



Spatial and temporal attention revealed by microsaccades

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ABSTRACT

We compared the spatial and temporal allocation of attention as revealed by microsaccades. Observers viewed several concurrent “rapid serial visual presentation” (RSVP) streams in the periphery while maintaining fixation. They continually attended to, and discriminated targets in one particular, cued stream. Over and above this continuous allocation, spatial attention transients (“attention shifts”) were prompted by changes in the cued stream location and temporal attention transients (“attentional blinks”) by successful target discriminations. Note that the RSVP paradigm avoided the preparatory suppression of microsaccades in anticipation of stimulus or task events, which had been prominent in earlier studies. Both stream changes and target discriminations evoked residual modulations of microsaccade rate and direction, which were consistent with the presumed attentional dynamics in each case (i.e., attention shift and attentional blink, respectively). Interestingly, even microsaccades associated with neither stream change nor target discrimination reflected the continuous allocation of attention, inasmuch as their direction was aligned with the meridian of the target stream. We conclude that attentional allocation shapes microsaccadic activity continuously, not merely during dynamic episodes such as attentional shifts or blinks.

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1. Introduction

In humans and their closer relatives, visual gaze is stabilized against head and body movements by compensatory eye movements which are guided by both visual and vestibular inputs (Kowler, 2011). These fixational eye movements include small, involuntary saccades which have been termed “microsaccades” and which exhibit the same dynamical characteristics (apart from size) as larger, voluntary saccades (Collewyn & Kowler, 2008; Hafed, 2011).

While microsaccades are irregular and infrequent (with rates on the order of 1 Hz, Engbert, 2006; Kowler, 2011), their statistics over many identical trials reflects both visual input transients and changes in cognitive state. Typically, visual onsets first decrease and then increase the microsaccade rate transiently, in each case by a factor of two or more (Engbert, 2006; Hafed, Lovejoy, & Krauzlis, 2011; Pastukhov & Braun, 2010). An even more pronounced reduction in microsaccade rate is observed in anticipation of the imminent appearance of task-relevant stimuli (Hafed, Lovejoy, & Krauzlis, 2011; Pastukhov & Braun, 2010; Steinman, Cunitz, Timberlake, & Herman, 1967). This preparatory saccadic suppres-

sion may serve to minimize the detrimental effects of ill-timed microsaccades on visual performance (Hafed & Krauzlis, 2010; Hafed, Lovejoy, & Krauzlis, 2011).

Covert attentional states influence the direction of microsaccades: when fixation is maintained but a peripheral location is cued as being task-relevant, microsaccades tend to aim first towards this location and later back towards fixation (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Horowitz et al., 2007; Laubrock et al., 2010). Moreover, successful allocation of attention (as indicated by task performance) is associated with microsaccades towards the task-relevant location (Hafed & Clark, 2002; Hafed, Lovejoy, & Krauzlis, 2011; Pastukhov & Braun, 2010). Microsaccades orient towards the task-relevant location both in response to a visual onset (“involuntary transient attention”) and in anticipation of a subsequent task-relevant stimulus (“voluntary sustained attention”, Carrasco, 2011). Paradoxically, this orientation of microsaccades increases during the saccadic suppression in anticipation of task-relevant stimuli (Hafed, 2011; Pastukhov & Braun, 2010).

The correlation between microsaccades and covert attention likely reflects shared neural mechanisms in the superior colliculus (Hafed, Goffart, & Krauzlis, 2009; Hafed, 2011; Hafed & Krauzlis, 2010) and elsewhere. Specifically, the superior colliculus (together with other brain structures) is thought to implement a ‘priority’ or ‘saliency’ map that guides both eye movements and shifts of visual attention in the absence of eye movements (Cavanaugh, Alvarez, & Wurtz, 2006; Fecteau & Munoz, 2006; Hafed & Krauzlis, 2008;

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Lovejoy & Krauzlis, 2010). Numerous behavioral studies have confirmed interactions between saccade planning and shifts of visual attention (e.g., Baldauf & Deubel, 2008; Deubel & Schneider, 1996; Gersch et al., 2009; Wilder et al., 2009).

Here, we modulate covert attention in space and over time in order to compare the respective effects on microsaccadic activity. In contrast to earlier studies, our experimental design largely avoided modulations of microsaccade rate due to visual onsets or to anticipation of task-relevant stimuli (residual modulation $\leq 20\%$). In earlier studies, the effects of covert attention were confounded by large (4- to 10-fold) modulations of microsaccade rate relating to visual onsets and/or to target anticipation (Betta, Galfano, & Turatto, 2007; Engbert & Kliegl, 2003; Galfano, Betta, & Turatto, 2004; Hafed & Clark, 2002; Laubrock, Engbert, & Kliegl, 2005; Pastukhov & Braun, 2010; Rolfs, Kliegl, & Engbert, 2008; Rolfs, Engbert, & Kliegl, 2005; Rolfs, Laubrock, & Kliegl, 2006).

Our observers attended continuously to one of several streams of successively presented items (“rapid serial visual presentation” (RSVP) (Potter & Levy, 1969)) in the visual periphery. To obtain “attention shifts” in space, we caused the attended stream to change its location from time to time. To modulate attentional allocation over time, we relied on the “attentional blink” (Raymond, Shapiro, & Arnell, 1992), a prolonged attentional deficit that follows successful discrimination of target items in the monitored stream (Dux & Marois, 2009; Hommel et al., 2006; Martens & Wyble, 2010). Thus, three kinds of attentional manipulations – continuously sustained, spatial shift, temporal blink – were combined in one experimental situation which, moreover, avoided simultaneous, large modulations of microsaccade rate.

All manipulations affected the prevailing direction(s) of microsaccades independently of modulations of microsaccade rate. Microsaccades were directed predominantly either towards the task-relevant location or back towards fixation, with a comparable degree of alignment during all three manipulations. Both microsaccade directions exhibited equal and stationary rates whether attention was sustained on target or on distractor items. However, when attention shifted to a new location, or when it disengaged from a target item, one direction transiently dominated over the other, consistent with prior results (Laubrock et al., 2010; Pastukhov & Braun, 2010; Valsecchi, Betta, & Turatto, 2007). Our findings provide several new constraints for computational models of microsaccade generation (Engbert et al., 2011; Engbert, 2012; Hafed, Goffart, & Krauzlis, 2009; Rolfs, Kliegl, & Engbert, 2008). We conclude that attentional allocation and eye movements may be controlled continuously – not just intermittently – by closely overlapping brain structures.

2. Material and methods

2.1. Observers

Four observers (three females), including one author (vv) participated in Experiment 1. Five observers (three females), including one author (vv) participated in Experiment 2. Procedures were approved by the medical ethics board of the Otto-von-Guericke-Universität, Magdeburg and informed consent was obtained from all observers. Apart from the author, all observers were naïve to the purpose of the experiment and were paid to participate.

2.2. Apparatus

Stimuli were generated in Matlab, using the Psychophysics Toolbox extensions (Brainard, 1997), and displayed on a CRT screen (Iiyama VisionMaster Pro 514, iiyama.com) with spatial resolution of 1600×1200 pixels and refresh rate of 100 Hz. The

viewing distance was 73 cm, so that each pixel subtended approximately 0.019° , and background luminance was 36 cd/m^2 . Ambient illumination was 80 cd/m^2 .

2.3. Stimuli and procedure

2.3.1. Experiment 1

Four streams of letters were presented concurrently at rates of 10 Hz (rapid serial visual presentation, RSVP, see Fig. 1), each stream in a unique color (orange, green, yellow, or light blue). Each stream contained 5–10 target letters (*N* and *Z*) and other letters as distracters. Targets appeared at random times in all four streams. Target identity was chosen randomly and independently for each stream. Letters measured 1.8° in height and were centered at eccentricities of 3.8° on the vertical or horizontal meridian. Stream colors and positions were randomized for each trial. Prior to each trial, observers were told which stream (color) was to be monitored during the trial. In general, observers were instructed to report the appearance of either target (*N* or *Z*) in the relevant stream as quickly as possible (by key press). Note that this was a compound detection (Sperling, Doshier, 1986), not a discrimination, in that observers reported target presence, but not target identity.

Each trial lasted for 30 s. In the *hold* condition, streams maintained their position/color during the entire trial (Fig. 1A, Movie 1). In the *switch* condition, all streams exchanged position/color every 2, 4 or 6 s with their counterparts on the same meridian (vertical or horizontal) (Fig. 1B, Movie 2).

