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Microsaccades uncover the orientation of covert attention

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Abstract

Fixational eye movements are subdivided into tremor, drift, and microsaccades. All three types of miniature eye movements generate small random displacements of the retinal image when viewing a stationary scene. Here we investigate the modulation of microsaccades by shifts of covert attention in a classical spatial cueing paradigm. First, we replicate the suppression of microsaccades with a minimum rate about 150 ms after cue onset. Second, as a new finding we observe microsaccadic enhancement with a maximum rate about 350 ms after presentation of the cue. Third, we find a modulation of the orientation towards the cue direction. These multiple influences of visual attention on microsaccades accentuate their role for visual information processing. Furthermore, our results suggest that microsaccades can be used to map the orientation of visual attention in psychophysical experiments.

Keywords: Attention; Microsaccade; Eye movements; Inhibition; Spatial cueing

1. Introduction

When we view a stationary scene, miniature (or fixational) eye movements are produced involuntarily (Ditchburn, 1955; Ratliff & Riggs, 1950; Steinman, Haddad, Skavenski, & Wyman, 1973; Yarbus, 1967). These micromovements are traditionally classified as noisy low-level oculomotor phenomena and are subdivided into tremor, drift, and microsaccades (for a review see Ciuffreda & Tannen, 1995). Generally, they serve to counteract retinal adaptation by generating small random displacements of the retinal image in stationary viewing (Riggs, Ratliff, Cornsweet, & Cornsweet, 1953). Retinal adaptation may have evolved as an elegant property of our visual system to force rapid detection of moving objects (e.g., an approaching predator). When viewing stationary objects, however, retinal adaptation is disastrous and causes the image to fade from perception (Riggs et al., 1953). Thus, micromovements serve an important purpose in the maintenance of stationary scenes.

So far a specific functional role for microsaccades (i.e., one that could differentiate them from drift) could not be demonstrated (Kowler & Steinman, 1980), in particular because microsaccades can be suppressed voluntarily without training in high-acuity observational tasks like threading a needle or rifle shooting (Bridgeman & Palca, 1980; Steinman, Cunitz, Timberlake, & Herman, 1967; Winterson & Collewijn, 1976). On the basis of these results it was concluded that microsaccades are not needed for visual information processing and, hence, represent an evolutionary puzzle (Kowler & Steinman, 1980; but see Martinez-Conde, Macknik, & Hubel, 2000).

Visual attention plays a central role in the control of saccades (Deubel & Schneider, 1996; Findlay, 1976; Kowler, Anderson, Dosher, & Blaser, 1995; Kustov & Robinson, 1996). A key finding in research about visual attention is that the orientation of attention can differ from the orientation of gaze position. In this case, the term *covert attention* is frequently used to indicate this separation, which is typically implemented in experimental conditions of attentional cueing (Posner, 1980). The aim of our investigation was to examine the effects of covert shifts of visual attention on microsaccade statistics. Such effects of attention during fixation may provide new insights into the function of microsaccades.

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2. An algorithm for the detection of microsaccades

Microsaccades can be detected in eye movement recordings when a participant is fixating a stationary object (Nachmias, 1959; Ratliff & Riggs, 1950). While small drifts induce a rather erratic trajectory (i.e., a random walk), microsaccades are ballistic movements and create small linear sequences embedded in the trajectory (Fig. 1a and b). Microsaccades occur at a rate of 1–2 per second and have a typical amplitude between 1′ and 25′ (Ciuffreda & Tannen, 1995).

We developed a new algorithm for the detection of microsaccades in two-dimensional (2D) velocity space. First, the time series of eye positions was transformed to velocities by

$$\vec{v}_n = \frac{\vec{x}_{n+2} + \vec{x}_{n+1} - \vec{x}_{n-1} - \vec{x}_{n-2}}{6\,\Delta t}, \tag{1}$$

which represents a moving average of velocities over 5 data sample to suppress noise. As a consequence of the random orientations of the velocity vectors during fixation, the resulting mean value is effectively zero (Fig. 1c and d). In this representation, microsaccades can be identified by their velocities, which are clearly separated from the kernel of the distribution, that is microsaccades are "outliers" in velocity space.

