had occurred. In total, this yielded an average of 752±45 (M±SD, out of 800) trials per participant for Experiment 1 and 633±74 for Experiment 2.

For our main analysis (the results of which are shown in [Figure 2](#)) we exclusively analysed directional microsaccade biases prior to the target event (i.e., the orientation change of either visual stimulus). This ensures our results are uncontaminated from potential responses related to the target event itself. To also ensure sufficient trials for analysing microsaccades, we included all trials where the orientation change occurred later than 1400 ms after cue onset. This provided a good trade-off between having sufficient trials, while also having sufficient time to capture microsaccade biases during the initial shifting phase and the ensuing phase in which attention was maintained on the cued stimulus after this shift.

Importantly, our conclusions remain unaffected when investigating the entire time course through a complementary analysis (see [Supplementary Figure S1](#)). In this analysis, all data occurring after the orientation change were removed on each trial (by replacing these data with NaNs), thereby also ensuring our results are uncontaminated from potential responses related to the

target event itself. While this complementary analysis does allow for examination of the full time course, the disadvantage of this approach is that the number of available data points decreases progressively towards the end. Consequently, statistical inferences become less stable at later time points. Because of this limitation, we did not adopt this approach as our main analysis.

Saccade detection and visualisation

To detect saccades, a previously established and validated velocity-based method was employed (18) (building on (15)). In this approach, saccades are detected by finding those samples where the 2-dimensional velocity exceeds a certain trial-based threshold. Gaze velocity was obtained as the derivative of gaze position that was smoothed in the temporal dimension with a Gaussian-weighted moving mean filter with a 7-ms sliding window (using the built-in MATLAB function ‘smoothdata’). The velocity threshold was set at 5 times the median velocity in any given trial, which is consistent with earlier work (14, 18, 23). A minimum delay of 100 ms between successive saccades was imposed to avoid counting the same saccade multiple times.

Saccade size (in degrees) and direction were calculated by estimating the difference between the pre-saccade gaze position (−50 to 0 ms before threshold crossing) and the post-saccade gaze position (50 to 100 ms after threshold crossing). Because stimuli were placed at a 45° angle *below* the central fixation dot we only included downwards saccades, following the same logic as in (30). This ensured that all saccades were either toward the cued stimulus or toward the other stimulus, while neglecting upward saccades back to the fixation marker. (Note how this deliberate analysis choice also renders saccade rates lower than in many other articles that include saccades in all directions). Depending on the direction of the saccade and the side of the cued item, we thus classified saccades as ‘towards the cued stimulus’ or ‘towards the other stimulus’. After detecting and classifying the saccades, the time courses of saccade rates (in Hz) was determined by using a sliding time window of 100 ms, advancing in steps of 1 ms.

To also investigate the size of the saccades that contributed to our findings without imposing an arbitrary threshold, we additionally decomposed saccade rates into a time-size representation, showing the time courses of saccade rates as a function of the saccade size (as also done in 14, 18, 23). For this, we used successive saccade-size bins of 0.5 degrees visual angle in steps of 0.1 degree.

Statistical analysis

For the analysis of the behavioural data, we employed paired-sample Student’s t-tests to compare average response times and accuracy scores between trials in which the target event occurred in the cued (valid cue) or other (invalid cue) stimulus, collapsed over all cue-target intervals.

To statistically evaluate the time series gaze data, we employ a non-parametric cluster-based permutation approach (44). The permutation analysis was conducted using Fieldtrip with default clustering settings (grouping adjacent time points that were significant in a mass-univariate comparison). A permutation distribution of the largest cluster size was acquired by randomly permuting the trial-average data at the group level 10,000 times and identifying the size of the largest clusters after each permutation. The p-values of the clusters observed in the original data were calculated as the proportion of random permutations where the largest cluster was equal to or larger than the cluster that we observed in the original data.