2.3.2. Experiment 2

The procedure was similar to the *hold* condition of Experiment 1. Three streams of letters, each of unique color (orange, green, or yellow), were presented at fixation (*Center*, letter height 1°), near fixation (*Near*, eccentricity 3° , letter height 2.3°), and in the periphery (*Far*, eccentricity 9.5° , letter height 5.5°), see Fig. 8A. Stream colors and positions were randomized from trial to trial and observers were instructed to monitor one particular stream and to report the appearance of a target (*N* or *Z*) in this stream.

2.4. Eye movement analysis

Eye movements were monitored binocularly and at a rate of 1000 Hz with a desk-mounted eye tracker (Eyelink 2000, SR Research, sr-research.com). Microsaccades and saccades were identified with the automated procedure described in Engbert and Kliegl (2003) and the analysis was limited to displacements $< 60'$. In addition, pairs of opposing microsaccades separated by less than 750 ms were flagged as “physiological square-wave-jerks” (SWJ) Hafed and Clark (2002). As expected for saccadic eye movements, peak velocity and amplitude were highly correlated in all conditions (Fig. 2AB). Pupil area during saccadic and non-saccadic intervals was identical (Fig. 2C).

3. Results

Our central aim was to investigate the relation between attentional state and microsaccadic (MS) activity. To this end, we combined three attentional manipulations in a single experimental situation. To minimize task-related variations of microsaccade rate (either by visual onsets or by anticipatory suppression), we employed streams of rapidly presented letter items. Observers performed an attentionally demanding discrimination with respect to these items, obliging them to sustain attention (almost) continuously on the task-relevant stream. Spatial attention shifts were induced by changing the location of the cued stream. Temporal attention transients were obtained by means of an “attentional

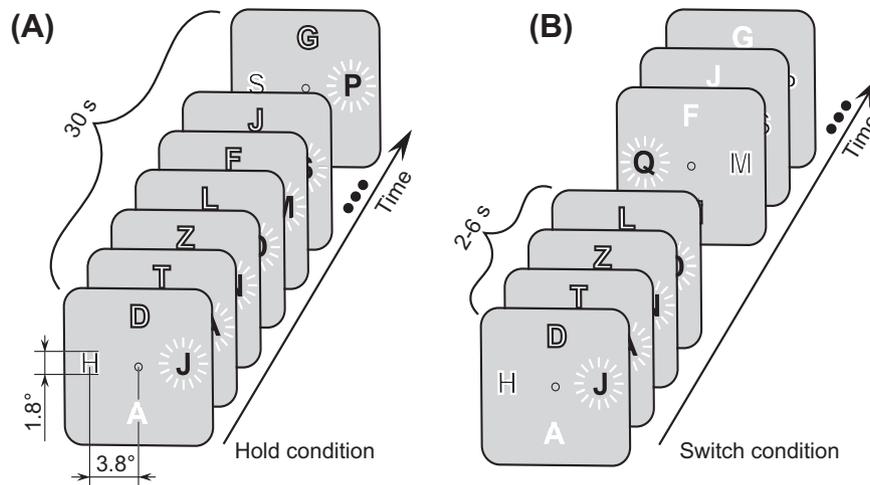


Fig. 1. Experimental design. Four RSVP streams of letters (each of different color) were presented at eccentric locations on the vertical and horizontal meridians. Observers maintained fixation and monitored the stream of one particular color (highlighted for purposes of illustration), reporting the appearance of a target (*N* or *Z*) by button press. Streams either held their location for the entire trial duration of 30 s (A, *hold condition*, see Movie 1), or exchanged positions with the opposite stream on the same meridian every 2, 4 or 6 s (B, *switch condition*, see Movie 2).

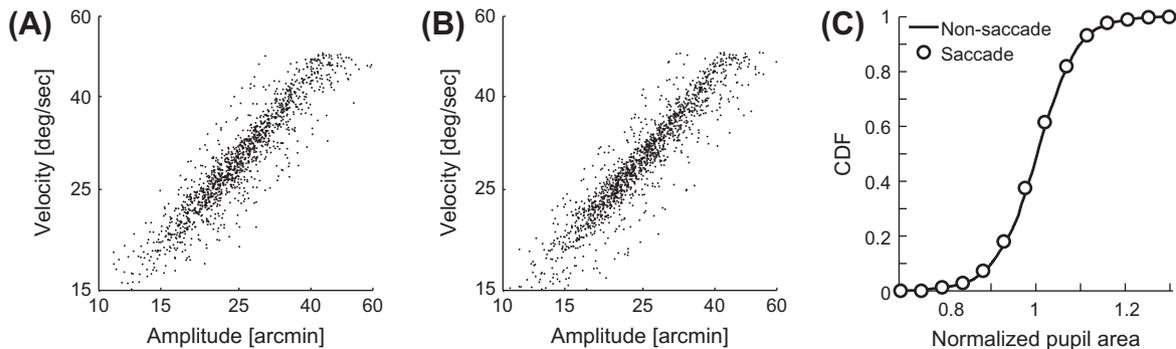


Fig. 2. Saccade properties. Saccadic main sequence for *hold* (A) and *switch* (B) conditions. The linear correlation between these measures was $R = 0.92$ ($p < .001$) and $R = 0.93$ ($p < .001$), respectively. (C) Cumulative distribution function (CDF) of pupil sizes, normalized to individual observer means, during saccade (open circles) and non-saccade intervals (continuous curve). The two distributions were virtually identical (Wilcoxon ranksum $p = 0.433 \pm 0.08$).

blink” (Raymond, Shapiro, & Arnell, 1992). “Attentional blinks” are prolonged attentional deficits which follow the successful discrimination of target items in rapid serial discrimination paradigms such as the one used here (Dux & Marois, 2009; Hommel et al., 2006; Martens & Wyble, 2010).

Observers were instructed to maintain fixation while monitoring one of four letter streams for 30 s and reporting the appearance of successive letter targets (see Section 2 for details). The to-be-monitored stream was identified by color and either retained its position during the entire trial (*hold condition*, Fig. 1A and Movie 1) or switched positions with its opposite number on the same meridian from time to time (*switch condition*, Fig. 1B and Movie 2). Importantly, both targets and position switches occurred at irregular intervals, forcing observers to attend continuously to the target stream. For the same reason, observers had to shift attention promptly to a new target stream location in the *switch condition*.

Observers reported target appearance reliably in both the *hold* and *switch* conditions, with performance levels ranging from 80% to 89% correct for all observers and conditions. The fraction of false alarms (mistakenly reported targets) ranged from 2.5% to 4%. No significant difference between *hold* and *switch* conditions was observed either in terms of behavioral performance (paired samples t -test: performance $T_3 = -0.24$, $p = .82$; reaction time $T_3 = 0.16$, $p = .16$), or in terms of MS rate ($T_3 = 0.04$, $p = .97$), or in terms of

MS amplitude ($T_3 = -0.4$, $p = .69$). The high level of performance implies that attention was continuously engaged during both *hold* and *switch* conditions. The probability of ‘attention lapses’ can be estimated as less than 0.2 (see below).

The visual onsets of letter items of the RSVP sequence failed to modulate microsaccade activity (residual modulation $\sim 5\%$, Fig. 3). This was an intended outcome of our rapid RSVP paradigm and differs from previous studies, in which visual onsets typically first suppressed and later enhanced the rate of microsaccades. For example, in the RSVP study of Valsecchi, Betta, and Turatto (2007), microsaccade rate was modulated approximately twofold in each direction (their Fig. 3). In the present paradigm, microsaccades were equally likely to occur at all latencies relative to letter items, thus uniformly sampling the temporal neighborhood of each display item. This allowed us to monitor attentional effects on microsaccade direction without the confound of substantial rate modulations (see also below).