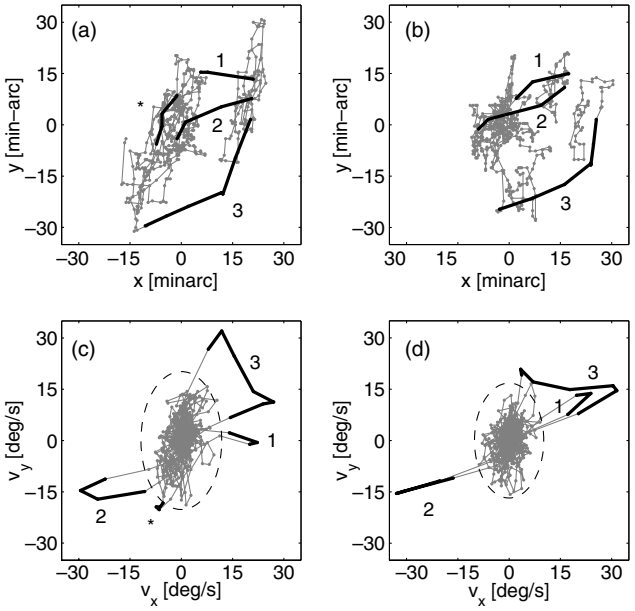

Fig. 1. Fixational eye movements and detection of microsaccades. (a) In a simple fixation task rather erratic miniature eye movements are observed. The example represents a fixation with a duration of 2348 ms (or 588 data samples), recorded from the left eye. Microsaccades are small but rapid events which can be identified by their approximately linear appearances (bold lines). (b) Plot of the corresponding data for the right eye positions. (c) A plot of the trajectory in 2D velocity space shows considerably higher peak velocities for microsaccades compared to other components of miniature eye movements. Detection thresholds were computed separately for horizontal and vertical components (see Section 2). (d) Plot of the corresponding data for the right eye velocity data. The numbers refer to binocular microsaccades, while the ★ symbol indicates a monocular microsaccade, which is discarded from the analysis presented here.

Second, computation of velocity thresholds for the detection algorithm was based on the median of the velocity time series to protect the analysis from noise. A multiple of the standard deviation of the velocity distribution was used as the detection threshold. To protect the computation of the standard deviation from noise, we applied a median estimator to the time series,

$$\sigma_{x,y} = \langle v_{x,y}^2 \rangle - \langle v_{x,y} \rangle^2, \tag{2}$$

where $\langle \cdot \rangle$ denotes the median estimator. Detection thresholds were computed independently for horizontal η_x and vertical η_y components and separately for each trial, relative to the noise level, i.e.

$$\eta_{x,y} = \lambda \sigma_{x,y}. \tag{3}$$

We used a value $\lambda = 6$ in all computations reported here. It is important to note that the detection threshold is chosen relative to the noise level in velocities of a single trial. Therefore, our algorithm is robust with respect to different noise levels between different trials and participants. Additionally, we assumed a minimal duration of three data samples (12 ms) to further reduce noise.

Third, microsaccades are traditionally defined as binocular events (Ciuffreda & Tannen, 1995). We addressed the aspect of binocular coordination in microsaccades in a recent study and suggested a distinction between monocular and binocular microsaccades (Engbert & Kliegl, 2003). Here, we focus on binocular microsaccades, defined as microsaccades occurring in left and right eyes with a temporal overlap, which is in agreement with the traditional definition. In more detail, we exploited binocular information in our detection algorithm by applying a temporal overlap criterion. If we observe a microsaccade in the right eye starting at time r_1 and ending at time r_2 and a microsaccade in the left eye beginning at time l_1 and stopping at time l_2, the criterion for temporal overlap can be implemented by the conditions

$$r_2 > l_1 \quad \text{and} \quad r_1 < l_2. \tag{4}$$

Examples for binocular and monocular microsaccades are given in Fig. 1. For a detailed discussion of binocular aspects in microsaccades, see Engbert and Kliegl (2003).

As microsaccades and macroscopic saccades share the same relation between peak velocity and amplitude due to their ballistic nature (Zuber, Stark, & Cook, 1965), we used this property as a criterion to check the validity of our detection algorithm. In good agreement with previous findings, a scatterplot of peak velocities of microsaccades over their amplitudes showed the expected relation between these two variables (Fig. 2).

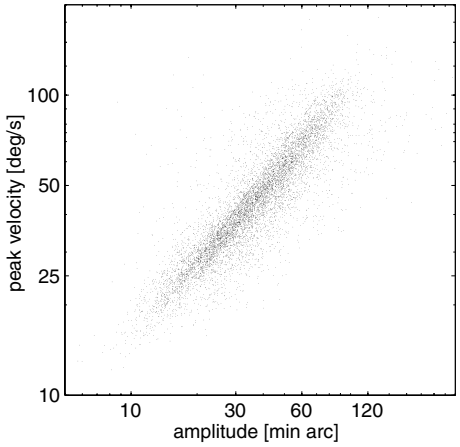

Fig. 2. Maximum velocities of microsaccades as a function of their amplitudes. Due to their ballistic nature, microsaccades show a fixed relation between peak velocity and amplitude. The plot contains 9183 microsaccades from all 30 participants in Experiment 3.

In summary, the detection threshold used in our algorithm is based on the standard deviation of the velocity components (computed with a robust median estimator). The temporal overlap criterion uses binocular information to reduce noise in the detection procedure. Because of these properties, we expect that our algorithm can easily be adapted to different noise levels produced by interindividual differences in participants or by different eye tracking technologies.

3. Experiment 1: spatial cueing of visual attention

We studied effects of visual attention on microsaccades with a classical spatial cueing paradigm (Posner, 1980). Most features of the experimental design were taken from the original work. In Experiment 1, participants fixated a cross presented centrally on a computer screen. After a random interval of presentation time, a cue (an arrow pointing to the left, right, or both directions) appeared centrally, indicating the most likely location for the next target (Fig. 3). We used longer presentation times (1.5–2 and 2–2.5 s) compared to the original study (0.9 s) for fixation cross and cue to facilitate the observation of microsaccades. Participants fixated the central cue until the target appeared. In half the blocks participants responded with a key press, in the other half with a saccade to the target.

3.1. Methods

3.1.1. Participants

Thirty participants, all undergraduate students of the University of Potsdam, performed 240 trials each. All subjects had normal or corrected-to-normal vision.