The cluster-based permutation approach only identifies temporal clusters of significance, but is not suited to directly compare modulations between the pre-defined time windows of shifting vs. maintaining attention. In order to compare the magnitude of the saccade bias between the two time windows of interest, we defined the shift window as the window between 200–600 ms after cue onset (determined a-priori, based on prior work, see 14, 18, 23 and consistent with ample related literature, see 32–34) and we defined the subsequent stage of attentional maintenance in the period following this (in the main analysis, this period lasts from 600 until 1400 ms after cue onset). This enabled us to average the saccade biases (defined as the difference in saccades rates toward the cued versus the other stimulus) in both a-priori defined time windows and to compare these biases using paired-sample Student’s t-tests. As this analysis resulted in a non-significant p-

value, we supplemented this analysis with a Bayesian analysis to also quantify evidence in favour of the absence of an effect. This was implemented in JASP using default settings (i.e., the prior distribution is a Cauchy distribution with location 0 and scale 0.707).

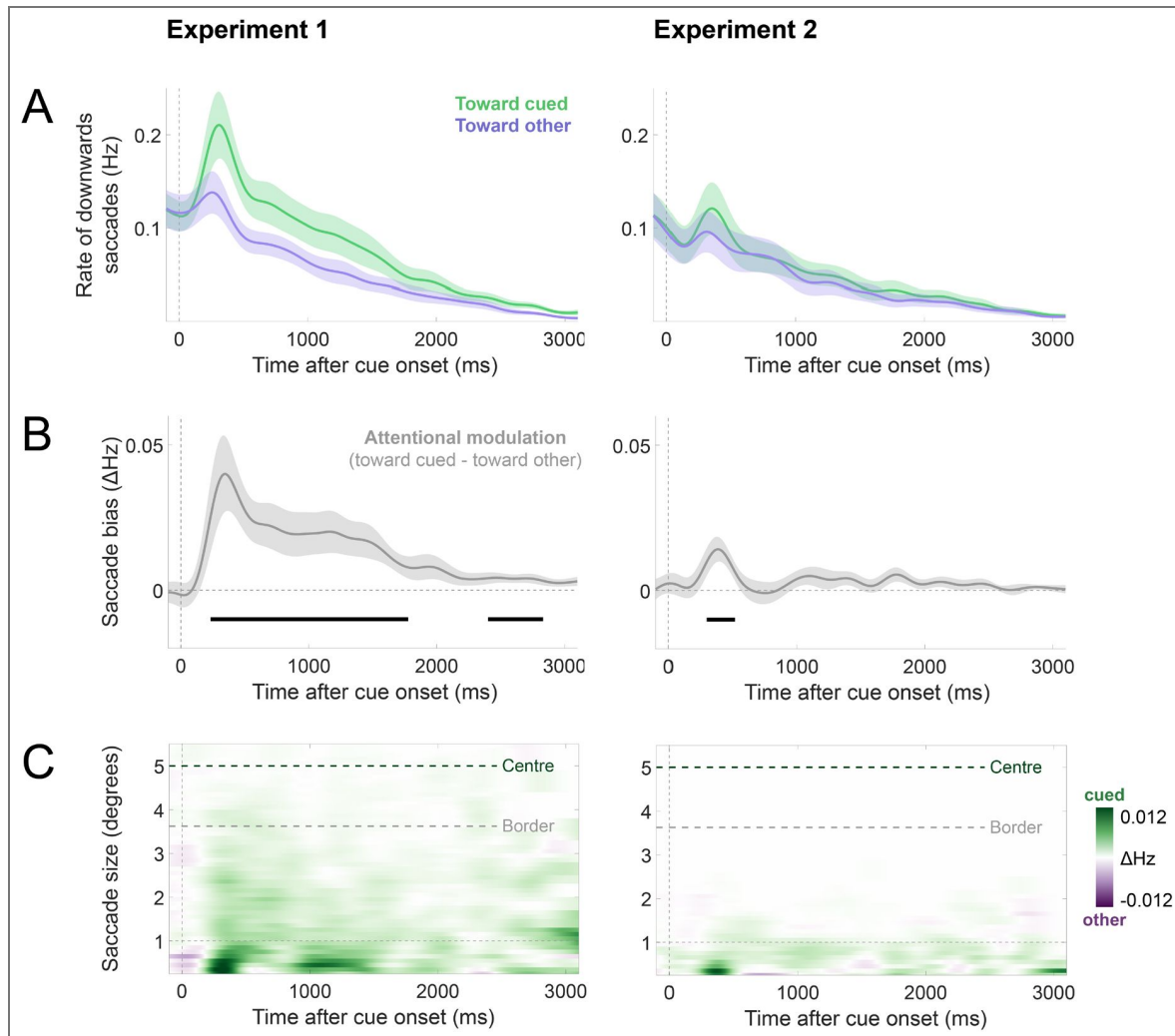
Data, Materials, and Software Availability

All study data and analysis code will be made public prior to publication. The code for the experimental task is already publicly available on [GitHub](#).