Each 30 s-long presentation comprised a number of display events – appearance of target items and location switches of the target stream – as well as several behavioral response events – microsaccades (MS) and target identification reports. The number of target items ranged from 3 to 7 per stream, spaced by variable intervals (both *hold* and *switch* condition). Targets appeared independently in all four streams. The number of color/location switches ranged from 3 to 10 per stream, again spaced by variable

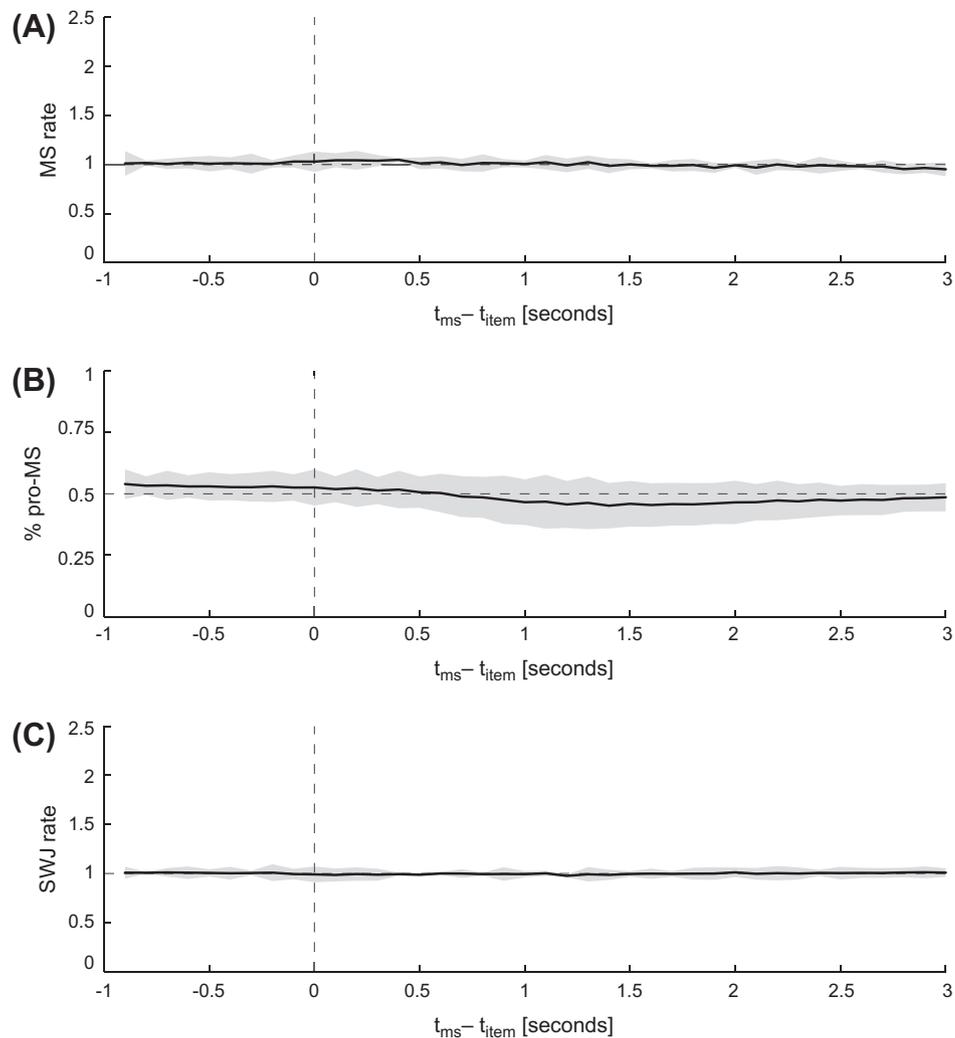


Fig. 3. MS activity associated with visual onsets. Visual onsets of letter items failed to modulate either (A) the rate of MS, (B) the direction of MS, or (C) the rate of square-wave-jerks (SWJ). This is an important difference to previous studies. The time axis represents latency between item onset (t_{item}) and MS onset (t_{ms}). The absence of directional biases in B implies that MS are directed equally often towards and away from the attended stream. This does not conflict with the MS alignment shown in Figs. 10 and 11.

intervals (*switch* condition only). Color/location switches occurred simultaneously in all four streams. The interval distribution for these events is shown in Fig. 4. Note that event rates were similar with 0.225 Hz for target appearances/identification reports and 0.25 Hz for stream switches, which implies that both kinds of events were sampled by a comparable number of microsaccades (average rate 0.27 Hz across observers) (see Fig. 4A).

3.1. Event-related attention effects

Previous work has shown that spatial attention shifts are associated with pronounced modulations in the rate and direction of MS (Hafed & Clark, 2002; Laubrock et al., 2010; Pastukhov & Braun, 2010). To replicate these findings under the present conditions, we established the MS activity associated with switching the target stream (*switch* condition).

We found the instantaneous MS rate to be weakly suppressed in anticipation of a stream switch (by approximately 20% at a latency of -400 ms) and to be strongly enhanced after the switch (by approximately 100% at a latency of 750 ms) (Fig. 5A). The total modulation of microsaccade rate was approximately 2.2-fold. After the switch, the majority of MS was directed *towards* the new target

stream location (Fig. 5B). Furthermore, grouping successive MS into square-wave-jerks (SWJ), revealed a more intricate pattern, in that the SWJ rate reached a first maximum around latencies of 250 ms and a second maximum around latencies of 1250 ms (Fig. 5C).

Previous evidence suggests that MS activity may also be modulated during attentional blink episodes (Valsecchi, Betta, & Turatto, 2007). Accordingly, we analyzed MS activity following the successful discrimination of letter targets (letters N or Z). We found the MS rate to be weakly enhanced in anticipation of a target (by approximately 10% around latencies of -300 ms) and subsequently suppressed (by approximately 40% around latencies of 500 ms) and then elevated significantly (by approximately 80% around latencies of 1100 ms, Fig. 6A). The total modulation of microsaccade rate was approximately 2.4-fold. The majority of MS was directed away from the target letter, consistent with an attentional disengagement (Fig. 6B). The rate of SWJ was suppressed significantly below its average level (Fig. 6C).

Consistent with an attentional blink, the pattern just described obtained only for successful discriminations. Following an unsuccessful target identification, the MS rate was first moderately suppressed (approximately 25% at latencies between 500 ms and

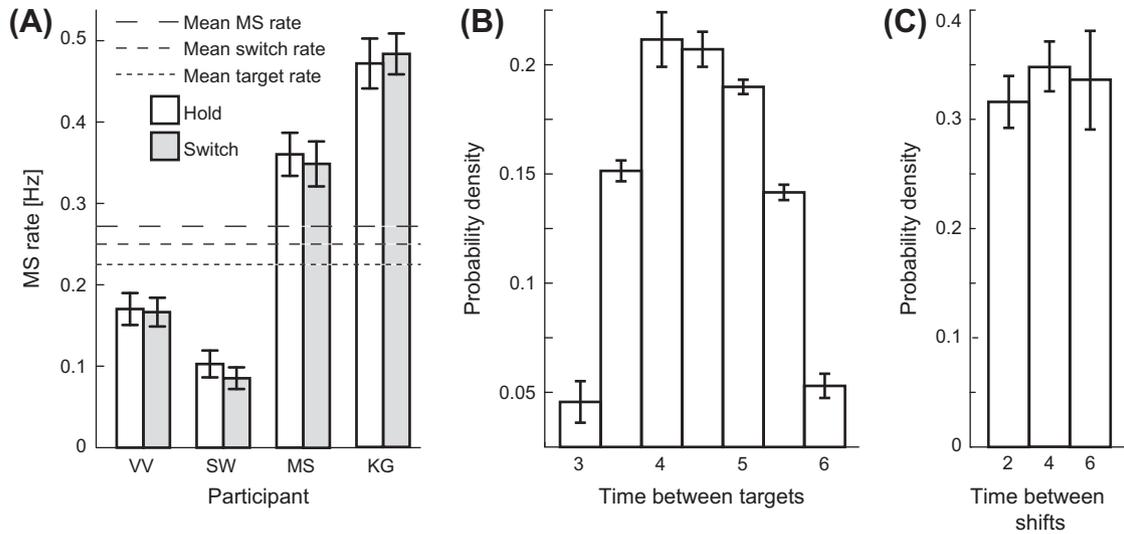


Fig. 4. Statistics of perceptual events. (A) Microsaccade rate (mean \pm s.e.m.) under *hold* and *switch* conditions (four observers). (B) Probability distribution of various interval durations between targets (mean \pm s.e.m.). (C) Probability distribution of various interval durations between stream switches (mean \pm s.e.m.).