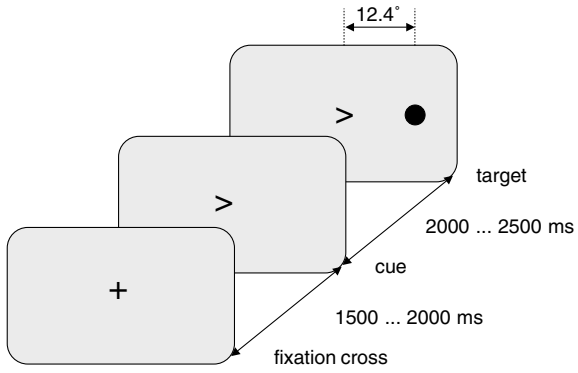

Fig. 3. Experimental displays in Experiment 1. A single trial comprised three different displays: a fixation cross, a cue, and a target to which participants responded with a saccadic eye movement or a key-press (for details see Section 3.1.2).

3.1.2. Stimuli and procedure

A trial started with a fixation cross (size: 0.73°; white on dark background), which was presented for 1500–2000 ms. A central cue (left: ⟨; right: ⟩; neutral: ⟨⟩; arrow symbols had a horizontal extension of 0.61° and a vertical extension of 0.98°) appeared for 2000–2500 ms. Time intervals were randomized within the given range in steps of approximately 100 ms. In the control condition, the fixation cross (+) remained unchanged. The target was presented peripherally (12.4°) for 2000 ms. A left/right cue was presented in 66.7% of the trials. Neutral cue and control condition were used in 16.7% of the trials each. A neutral cue (⟨⟩) indicated that the target could appear on the left or on the right with equal probability. Furthermore, we used a valid cue condition, which correctly predicted the later target location, and an invalid cue condition, which pointed to the opposite direction of the later target location. The difference in reaction times between invalid and valid cue condition is a convenient measure of attentional cueing. The cue was valid in 80% of the trials (20% invalid). Participants were instructed to respond to the stimulus with a saccadic eye movement to the stimulus or with a key-press in different blocks of 60 trials. Participants maintained fixation of the cue, until the stimulus occurred. Trials were run in blocks of 60 with rest periods as-needed. Blocks were alternating with saccadic and key-press responses to target stimuli. To exclude possible influences arising from manual motor preparation in blocks with key-press responses, participants were instructed to press the "space" button on a computer keyboard with the same finger in all conditions.

3.1.3. Eye movement recording

Experiments were presented on a 21-in. EYE-Q 650 Monitor (832×624 resolution; frame rate 75 Hz) controlled by an Apple Power Macintosh G3 computer. Eye movements were recorded using a video-based SMI

Eyelink System (SensoMotoric Instruments) with a sampling rate of 250 Hz and an eye position resolution of 20″. Eye movements were recorded by the same technique for all experiments reported here.

3.1.4. Data pre-processing

In all experiments reported here, correct fixation was checked with eye movement data. Trials with incorrect fixation, eye blinks or other errors in data acquisition were discarded. After pre-processing, we used 4773 trials (from 7200 or 66%) of Experiment 1 in our final data analysis for producing Fig. 5.

3.2. Results and discussion

3.2.1. Response latencies

An analysis of response latencies was used to validate that participants shifted attention in Experiment 1 as instructed while maintaining fixation on the central cue. Participants responded faster (both with a key-press or a saccade) to the target stimulus when the cue correctly predicted the target's location; they were also slower to respond to targets at unexpected locations (Fig. 4). Thus, as in the original paradigm (Posner, 1980), participants were able to shift their visual attention to the most likely location of the target stimulus.

3.2.2. Microsaccade rate

The effects of shifts of covert attention on microsaccades were investigated by comparing the time evolution of several statistical measures before and after presentation of the cue. First, we computed the rate of occurrences of microsaccades (number per second) averaged over all trials of 30 participants in Experiment 1 (Fig. 5) and obtained a mean rate of about one per second (computed within a moving window of 100 ms). This baseline rate is in good agreement with previous investigations (Ciuffreda & Tannen, 1995).

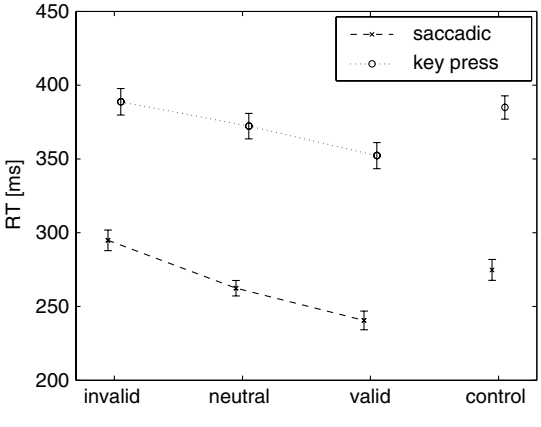

Fig. 4. Effects of covert shifts of visual attention on response latency, i.e. time from target onset in [ms], in Experiment 1. A valid cue correctly predicted the later target location, an invalid cue pointed to the direction opposite to the later target location, and a neutral cue indicated that the later target stimulus appeared with equal probability on the left or right target locations. There were benefits for valid and neutral cues and costs for invalid cues compared to the control condition, in which the fixation cross was unchanged. These results indicate successful attentional cueing in the experiment.