Supplementary Information

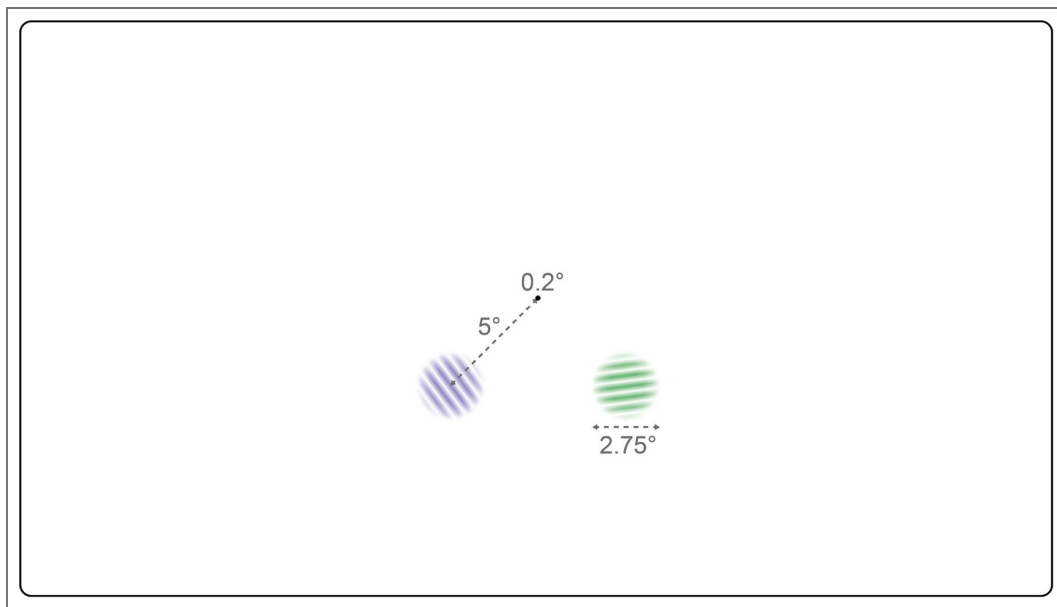
Reaction time						
	Experiment 1			Experiment 2		
Cue-target interval (ms)	t-value	p-value (uncorrected)	p-value (Bonferroni)	t-value	p-value (uncorrected)	p-value (Bonferroni)
500	3.431	0.002**	0.02*	3.876	7.66e-04***	0.008**
800	3.482	0.002**	0.02*	3.211	0.004**	0.04*
1100	3.007	0.006**	0.06	3.822	8.74e-04***	0.009**
1400	4.022	5.33e-04***	0.005**	3.864	7.88e-04***	0.008**
1700	3.299	0.003**	0.03*	3.384	0.003**	0.03*
2000	3.322	0.003**	0.03*	2.717	0.012*	0.12
2300	3.278	0.003**	0.03*	3.347	0.003**	0.03*
2600	2.604	0.016*	0.16	2.826	0.010*	0.1
2900	3.629	0.001**	0.01*	3.422	0.002**	0.02*
3200	1.603	0.122	1.22	3.390	0.003**	0.03*
Accuracy						
	Experiment 1			Experiment 2		
Cue-target interval (ms)	t-value	p-value (uncorrected)	p-value (Bonferroni)	t-value	p-value (uncorrected)	p-value (Bonferroni)
500	2.389	0.025*	0.25	3.505	0.002**	0.02*
800	2.322	0.029*	0.29	2.713	0.012*	0.12
1100	2.934	0.007*	0.07	3.488	0.002**	0.02*
1400	2.310	0.030*	0.3	3.190	0.004**	0.04*
1700	1.893	0.071	0.71	2.356	0.027*	0.27
2000	1.363	0.186	1.86	1.728	0.097	0.97
2300	1.976	0.060	0.6	2.382	0.026*	0.26
2600	1.399	0.175	1.75	1.804	0.084	0.84
2900	2.419	0.024*	0.24	1.303	0.205	2.05
3200	1.783	0.088*	0.88	2.039	0.053	0.53

Supplementary Table 1. Cue-validity effects at each of the tested cue-target intervals. This table splits the cue-validity effects from [Figure 1](#) into the ten possible cue-target intervals. The top half of the table shows the effects of cue-validity on reaction time; the bottom half of the table shows the effects of cue-validity on accuracy. Results from Experiment 1 and 2 are shown, respectively, on the left and right sides of the table. The table shows both uncorrected and Bonferroni corrected p-values, along with their significance levels: *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.