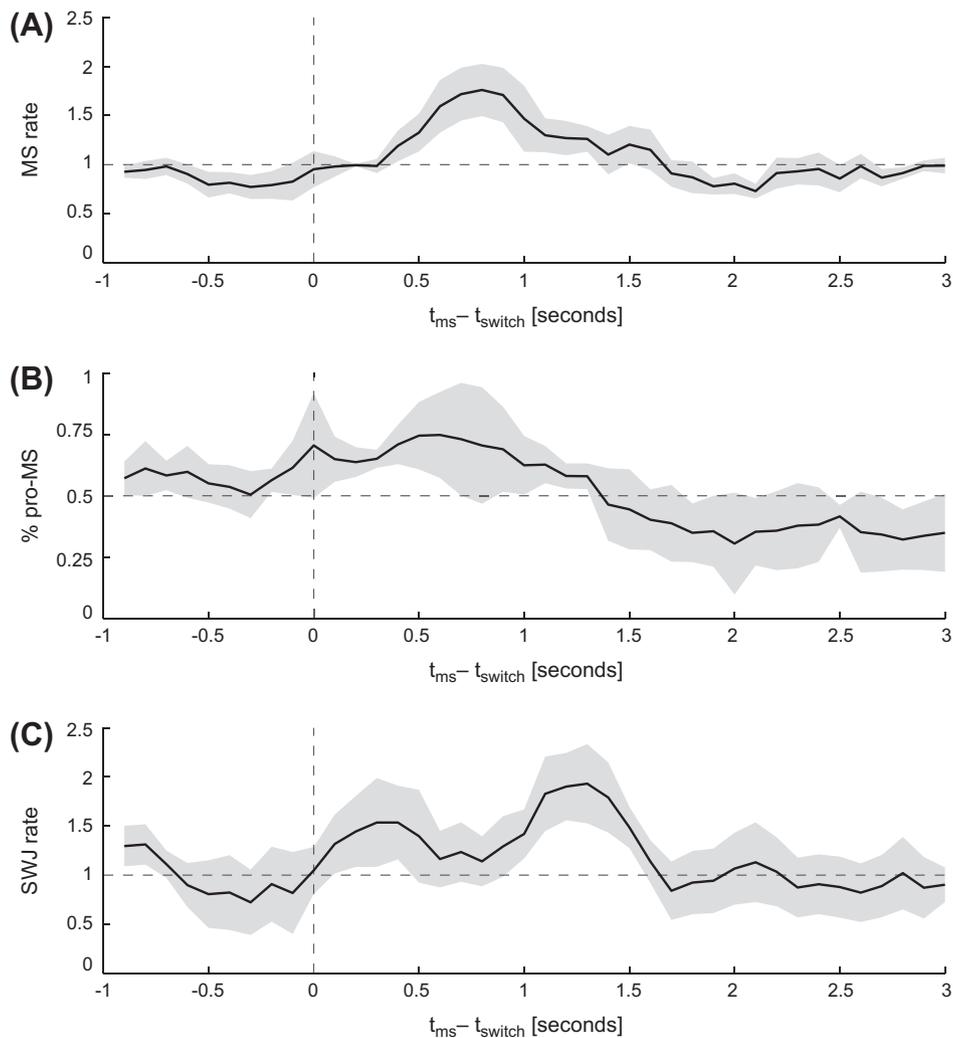


Fig. 5. MS activity associated with spatial attention transient (stream switch). Following a switch in the target stream, rate and direction of MS were modulated transiently. Mean (solid line) \pm s.e.m. (gray area) across observers was computed for temporal bins of 500 ms in 100 ms steps. The time axis represents latency between stream switch (t_{switch}) and MS onset (t_{ms}). (A) Rate of MS, normalized to mean rate of individual observers. (B) Fraction of MS toward the new target stream location (pro-MS), compared to chance level. (C) Square-wave-jerk (SWJ) rate, normalized to mean rate of individual observers.

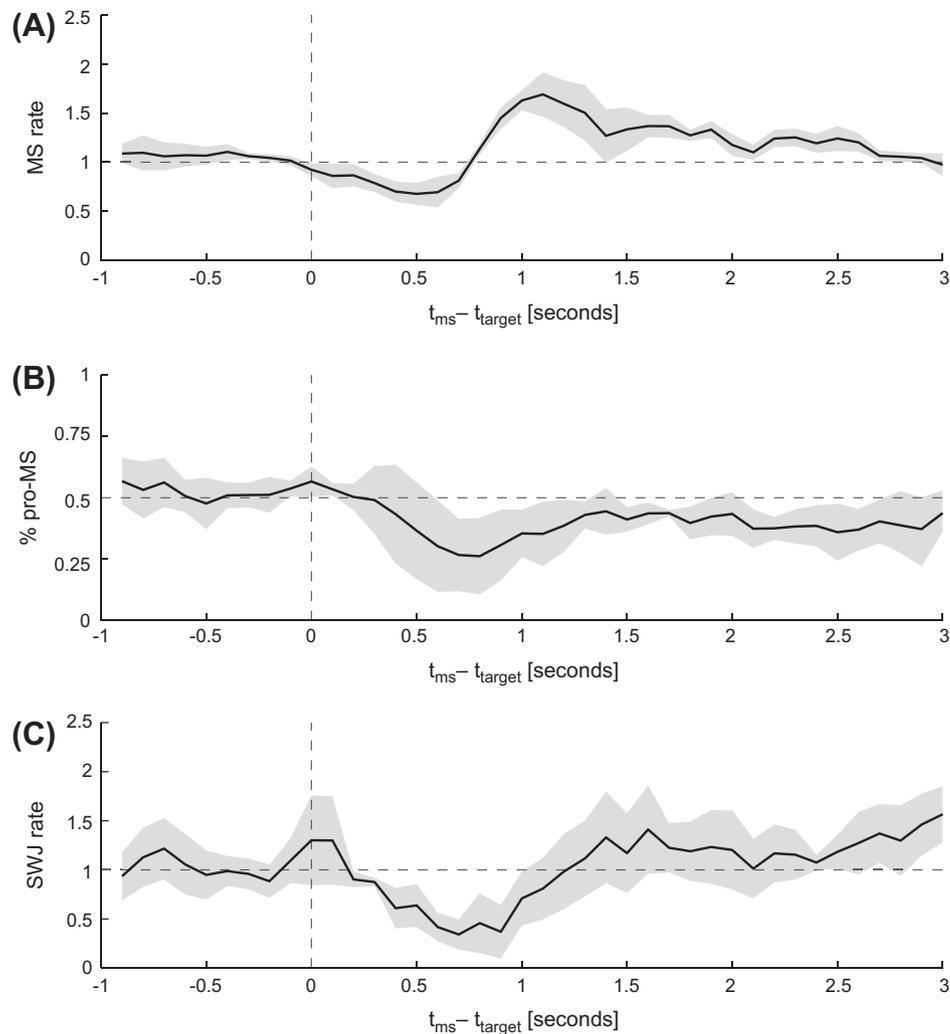


Fig. 6. MS activity associated with temporal attention transient (attentional blink). Following the successful discrimination of a target item (letters N or Z), rate and direction of MS were modulated transiently. The time axis represents latency between target onset (t_{target}) and MS onset (t_{ms}). Mean (solid line) \pm s.e.m. (gray area) across observers was computed for temporal bins of 500 ms in 100 ms steps. (A) Rate of MS, normalized to mean rate of individual observers. (B) Fraction of MS toward the target location (pro-MS), compared to chance level. (C) Rate of square-wave-jerks (SWJs), normalized to mean rate of individual observers.

1500 ms) and later moderately elevated (approximately 25% about latencies of 2000 ms)(Fig. 7A), with an approximately 2.3-fold total modulation. The direction of MS was not modulated significantly (Fig. 7B). The rate of SWJ exhibited a significant elevation at latencies between 1500 ms and 2500 ms (Fig. 7C). This late elevation coincides with the presumed end of the attentional blink period and exhibits characteristics of a spatial attention shift (see above). Accordingly, this late elevation may reflect a re-focusing of spatial attention after having lapsed.

To summarize, the spatial attention shift occasioned by a stream switch is characterized by MS towards the target location at latencies of approximately 750 ms. In addition, there is a high probability of a SWJ towards the target location at latencies of approximately 250 ms and of approximately 1250 ms. In contrast, the temporal engagement of attention during successful target identification is associated with MS directed back towards fixation, most often at latencies of approximately 1000 ms, consistent with a relaxation of the attentional focus. Yet another pattern of MS activity is observed after unsuccessful target identification. In this instance, MS activity is moderately suppressed until 750 ms after the event, at which time there is an elevated probability of MS and SWJ towards the target location, perhaps reflecting the re-focusing of attention on the cued stream.

3.2. Effect of eccentricity

Given the detailed information revealed by MS activity about the (average) timing and direction of attention shifts, we wondered whether MS activity might prove informative also about the visual eccentricity of the attended location. To investigate this possibility, we modified the display layout and presented three letter streams (each of unique color), one at fixation, a second at 3° eccentricity, and a third at 9.5° eccentricity (Fig. 8A). Each letter stream maintained its color/location for the entire 30 s presentation (as for the *hold* condition of the previous experiment). Observers were instructed to maintain fixation at display center while monitoring (and reporting target appearances in) one particular stream.