The presentation of the cue induced a decrease of the rate of microsaccades to about 20% of the baseline level about 150 ms after cue onset (Fig. 5). Following this decrease, the microsaccade rate increased to a maximum of about twice the baseline level at about 350 ms after presentation of the cue before returning to baseline level at about 500 ms after cue onset. The characteristic signature of modulation of the microsaccade rate occurred both for directional and neutral cues.

Next, we investigated interindividual differences in the modulation of microsaccades. While the quasi-continous time course of the microsaccades rate (Fig. 5a) cannot be computed for individual participants due to an insufficient number of microsaccades, we counted the number of microsaccades in three time windows: a pre-cue window for estimating the baseline rate r_0 $(-200 \leqslant t < 0)$, a window around the inhibition phase r_- $(50 \leqslant t < 250)$, and a window around the microsaccadic enhancement epoch r_+ $(250 \leqslant t < 400)$. Values for each participant are given in Table 1, where asterisks (★) in the last column indicate that 21 of 30 participants showed the pattern of rate modulation observed in Fig. 5a, i.e. $r_- < r_0 < r_+$. In a repeated measures analysis of variance (ANOVA) with time window (pre-cue, inhibition and enhancement epoch) as within-subject factor, differences between time windows were highly significant $(F(2,58) = 58.17,\ p < 0.001)$.

The modulation of the microsaccade rate reported here is similar to findings published recently for large (or "macroscopic") saccades (Reingold & Stampe, 2000, in press). Because of the initial decrease of saccade rate in response to a display change, the effect is called saccadic inhibition and is interpreted as a low-level phenomenon of the saccadic system to any change in visual input. Voluntary microsaccadic suppression had been reported for microsaccades in foveal high-acuity tasks previously (Bridgeman & Palca, 1980; Winterson & Collewijn, 1976). In addition to these results, we observed microsaccadic enhancement about 200 ms after saccadic inhibition.

3.2.3. Orientation of microsaccades

Experiments on attentional cueing (Deubel & Schneider, 1996; Kowler et al., 1995; Kustov & Robinson, 1996) unveiled a common mechanism underlying attention shifts and programming of saccades. These results and theoretical models of saccade generation (Findlay & Walker, 1999) suggest that the orientation of microsaccades might be influenced by shifts of visual attention. To study a possible interaction with the orientation of attention, we analyzed the angular distri-

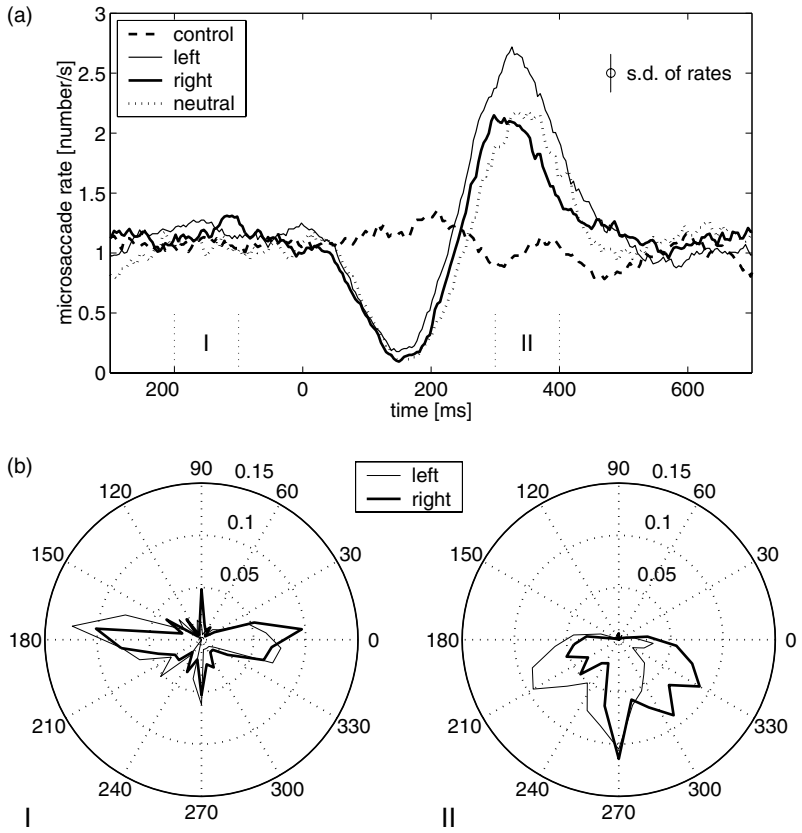

Fig. 5. Modulation of microsaccade statistics in Experiment 1. (a) The time evolution of the rate of microsaccades yielded a fast response to the stimulus, which led to a decrease of the microsaccade rate from one per second to 20% of this baseline level (150 ms after cue onset). A later response was an increase of the microsaccade rate to more than twice the baseline level about 350 ms after cue presentation (microsaccadic enhancement). The standard deviation computed from the pre-cue interval ($t < 0$) as a measure of stochasticity in rate fluctuations is shown in the upper right corner of the panel. The target onset was between 2000 and 2500 ms, i.e. much later than the time intervals chosen for our analysis of microsaccade statistics. Furthermore, it is important to note that valid and invalid cues were indistinguishable before target onset. Therefore, we did not perform separate analyses of microsaccade statistics for these cases. (b) Panel I: The directional distributions of microsaccades (probability densities computed from 30 bins) showed a horizontal preference in the selected pre-cue interval (I: $-200 < t < -100$ ms) without significant differences between the distributions corresponding to left and right cue conditions. Panel II: During microsaccadic enhancement (II: $300 < t < 400$ ms), we observed a mean orientation towards the cue direction with an additional downward component.