Supplementary Figure 1. Attention was successfully shifted and maintained throughout entire trial period.

Full time courses of saccade data. This figure replicates the results shown in Figure 2 using the complementary analysis described in the Methods section. (A) Time courses of saccade rates for saccades towards the cued and the other item. This analysis only includes downward saccades, as stimuli were positioned at a 45° angle below fixation, allowing us to distinguish saccades toward the item from those returning to central fixation. The time courses indicate mean values, with shaded areas indicating the standard error of the mean. (B) Time courses of the attentional modulation of saccade direction (toward cued – toward other). The time courses indicate mean values, with shaded areas indicating the standard error of the mean. Black horizontal lines indicate significant temporal clusters (as determined by a cluster-based permutation test). (C) Time courses of attentional modulation (as shown in B) as a function of saccade size. For reference, dashed horizontal lines indicate 1 degree visual angle, as well as the original locations of the centre and closest border of the visual stimulus.



Supplementary Figure 2. Size of the experimental screen, stimuli, and distances to scale.

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Author ORCID iDs

Anna M van Harmelen: <http://orcid.org/0000-0003-3935-2209>

Freek van Ede: <http://orcid.org/0000-0002-7434-1751>

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Peer reviews

Reviewer #1 (Public review):

Summary:

This manuscript describes a study examining the relationship between microsaccades and covert attention. This question has been widely investigated, with numerous studies showing that during sustained fixation, when subjects covertly attend to a peripheral stimulus, microsaccades tend to be biased toward the attended location. Here, the authors ask whether this microsaccade bias reflects a shift of covert attention or the maintenance of covert attention. They conclude that the bias is primarily driven by attention shifts, a finding that also helps reconcile the seemingly conflicting results of prior research, where the bias was questioned in paradigms that largely involved attention maintenance rather than shifting.

Strengths:

The paradigm and conclusions appear sound and supported by the results. A large sample size was used.

Weaknesses:

Weaknesses are mostly related to how the authors enforced fixation in the task, and clarifications are needed regarding some methodological details. A more direct comparison of the effect in the two experimental conditions is missing.

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Reviewer #2 (Public review):

Summary:

This study aims to test the hypothesis that microsaccades are linked to the shifting of spatial attention, rather than the maintenance of attention at the cued location. In two experiments, participants were required to judge an orientation change at either a validly cued location (80% of the time) or an invalidly cued location (20% of the time). This change was presented at varying intervals (ranging from 500 to 3,200 ms) after cue onset. Accuracy and reaction times both showed attentional benefits at the valid versus invalid location across the different cue-target intervals. In contrast, microsaccade biases were time-dependent. The authors report a directional bias primarily observed around 400 ms after the cue, with later intervals (particularly in Experiment 2) exhibiting no biases in microsaccade direction towards the cued location. The authors argue that this finding supports their initial

hypothesis that microsaccade biases reflect shifts in attention, but that maintaining attention at the cued location after an attention shift is not correlated with microsaccade direction.

Strengths:

The results are straightforward given the chosen experimental design. The manuscript is clearly written, and the presentation of the study and its visualisations are both of a high standard.

Weaknesses:

The major weakness of this paper is its incremental contribution to a widely studied phenomenon. The link between attention and microsaccades has been the subject of extensive research over the past two decades. This study merely provides a limited overview of the key insights gained from these papers and discussions. In fact, it attempts to summarise previous work by stating that many experiments found a link, while others did not, and provides only a relatively small number of references. To make a significant contribution, I believe the authors should evaluate the field more thoroughly, rather than merely scratching the surface.