The results are summarized in terms of the average rate and amplitude of MS observed in each condition (Fig. 8BC). They show a clear difference between attending to a central and an eccentric location: MS were significantly less frequent (paired samples t -test $T_3 = -6.4$, $p = 0.008$), and significantly smaller (paired samples t -test $T_3 = -5$, $p = 0.015$ and $T_3 = -6$, $p = 0.001$), when observers attended at fixation. Interestingly, MS rate and amplitude did not differ significantly when observers attended either one of the two peripheral target streams. We conclude that MS amplitude does

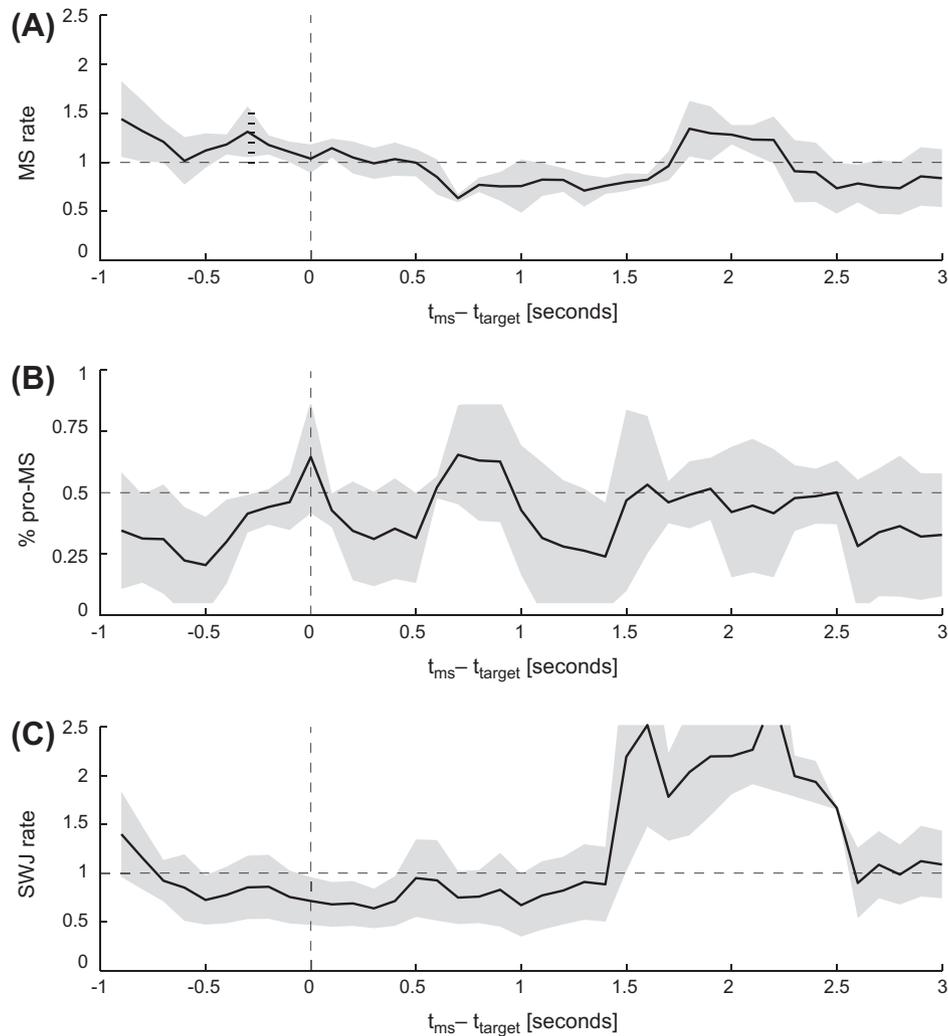


Fig. 7. MS activity associated with missed target. Subsequent to an unreported (missed) target, rate and direction of MS were modulated differently. Mean (solid line) \pm s.e.m. (gray area) across observers was computed for temporal bins of 500 ms in 100 ms steps. The time axis represents latency between target onset (t_{target}) and MS onset (t_{ms}). (A) Rate of MS, normalized to mean rate of individual observers. (B) Fraction of MS toward the target location (pro-MS), compared to chance level. (C) Rate of square-wave-jerks (SWJs), normalized to mean rate of individual observers.

not (readily) differentiate between extrafoveal attended locations of different eccentricity.

3.3. Non-event-related ('unrelated') microsaccades

In addition to the event-related attention effects described above, we wondered whether there might also be attention effects during periods associated with neither target events nor stream switches. As mentioned, our experimental situation required observers to attend continuously to the cued stream. Accordingly, it seemed possible that this (mostly) steady allocation of attention to a peripheral location might influence microsaccade activity even in the absence of targets events or stream switches.

To distinguish 'unrelated' from 'event-related' microsaccades, we excluded from the analysis a 3000 ms window around each target onset and each stream switch (from -750 ms before to 2250 ms after each event). In the *hold* condition, which contained only target events, this criterion excluded $70 \pm 7\%$ of the presentation time and $66 \pm 7\%$ of the MS activity. In the *switch* condition, which contained both target events and stream switches, it excluded $92 \pm 5\%$ of the presentation time and $91 \pm 6\%$ of the MS activity.

To our surprise, mean MS activity was comparable during unrelated and event-related periods. When MS frequency was normalized to the individual observer mean (which varied considerably between observers), the *switch* condition yielded a normalized mean rate of 0.99 ± 0.03 Hz for event-related and 1.04 ± 0.17 Hz for unrelated MS activity. In the *hold* condition, we measured 0.90 ± 0.02 Hz for event-related and 1.14 ± 0.03 Hz for unrelated MS activity. When the window of exclusion defining unrelated MS was narrowed to 1500 ms around each event, the results remained essentially unchanged.

A more detailed analysis of MS timing and amplitude provided further evidence that MS activity was quantitatively comparable in unrelated and event-related periods. As shown in Fig. 9A–C, we obtained no significant difference between unrelated, target-related, and switch-related periods with respect to either the mean inter-MS-interval, or the variability of inter-MS-intervals, or the amplitude of MS. Two sample *t*-tests were performed for each observer (4), observable (3), and each pair of conditions (3). All *p*-values were greater than the uncorrected significance level of $\alpha = 0.05$. These observations suggest that MS may occur spontaneously (due to some independent random process with stationary statistics), rather than being triggered by attentional transients.

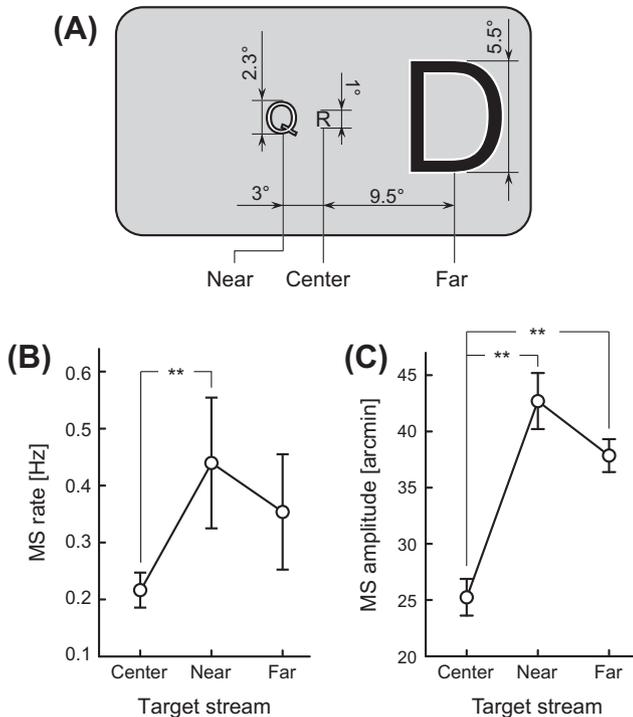


Fig. 8. Effect of eccentricity. (A) Display layout (schematic). Three streams of letters (each of unique color) were presented at fixation (letter 'R'), at 3° eccentricity (letter 'Q'), and at 9.5° eccentricity (letter 'D'). Observers were instructed to maintain fixation at display center while monitoring one particular stream. (B) Average MS rate from five observers (mean \pm s.e.m.). MS were significantly less frequent with attention focused at fixation. (C) Average MS amplitude from five observers (mean \pm s.e.m.). MS amplitudes were significantly smaller with attention focused at fixation.

But how can we be sure that the MS we consider 'unrelated' were not in fact associated with attentional shifts (i.e., lapses in the attentional monitoring of the cued stream)? Although it is likely that attention lapsed occasionally, our argument is simply that there must have been fewer attention shifts (per unit time) in periods in which the cued stream remained in place than in periods in which the cued stream switched to a new location. While we cannot know how often attention may have lapsed from a stationary cued stream, we can estimate the fraction of time during which attention remained on this stream.