butions of microsaccades in several time windows of Experiment 1 (Fig. 5, panels I and II). All time windows were chosen by visual inspection. We computed the 2D distributions of all microsaccade vectors in two different time windows (width 100 ms) starting at $t = -200$ ms (I) and 300 ms (II) relative to cue onset for the left and right cue conditions. The first time window (I) shows the baseline directional distributions of microsaccades for left and right cues, indicating a preference for horizontal orientations (Engbert & Kliegl, 2003). In the second time window (II), we find a shift of the directional distributions of microsaccades to the direction of the cue with an additional downward component. [1] We performed a Kolmogorov–Smirnov (KS) test for the null hypothesis that the orientations of microsaccades for left and right cue conditions have the same continuous distribution at the 5% level of significance. For the pre-cue time window I we cannot reject the hypothesis, while in time window II the distributions are significantly different ($K(29) = 0.236$, $p < 0.001$).

As for microsaccade rates, we examined interindividual differences in microsaccade orientations. Our analysis was performed in the time window showing microsaccadic enhancement ($300 < t < 400$ ms). In each cue condition, we observed a number N_R of microsaccades to the right, i.e. orientation angle $-\pi/2 < \phi < \pi/2$, and N_L microsaccades to the left, i.e. orientation angle $\phi < -\pi/2$ or $\pi/2 < \phi$. [2] Using the numbers $N_{L,R}$ we compute the fraction of microsaccades to the right,

[1] We have tested the hypothesis that the downward component is related to the key-press responses but we found no correlation of the strength of the downward shift of the distribution with responses type. However, the downward shift might be related to the greater vertical orientation of the arrow stimuli (0.98°) compared to the fixation cross (0.73°); see Section 3, Section 3.1.2.

[2] The numbers $N_{L,R}$ were normalised with respect to the total number of microsaccades pointing to the left or to the right.

Table 1
Interindividual differences in microsaccade rate modulation

Participant	Pre-cue r_0 $(-200 \leqslant t < 0)$	Inhibition r_- $(50 \leqslant t < 250)$	Enhancement r_+ $(250 \leqslant t < 450)$	Ranking[a]
1	0.15	0.15	0.28	
2	1.30	1.30	2.82	
3	2.45	1.16	2.18	
4	1.53	0.40	4.27	★
5	1.27	0.34	2.03	★
6	0.50	0.42	2.42	★
7	1.55	2.12	1.77	
8	0.69	0.29	1.57	★
9	1.74	0.29	2.50	★
10	0.86	0.22	0.86	
11	0.67	0.21	1.98	★
12	2.33	0.40	1.79	
13	1.78	0.22	3.19	★
14	1.04	0.24	1.22	★
15	1.72	0.16	1.72	
16	1.21	1.70	3.30	
17	1.10	0.27	1.88	★
18	0.18	0.05	0.54	★
19	2.31	0.38	3.46	★
20	1.47	0.53	2.68	★
21	1.12	0.56	3.12	★
22	0.89	0.56	2.40	★
23	0.96	0.22	3.01	★
24	0.37	0.13	0.66	★
25	1.38	0.69	3.97	★
26	0.79	0.13	1.71	★
27	1.47	0.32	2.39	★
28	2.54	1.07	2.57	★
29	2.43	0.79	4.00	★
30	0.24	0.32	0.38	
Mean	1.27	0.52	2.22	
SD	0.69	0.49	1.07	

[a] An asterisk (★) indicates that the rate modulation of the participant follows the pattern observed in Fig. 5, i.e. $r_0 > r_- > r_+$.

$f_{\mathrm{l,r}} = N_{\mathrm{R}}/(N_{\mathrm{L}} + N_{\mathrm{R}})$, where the index l, r denotes the cue conditions. From the pattern of the orientation distributions in Fig. 5b (panel II), we expected $f_{\mathrm{l}} < 0.5$ and $f_{\mathrm{r}} > 0.5$. Values for each participant are given in Table 2, where asterisks (★) in the last column indicate that 19 of 29 participants showed the pattern consistent with Fig. 5b, i.e. $f_{\mathrm{l}} < 0.5$ and $f_{\mathrm{r}} > 0.5$. In a repeated measures ANOVA with cue direction (left and right) as within-subject factor, differences were highly significant ($F(1,28) = 16.18,\ p < 0.001$). In summary, in Experiment 1 we demonstrated an effect of covert shifts of attention on the orientation of microsaccades.