The authors then present a potential solution to the conflicting past findings, arguing that attention should be considered a dynamic process that can be broken down into an attention shift and a sustained attention phase. Although the authors present this as a novel concept, I cannot think of anyone in the field who considers spatial attention to be a static entity. Nevertheless, I was curious to see how the authors would attempt to determine the precise timing of the attention shift and manipulate the different stages individually. However, the authors only varied the interval between the onset of the attention cue and the test stimulus, failing to further pinpoint their dynamic attention concept.

The current version of the experiment, therefore, takes a correlational approach, similar to initial studies by Engbert and Kliegl (2003) and Hafed and Clark (2002). Meanwhile, we have learned a great deal about the link between microsaccades and attention. Below, I will list just a few of these findings to demonstrate how much we already know. It is important to note that, while the present study cites some of these papers, it does not provide a clear overview of how the current study goes beyond previous research.

(1) Yuval-Greenberg and colleagues (2014) presented stimuli contingent on online-detected microsaccades. A postcue indicated the target for a visual task, and the target could be congruent or incongruent with the microsaccade direction. The authors showed higher visual accuracy in congruent trials. The authors cited that paper, but it is still important to emphasize how this study already tried to go beyond purely correlational links on a single trial level.

(2) The Desimone lab (Lower et al., 2018) showed that firing rates in monkey V4 and IT were increased when a microsaccade was generated in the direction of the attended target.

(3) However, attention can modulate responses in the superior colliculus even in the absence of microsaccades (Yu et al., 2022)

(4) Similarly, Poletti, Rucci & Carrasco (2017) observed attentional modulations in the absence of microsaccades, or comparable attention effects irrespective of whether a microsaccade occurred or not (Roberts & Carrasco, 2019).

Thus, in light of these insights, I believe the current study only adds incrementally to our understanding of the link between microsaccades and spatial attention.

In general, it is important to have an independent measure of the dynamics of an attention shift. I think a shift of 200-600 ms is quite long, and defining this interval is rather arbitrary.

Why consider such a long delay as the shift? Rather than taking a data-driven approach to defining an interval for an attention shift, it would be more convincing to derive an interval of interest based on past research or an independent measure.

The present analyses report microsaccade statistics across all trials, but do not directly link single-trial microsaccades to accuracy. Similarly, reaction times and accuracy were analyzed only with respect to valid vs. invalid trials. Here, it would be important to link the findings between microsaccades and performance on a single-trial level. For instance, can the authors report reaction times and accuracy also separately for trials with vs. without microsaccades, and for trials with congruent vs. incongruent microsaccades?

The study would benefit greatly from including a neutral condition to substantiate claims of attentional benefits and costs. It is highly probable that invalid trials would also demonstrate costs in terms of reaction times and accuracy. It would be interesting to observe whether directional biases in microsaccades are also evident when compared to a neutral condition.

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Author response:

We wish to thank the reviewers and the editors for their careful evaluation of our article and for their valuable input that we will embrace to strengthen our article. We will still respond in full when we have had time to perform further analyses, which we anticipate will corroborate our main conclusions and make our article more comprehensive.

For now, we provide a provisional response to the major points brought forward by both the editorial summary and the public reviews. As we understood, the two main points that were raised regard: (1) the novelty and, accordingly, the theoretical importance of our work and (2) the (in)completeness of our results. We provide our provisional response to both of these points below.

Novelty and theoretical relevance of the work

Regarding the novelty of our work, we believe the reviews—and, by extension, the editorial summary—underappreciated the main theoretical value of the question we addressed. Our work set out to investigate whether microsaccades track covert attentional shifting, attentional maintenance, or both. We fully recognise that there are ample prior studies that investigated and reported a link between microsaccades and covert attention, but also underscore how other studies report seemingly contradicting evidence by reporting that there is no such link. One such example is a recent high profile paper by Willett & Mayo in PNAS (2023). Prompted by the recent hypothesis that this seemingly conflicting evidence may be due to prior work investigating attention ‘in different stages’ (van Ede, PNAS, 2023), we set out to address precisely this using a dedicated task that we designed for this purpose. As acknowledged by the summary and public reviews, this helps to reconcile seemingly opposing views in the literature. In our view, such reconciliation has substantial theoretical value.

While we appreciate that our reported insights may resonate and appear plausible to those working on this topic, we are not aware of any prior studies that directly addressed whether the link between covert attention and microsaccades may fundamentally depend on the ‘stage’ of attentional deployment (‘shift’ vs. ‘maintain’).