Discriminating target letters (*N* or *Z*) embedded in a stream of distractor letters places a considerable demand on attention (Braun, 1998), so that the performance level of this task provides a sensitive measure of attentional allocation. Specifically, a complete lapse of attention reduces performance to chance level and a partial lapse leads to a proportionately smaller reduction (Lee, Koch, & Braun, 1999; Pastukhov, Fischer, & Braun, 2009). In the present case, the performance level was 80–89% correct, while chance performance was 17% correct. Given these values, we can estimate the fraction of time α , during which attention was fully allocated to the target stream, to be $\alpha = 0.76\text{--}0.87$ (from $100\alpha + 17(1 - \alpha) = 80\text{--}89\%$).

In short, assuming that our attentional manipulations were mostly effective (so that attentional shifts were more frequent during event-related than during non-event-related periods), it follows that MS occurred spontaneously and with (overall) stationary statistics.

3.4. Attentional alignment of event-related and non-event-related ('unrelated') MS

As mentioned above, switch-related and target-related MS seemed to be often directed either towards the target stream or away from it (i.e., back towards fixation). In other words, MS seemed to align predominantly with the meridian of the attended stream. Accordingly, if observers attended a target stream on the horizontal (vertical) meridian, the predominant direction of MS was also horizontal (vertical). Representative examples of aligned MS are shown Fig. 10A.

To quantify this apparent alignment, we computed the mean *absolute* size of horizontal and vertical MS components, averaging over the entire trial duration of 30 s. As expected, the mean *absolute* horizontal and vertical MS size varied significantly with the attended meridian (Fig. 10B): horizontal amplitudes were larger than vertical amplitudes when the attended stream lay on the horizontal meridian, and *vice versa*. Indeed, when examining Fig. 10B, it is evident that the results from trials with different attended meridians (horizontal and vertical) form two distinct clusters. Accordingly, the attended meridian of an individual trial could be inferred reliably from the relative size of horizontal and vertical MS components by applying a simple linear criterion (straight lines in Fig. 10B). This inference was equally reliable for *hold* and *switch* conditions (92% and 92.5%, respectively). For individual observers, the reliability of this inference ranged from 88% to 96% (*hold*

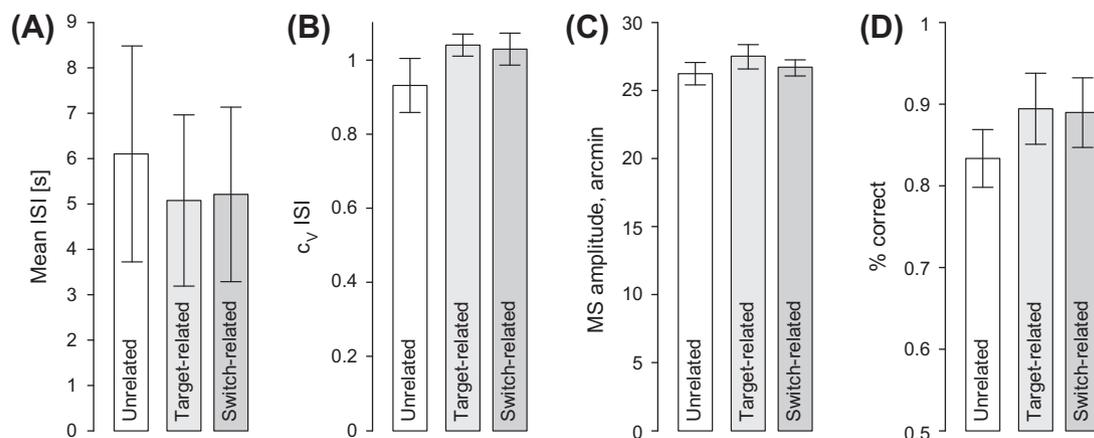


Fig. 9. Comparison of event-related and non-event-related MS. Classifying MS as being associated either with a stream switch (switch-related), or with a target event (target-related), or with none of the above (unrelated), we compared the mean interval between successive MS (A), the coefficient of variation of this interval (B), the amplitude of MS (C), and the informativeness of MS direction about the attended meridian (D). See Fig. 10 for further details about the measure of informativeness. No significant differences were observed (two-sample *t*-test, all *p*-values greater than $\alpha = 0.05$).

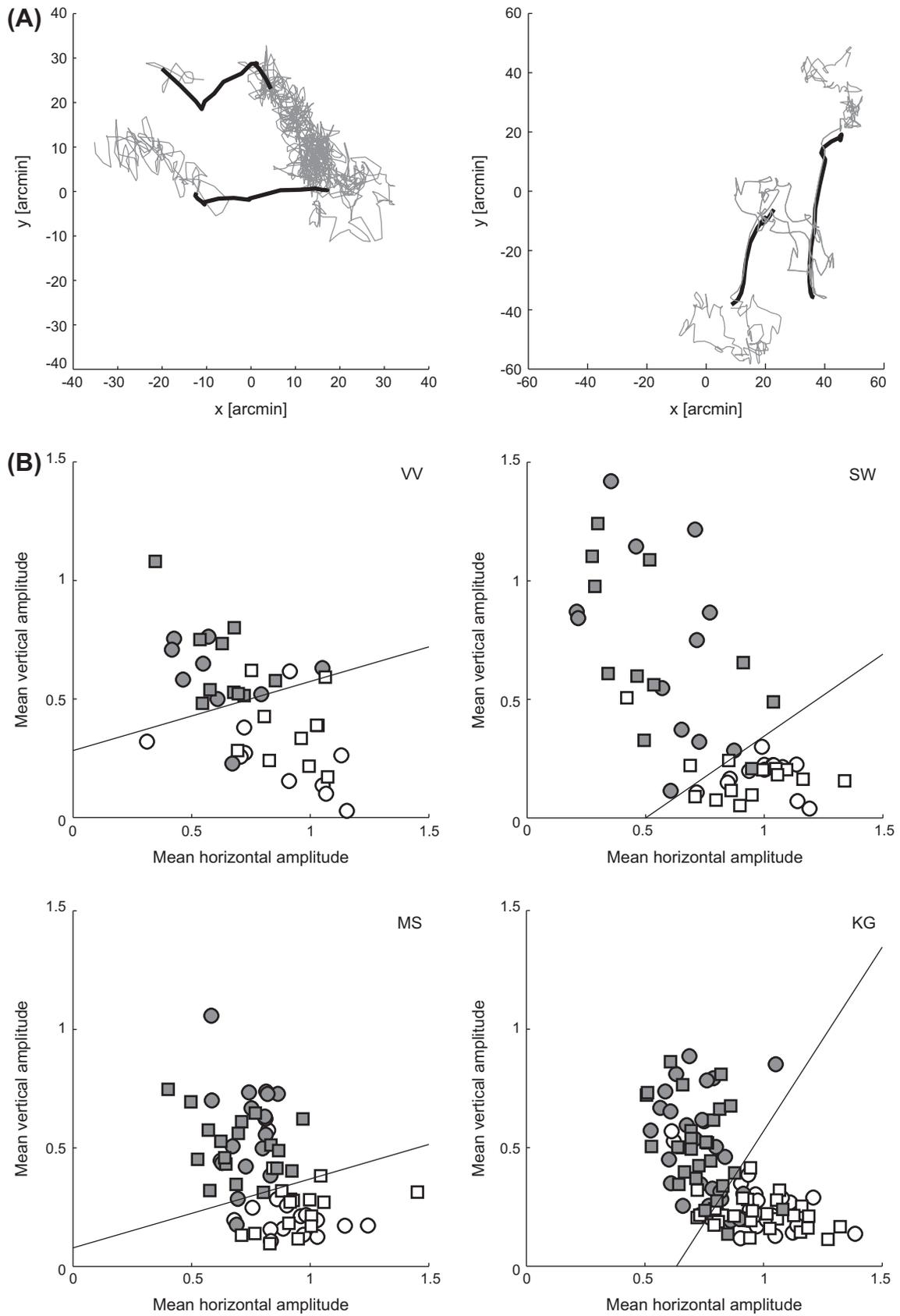


Fig. 10. Alignment with attended meridian (all MS). (A) Representative eye position recordings illustrating alignment of MS (bold traces). Left: target stream on the horizontal meridian. Right: target stream on the vertical meridian. (B) MS alignment reveals the target meridian of individual trials (results of four observers). Mean absolute horizontal and vertical components of MS amplitude observed in individual trials, for target streams on the horizontal (open symbols) or vertical meridian (closed symbols). To facilitate comparison across observers, amplitude components are normalized to individual observer means. Also shown is the optimal discrimination criterion (straight line, K-means algorithm) for each observer. Circles: *hold* condition, 92% of trials classified correctly. Squares: *switch* condition, 92.5% of trials classified correctly.

condition, paired samples t -test against chance level performance of the algorithm obtained for each individual observer by bootstrapping, $T_3 = 7.01$, $p = 0.005$) and from 88% to 98% (*switch* condition, $T_3 = 9.91$, $p = 0.002$).