4. Experiment 2: spatial cuing by color cues

In Experiment 1, the modulation of microsaccade rate might have been triggered by the change in visual form from a fixation cross to arrow cues with an inherent directionality. Therefore, in Experiment 2, attention shifts were cued by changing the color of the fixation cross to red or green. Thus, the display change was limited to a change in color only, compared to a form change in Experiment 1.

4.1. Methods

4.1.1. Participants

Thirty participants performed 240 trials each. Again, all participants were undergraduate students of the University of Potsdam and had normal or corrected-to-normal vision.

4.1.2. Stimuli and procedure

For general procedures see Experiment 1 (Section 3.1.2). In Experiment 2, participants were cued to shift attention by a color change of the fixation cross to green (cue to the left) or red (cue to the right) without neutral and control conditions.

4.1.3. Data pre-processing

With the same criteria as used for Experiment 1, 3515 trials (from 7200 or 49%) were selected for further data analysis. These trials were used to produce Fig. 6.

Table 2
Interindividual differences in microsaccade orientation

Participant[a]	Cue left, f_l	Cue right, f_r	Pattern[b]
1	0.33	1.00	★
2	0.40	0.43	
3	0.36	0.62	★
4	0.51	0.57	
5	0.37	0.83	★
6	0.24	0.72	★
7	0.00	0.74	★
8	0.58	0.41	
9	0.50	0.61	★
10	0.00	0.54	★
11	0.00	0.81	★
12	0.27	0.75	★
13	0.42	0.51	★
14	0.69	0.39	
15	0.00	0.80	★
16	0.27	0.74	★
17	0.00	0.95	★
18	0.56	0.30	
19	0.53	0.70	
20	0.43	0.58	★
21	0.25	0.78	★
22	0.37	0.62	★
23	0.30	0.76	★
25	0.56	0.47	
26	1.00	0.73	
27	0.41	0.70	★
28	0.59	0.42	
29	0.41	0.52	★
30	1.00	1.00	
Mean	0.39	0.65	
SD	0.26	0.18	

[a] Participant 24 was excluded in this analysis due to absence of microsaccades in the time window.

[b] We computed the fraction of microsaccades to the right in relation to all microsaccades, $f_{l,r} = N_R/(N_R + N_L)$, where the index l, r indicates the cue direction. The numbers $N_{L,R}$ were normalised to the total number of microsaccades to left and right directions. An asterisk (★) indicates that the preferred orientation to the left ($f_l < 0.5$) was observed for the cue to the left and a preferred orientation to the right ($f_r > 0.5$) was found for the cue to the right.

4.2. Results and discussion

4.2.1. Response latencies

Response latencies were comparable to Experiment 1, however color mapping of orientation cues slowed response times by 10–20 ms.

4.2.2. Microsaccade rate

The temporal modulation of the microsaccade rate was qualitatively similar to Experiment 1, but the microsaccadic enhancement was considerably weaker, i.e. the maximum rate was less than twice the baseline level (Fig. 6). Thus, as already reflected in response latencies (Section 4.2.1), color cues were indeed weaker than arrow cues but the modulation of microsaccade rate was still observed.

4.2.3. Orientation of microsaccades

An analysis of the orientation of microsaccades also supports our interpretation that color cues are weaker than arrow cues. We find only slight distortions of the angular distribution (Fig. 6, panel II) with a lack of the downward shift observed in Experiment 1 (Fig. 5, panel II). However, the KS statistic again indicated that the distributions differ significantly in time window II ($p = 0.036$). Note that we had to increase the lengths of the time windows as well as slightly shift time window II (I: −250 to 0 ms; II: 350–600 ms) to accommodate the weaker color cues.

In Experiment 1 (arrow cues) mean reaction times were 10–20 ms faster than in Experiment 2 (color cues). Furthermore, effects in the orientations of microsaccades were stronger in Experiment 1. Therefore, the smaller and later effect associated with the orientation of microsaccades in Experiment 2 is compatible with longer response latencies and a weaker modulation of microsaccade rate. Taken together, the results suggest an interaction of microsaccadic enhancement with shifts of attention.

5. Experiment 3: simple fixation task

In Experiment 3, we determined the effect of display change on microsaccade rate in the absence of attention shifts. In Experiment 1, the neutral cue (i.e., a double arrow) had a similar effect as the directional cues (see Fig. 5) suggesting that any display change suffices to trigger the modulation. However, the neutral cue effect could have resulted from participants' mental setting, that is they were always preparing for attention shifts in Experiment 1. Therefore, we carried out a control experiment (Experiment 3) with the same cues as in Experiments 1 and 2 but asked participants to respond to the offset of the cue. Thus, we converted the task to a simple reaction time study without attention shifts.

5.1. Methods

5.1.1. Participants

Twenty participants performed 240 trials each. All participants (undergraduate students of the University of Potsdam) had normal or corrected-to-normal vision.