To fill this key gap and address this timely issue, we developed a dedicated experiment designed to evaluate the relationship between microsaccades and the different stages of attention within a single paradigm. We did so by varying the cue-target intervals to uniquely incentivise early shifting (by having short intervals), while also being able to assess

microsaccade biases during subsequent maintenance (in the longer trials). To our knowledge, no previous task has jointly examined these components in this manner. Moreover, our inclusion of two widely adopted approaches to fixational control provides yet another source of novelty. Together, we believe that these features position our work as a substantive advance that reconciles seemingly opposing theoretical views.

Completeness of results

Regarding the completeness of our results, the editorial summary points to “the absence of independent measures, single-trial analyses, and neutral-condition controls needed to substantiate the central claims”. In our view, while the raised points are valuable, they pertain to issues that are tangential to our primary question and stem from misunderstandings of key analytical choices. We consider our results complete and comprehensive with regards to the main question our studies set out to answer. We briefly clarify each of the raised points below, and will respond more elaborately as part of our forthcoming revision.

First, regarding the portrayed “need” for independent measures to define the ‘shift window’ of interest, we wish to clarify how our main analysis is completely agnostic to predetermined time windows, as we employ a cluster-based permutation approach to assess our rich time-resolved data across the full time axis. For the complementary analyses that address the ‘shift’ and ‘maintain’ windows more directly, we use a priori defined windows that are based on ample prior literature (from prior literature studying microsaccade biases, as well as from prior literature on the time course of top-down attention as studied through SOA manipulations). Accordingly, even these ‘zoomed in’ analyses rely on time windows that are empirically grounded in ample prior research.

Second, regarding the use of single-trial analyses, we want to emphasise that single-trial predictability is not where our theoretical question resides. We start from the perspective that the relationship between covert visual-spatial attention and microsaccades is inherently probabilistic. Our aim is not to address or question this. Rather, our aim is to determine whether this probabilistic relationship behaves similarly during attentional shifting and maintenance—an issue our analyses directly and appropriately address. In addition, we also explicitly discuss how the link between microsaccades and attention is fundamentally probabilistic at the single-trial level in our discussion, and prompted by the valuable feedback, we plan to expand on this important contextualisation as part of our revision.

Finally, regarding the portrayed “need” for a neural-attention control condition, we agree that inclusion of a neutral attention condition could be informative for disentangling the ‘benefits’ versus ‘costs’ of attentional cueing. However, such disambiguation is tangential to our central aim. Rather, our behavioural data primarily serve to verify attentional ‘allocation’ at later cue-target intervals. Observing a difference between valid and invalid cues suffices for this central aim. We also note how inclusion of a neutral condition would have reduced trial-numbers and statistical power for our critical conditions of interest. Accordingly, we do not see this as a limitation that in any way challenges our main conclusions. Prompted by this reflection, during our revision we will ensure to not mention selective ‘benefits’ or ‘costs’ of our cueing manipulation, but to refer to ‘the presence of an attentional modulation’ instead.

Therefore, we believe that the explicit design and analysis choices that we made aligned with the theoretical aims of our study, and that our data provide a complete and coherent test of our central question. The raised points are valuable and we will leverage them to improve our article, but they do not render our findings “incomplete” (as currently portrayed) with regards to the key goal of our article.

Future changes

Naturally, we consider the feedback from the editors and the reviewers of great value, and we will incorporate their suggestions to further strengthen our article. Concretely, we plan to implement the following revisions:

- In our introduction we plan to elaborate on the prior state of knowledge to provide a more complete context.
- We plan to add precise clarifications throughout the paper, ranging from methodological details and methodological choices to interpretation of the results. This should increase the comprehensiveness and transparency of our article.
- We will run and incorporate the outcomes of various additional analyses that we anticipate will further substantiate our conclusions and provide a more comprehensive view of our data and key findings.

We are confident that these revisions will enhance clarity and accessibility while reinforcing the theoretical contributions of the work.

References

Willett, S. M., & Mayo, P. J. (2023). Microsaccades are directed toward the midpoint between targets in a variably cued attention task. *Proceedings of the National Academy of Sciences of the United States of America*, 120(20). <https://doi.org/10.1073/pnas.2220552120> 
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