As MS alignment proved comparably informative for *hold* and *switch* conditions, it was not a specific correlate of spatial attention shifts (which we assume to have been less frequent during the *hold* condition). To ascertain whether or not non-event-related MS activity also exhibited this alignment, we computed the informativeness of unrelated MS during the *hold* condition. As shown in Fig. 11, MS unrelated to target appearances ($30 \pm 7\%$ of the total) proved comparatively informative about the target meridian, with $84 \pm 4\%$ of trials classified correctly (significantly above chance, $T_3 = 9.13$, $p = 0.003$). Thus we found the degree of alignment with the target meridian to be comparable for target-related, switch-related and unrelated MS activity (Fig. 9D, paired t -test, all p -values were greater than $\alpha = 0.05$).

Our analysis excluded from consideration all eye movements larger than 1° (0.4% of the total). This cut-off was arbitrary and other values have been used in the literature (Martinez-Conde, Macknik, Troncoso, & Hubel, 2009). Analysis of MS amplitude showed that this cut-off could be lowered substantially, as most of observed microsaccades were smaller than $40'$, see Fig. 12A. To

ascertain whether MS alignment varies with MS amplitude, we repeated the analysis for a range of different amplitude values. As shown in Fig. 12B, the alignment of smaller MS also predicts the attended meridian, albeit with diminished prediction performance. However, even for MS amplitudes as low as $15.25'$, the predicted performance was above 80% and significantly above the chance level (paired samples t -test $T_3 = 8.7$, $p = 0.003$).

Taken together, our analysis revealed a ubiquitous MS alignment, which was comparable at all times (switch-related, target-related, and non-event-related MS). This observation strongly suggests that attention was directed (almost) continuously at the target stream and that MS continuously reflected this attentional allocation. Whereas the influence of attention did not entail any directional bias – in that MS were directed equally often towards and away from the attended stream – it did impose a biased alignment: MS were directed more often along the attended meridian than orthogonal to it.

4. Discussion

We studied the relation between covert attention and microsaccadic activity by combining several attentional manipulations in a single experimental situation. Our paradigm – discriminating

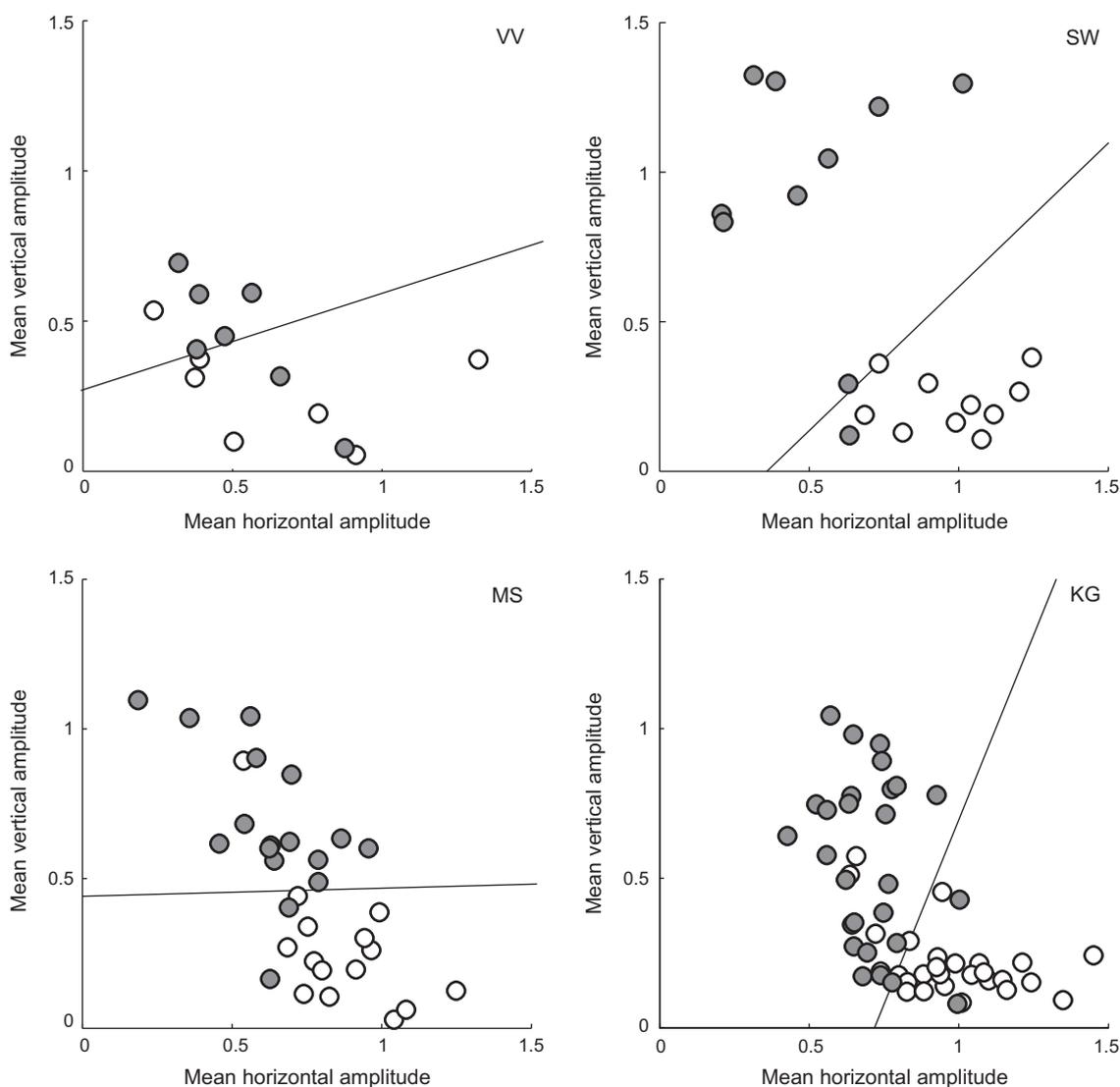


Fig. 11. Alignment with attended meridian (non-event-related MS). In the *hold* condition, $34 \pm 7\%$ of all MS were unrelated to target appearances. Unrelated MS were highly informative about the target meridian, with $84 \pm 4\%$ of trials classified correctly. See Fig. 10 for further details.

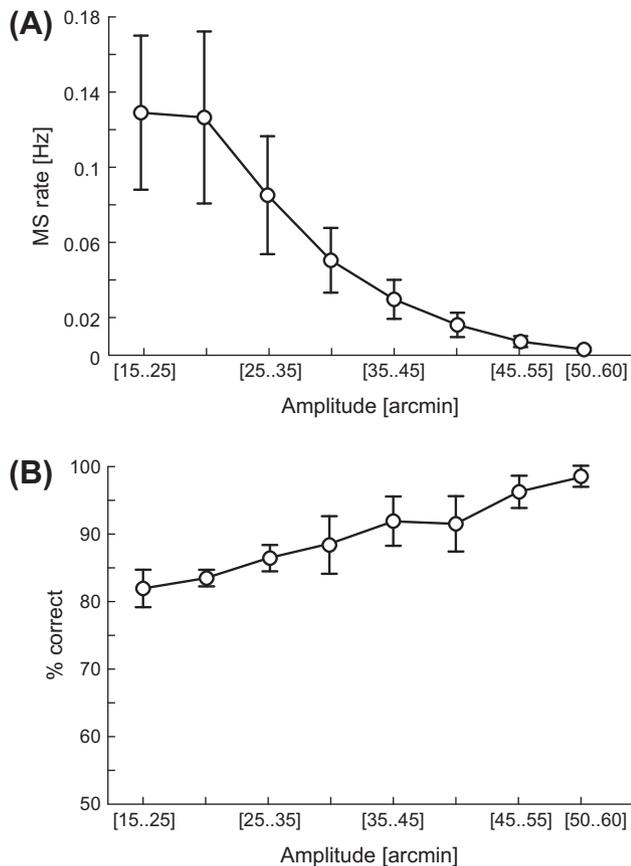


Fig. 12. MS alignment with attended meridian and amplitude. Predictiveness of MS alignment with attended meridian as a function of MS amplitude. (A) Mean MS rate from different MS subsets. (B) Discrimination of target meridian (% correct, mean \pm s.e.m.) from different MS subsets.

a stream of successively presented items – was a proven method for engaging attention continuously and also afforded opportunities for spatial and temporal attention transients. Furthermore, this paradigm largely eliminated the modulation of microsaccade rate either by visual onsets or in anticipation of task-relevant items, both of which had been prominent (and potentially confounding) features of previous studies.