5.1.2. Stimuli and procedure

For general procedures see Experiment 1 (Section 3.1.2). The fixation cross was presented for 1500–2000 ms as in Experiment 1. Then, the fixation cross was replaced by one of the stimuli used in Experiments 1 and 2 (⟨; ⟩; ⟨⟩; green cross; red cross). Participants were

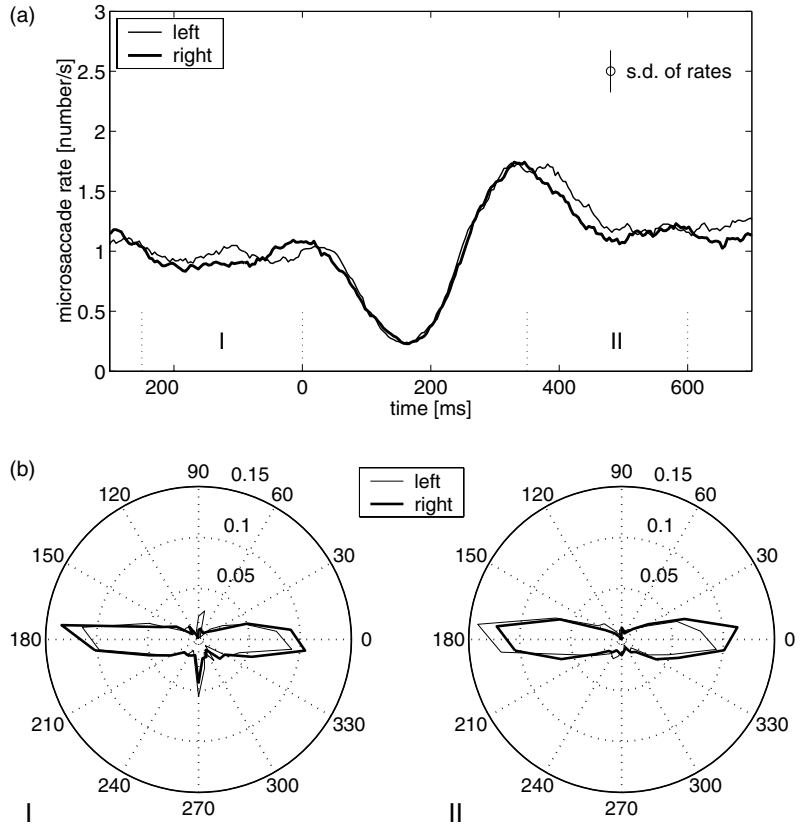

Fig. 6. Modulation of microsaccade statistics in Experiment 2. The characteristic time course of modulation of the microsaccade rate found in Experiment 1 was reproduced in Experiment 2 with color cues, however, the microsaccadic enhancement was weaker compared to Experiment 1. Panel I: The directional distributions of microsaccades showed a horizontal preference in the selected pre-cue interval (I: $-250 < t < 0$ ms) without significant differences between left and right cue conditions. Panel II: During the microsaccadic enhancement (II: $350 < t < 600$ ms), we observed a mean orientation towards the cue direction, which was significant at the 5% level (see text for the details). The additional downward shifts of the distributions found in Experiment 1 were absent here.

instructed to ignore this display change. After a time interval of 2000–2500 ms, the stimulus disappeared. Participants were asked to respond with a key-press as fast as possible.

5.1.3. Data pre-processing

Using the same criteria as used for Experiment 1, 4040 trials (from 4800 or 84%) were selected for final data analysis.

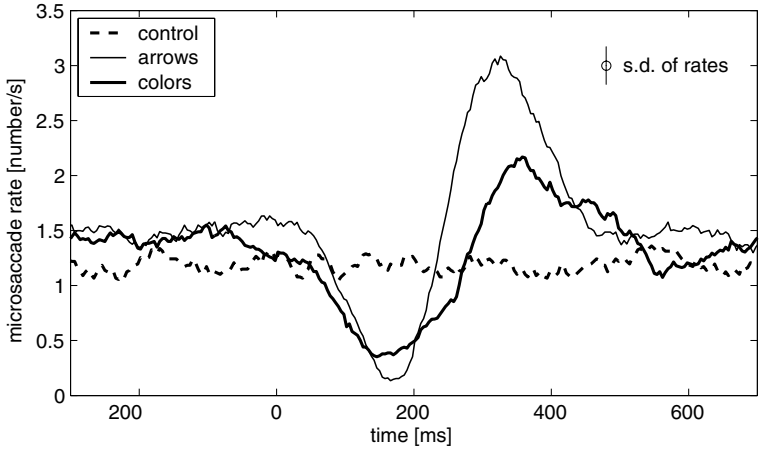

Fig. 7. Modulation of microsaccade statistics in Experiment 3. The modulation of the microsaccade rate found in Experiments 1 and 2 was reproduced in Experiment 3 with a simple fixation task, i.e. without shifts of visual attention. The microsaccadic enhancement was weaker for color symbols than for arrow symbols.

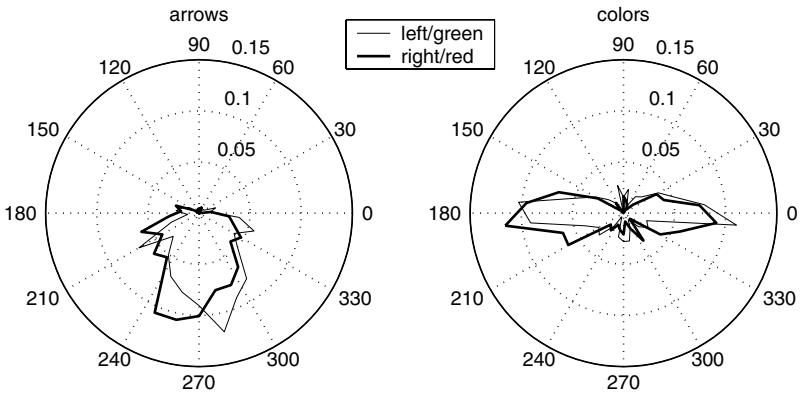

Fig. 8. Orientations of microsaccades in Experiment 3. The different stimuli, which were used as arrow or color cues in Experiment 1, did not induce significant effects in the angular distributions of microsaccades. The time windows for the analysis of the distribution were the same as in Fig. 5 (arrows, II: $200 < t < 300$ ms) and Fig. 6 (colors, II: $350 < t < 600$ ms).