Consistent with numerous previous reports (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Hafed, Lovejoy, & Krauzlis, 2011; Horowitz et al., 2007; Laubrock et al., 2010; Pastukhov & Braun, 2010), we found that microsaccades tend to be directed towards a peripheral location when attention was being shifted towards this location. We also confirmed the tendency of microsaccades to cluster into ‘back and forth’ patterns that have been termed “square-wave-jerks” (Hafed & Clark, 2002; Hafed, Lovejoy, & Krauzlis, 2011), presumably reflecting corrective mechanisms for maintaining fixation. Finally, we confirmed that microsaccades tend to be directed away from an attended peripheral location during an attentional blink episode (Valsecchi, Betta, & Turatto, 2007).

In addition, our results contributed several new findings, which we describe in detail below. In a nutshell, our observations suggest a simple relation between attentional allocation and microsaccade direction: (i) While an attentional focus builds up at a task-relevant location, microsaccades aim predominately towards this location. (ii) When such a focus relaxes, microsaccades aim predominantly back towards fixation. (iii) When an attentional focus is sustained continuously, microsaccades aim equally often in both directions, aligning themselves with the meridian of the task-relevant location. Thus, the association between attention

and microsaccades is not restricted to exceptional episodes such as attentional shifts, but is continuous and lasts throughout the formation, maintenance, and relaxation of an attentional focus. Accordingly, attentional allocation and eye movements seem to be controlled continuously – not just episodically – by closely overlapping brain structures.

4.1. Formation, relaxation, and re-formation of attentional focus

We observed microsaccades (and square-wave-jerks) towards a behaviorally relevant location when attention shifted there for the first time (switches in the cued stream location, Fig. 5) and when attention re-focused on a location after having lapsed (following unsuccessful target discrimination, Fig. 7). In addition, we observed microsaccades (but not square-wave-jerks) back towards fixation when an attentional focus temporarily relaxed (“attentional blink” following successful target discrimination, Fig. 6).

The ‘back and forth’ between microsaccades towards the attended location and corrective microsaccades that restore fixation served to “align” microsaccade direction with the meridian of the attended location. This alignment was sufficiently reliable to infer the attended meridian in approximately 80% of trials (Fig. 9D).

4.2. Continuously sustained attention

When attention was sustained continuously on a task-relevant location, the appearance of a task-relevant target failed to increase the probability of microsaccades towards this location (Fig. 6AB). However, between approximately 750 ms and 2000 ms after the target onset, we observed an increase in the probability of microsaccades away from the task-relevant location, presumably reflecting a temporary relaxation of the attentional focus (“attentional blink”).

These results contrast with a recent study of non-human primates (Hafed, Lovejoy, & Krauzlis, 2011), in which microsaccades tended to be directed towards the cued location just before and during the appearance of a task-relevant stimulus. However, microsaccades in that study (unlike ours) also exhibited a prominent preparatory suppression in anticipation of a task-relevant stimulus, consistent with a preparatory re-focussing of attention at the cued location. In other words, unlike the present study, Hafed, Lovejoy, and Krauzlis (2011) do not appear to have attained a true steady-state of attentional allocation (i.e., continuously sustained attention).

4.3. Continuous alignment with task-relevant location

Our results show that microsaccade direction remained aligned to the meridian of the location at which attention was sustained. The degree of alignment was comparable during periods of continuously sustained attention, periods with spatial attention shifts, and periods with attentional blinks (Fig. 9D). Thus, microsaccade alignment continuously reflected the task-relevant location.

In contrast, previous studies have concluded that microsaccade direction best reflects the task-relevant location around the time of an attentional shift. For example, Laubrock et al. (2010) stated that “if the attentional signal is not smeared over time, ... it will be expressed in microsaccade direction”. Similarly, we have reported that the correlation between microsaccade direction and task-relevant location is maximal at the very moment of an attentional shift (Pastukhov & Braun, 2010).

The present results suggest a more nuanced conclusion: while microsaccade direction indeed reveals attentional transients, microsaccadic alignment equally reflects both attentional transients and continuously sustained attention. Accordingly, the full

effect of attending to a task-relevant location becomes evident only when both direction and alignment of MS are analyzed.

4.4. Dissociating rate and direction of microsaccades

For the first time, our observations distinguish between attentional effects on the rate and on the direction of MS. This became possible because our experimental paradigm (rapid serial visual presentation, RSVP) eliminated almost entirely rate modulations due to visual onsets (residual modulation ~5%, Fig. 3) and due to anticipation of imminent targets (~20%, Fig. 6) or imminent stream switches (~10%, Fig. 5). In previous studies, substantial (4- to 10-fold) modulations related to onsets and/or target anticipation were superimposed over any attentional modulations of MS rate (Betta et al., 2007; Betta, Galfano, & Turatto, 2007; Engbert & Kliegl, 2003; Galfano, Betta, & Turatto, 2004; Hafed & Clark, 2002; Laubrock, Engbert, & Kliegl, 2005; Pastukhov & Braun, 2010; Rolfs, Kliegl, & Engbert, 2008; Rolfs, Engbert, & Kliegl, 2005; Rolfs, Laubrock, & Kliegl, 2006).

Following the appearance of a target, or a switch of the cued stream, we observed 2.2- to 2.4-fold modulations of MS rate. These rate modulations extended over approximately 2 s and roughly coincided with modulations of MS direction (switch-related MS, Fig. 5; target-related MS, Fig. 6, and missed-target-related MS, Fig. 7). Accordingly, we took these modulations to be purely attentional in nature. Interestingly, the respective time-courses of rate and direction modulations did not mirror each other, suggesting that the underlying mechanisms may be complex (see below).

One may well ask whether the substantial (4- to 10-fold) modulations of MS rate observed in previous studies were always exclusively attentional in nature. On the one hand, it is quite plausible that visual onsets would attract exogenous attention and that imminent targets would be anticipated by a focussing of endogenous attention (both of which could, in turn, suppress MS activity). On the other hand, the preparatory suppression of MS detrimental to task performance may also reflect trace conditioning at the level of premotor nuclei or motor neurons (Hafed, 2011). Further work is needed to distinguish these possibilities.

4.5. Effect of extrafoveal eccentricity

The amplitude of microsaccades carries some information about the eccentricity of the attended location. We observed significantly smaller amplitudes when attention focused at fixation than when it focused in the near or far periphery (3° or 9.5°). However, the amplitude of microsaccades failed to distinguish between extrafoveal locations of different eccentricity (near and far periphery, Fig. 8).

4.6. Implications for modeling

Several groups have modeled fixational eye movements in terms of the fluctuating activity distribution of a retinotopic representation in superior colliculus (Engbert et al., 2011; Engbert, 2012; Hafed, Goffart, & Krauzlis, 2009; Rolfs, Kliegl, & Engbert, 2008). Typically, these models assume that small deviations of the center-of-activity from the fixated location generate continuous fixational eye movements whereas large deviations trigger restorative microsaccades. The preparation of saccades, or the shifting of attention, to peripheral locations is assumed to involve the formation of a secondary activity peak at the corresponding retinotopic location. Presumably, such a secondary peak deforms the primary activity peak around fixation, thereby modulating fixational eye movements including microsaccades.

A key feature of current models (e.g., Engbert et al., 2011; Engbert, 2012) is that both the instantaneous probability and

direction of MS are assumed to be byproducts of large dynamical shifts in the collicular activity distribution (i.e., shifts of the attention focus). These assumptions appear doubtful in the light of the present findings. Firstly, the probability of MS is comparable whether an attentional focus builds up, relaxes, or is continuously sustained, suggesting that MS reflect small spontaneous fluctuations (not large dynamical shifts) in an activity distribution. Secondly, if anticipatory saccadic suppression is eliminated, MS probability and direction can be dissociated (and the close association observed in many previous studies dissolves, e.g., Pastukhov & Braun (2010)). Thus, it is not clear that one should seek to account for attentional modulations of the probability and direction of MS with a common mechanism. Instead, it may become necessary to also consider mechanisms of saccadic suppression that do not operate through a collicular activity distribution, for example, conditioning at the level of premotor or motor structures (Hafed, 2011).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.visres.2012.11.004>.

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