5.2. Results and discussion

5.2.1. Microsaccade rate

In the simple fixation task, we still observed the characteristic modulation of the microsaccade rate (Fig. 7). Again, color symbols induced a weaker response. We conclude that the characteristic modulation of microsaccade rate was triggered by a display change in the absense of attention shifts.

5.2.2. Microsaccade orientation

The angular distributions of microsaccades showed only small differences in time window II for the arrow cues. The symbol $\langle$, which was used as a cue to the left in Experiment 1, induced a small bias in the orientation of microsaccades to the right (and vice versa with the symbol $\rangle$). This result indicates that the arrow symbols alone does not produce the modulations of microsaccade orientations observed in Experiment 1. In both cases (arrow and color symbols) the distributions were not significantly different between different arrows or colors at the 5% level using the KS statistic (Fig. 8). We conclude that in Experiments 1 and 2 the orientation of microsaccades was modulated by shifts of visual attention.

6. General discussion

Temporal rates of microsaccades responded to shifts of visual attention with a decrease (showing a minimum around 150 ms) and a subsequent increase (maximum around 350 ms) with a simultaneous shift in the directional distributions towards the cue direction. In conditions with color cues the microsaccadic enhancement was temporally decoupled from the directional shifts. Thus, microsaccades were clearly modulated by visual attention.

Recently, microsaccades were shown to be correlated with bursts of firing of single cells in primary visual cortex (V1) of macaque monkeys (Martinez-Conde et al., 2000). While this important finding may contribute to an understanding of the functional significance of microsaccades, generation of microsaccades may still be looked upon as a primarily noise-producing low-level oculomotor phenomenon. Since we find a modulation of microsaccades by visual attention, our results challenge the interpretation of microsaccades as strictly low-level oculomotor phenomena. While microsaccades are—like drift and tremor—most probably generated to provide stochastic displacements of retinal images, shifts of visual attention can produce a bias in this inherent randomness by inducing correlations of successive displacements.

The typical fixational control procedure employed in spatial cueing paradigms allows for a dissociation of the locus of attention and eye fixation but, given our results, it may not eliminate oculomotor activity associated with the preparation of microsaccades and presumably also the preparation of saccades in the cued direction. Consequently, the common activation of brain areas in overt and covert shifts of attention (e.g., Corbetta, 1998; Nobre, Gitelman, Dias, & Mesulam, 2000) which is sometimes interpreted as evidence for common mechanisms of pure attention shifts and saccade generation might still be "contaminated" by oculomotor activity common to overt and covert shifts of visual attention (e.g., in Experiment 1 we found microsaccades with a mean amplitude below 1° of visual angle, $M = 32'$ and $SD = 18'$). Thus, "fixational control" is somewhat of a misnomer; in a conservative procedure one might want to eliminate trials with microsaccades. Nevertheless, our results can also be interpreted as further evidence for the close link between visual spatial attention and the programming of eye movements (Corbetta, 1998; Rizzolatti & Craighero, 1998).

In a recent study, Tse, Sheinberg, and Logothetis (2002) reported that fixational eye movements, and in particular microsaccades, are not affected by abrupt onsets that capture attention. These results are not necessarily in contradiction to the present ones. There are at least three differences between the experimental paradigms that can be expected to differentially affect microsaccade rate. First, our cue-target interval was four times longer than the intervals in that study. Given the low base rate of only one or two microsaccades per second, a long interval is necessary for a statistical analysis of fluctuations in the rate of microsaccades. Second, Tse et al. (2002) used a very small three-pixel fixation spot. Thus, their paradigm resembled a high-acuity observation task for which microsaccadic inhibition was reported by Bridgeman and Palca (1980) and Winterson and Collewijn (1976). Third, a trial in the Tse et al. experiment involved five display changes. From our results, we would expect that these frequent display changes should strongly reduce the number of microsaccades. In general, our experiments apparently maximized whereas the Tse et al. paradigm minimized the occurrence of microsaccades.

Our observation of microsaccadic enhancement is a new finding expanding on the previously reported microsaccadic inhibition (Bridgeman & Palca, 1980; Winterson & Collewijn, 1976). Microsaccadic inhibition was studied in foveal vision. In our experiments, however, targets were presented in the periphery. Therefore, the increase in the rate of microsaccades observed around 350 ms after cue onset may be relevant in the case of parafoveal information processing. One possible interpretation is that, compared to foveal vision, a higher rate of microsaccades enhances parafoveal information processing. This interpretation is supported by preliminary results obtained from a crossmodal cueing experiment, with auditory and visual cues and targets (Rolfs, Engbert, & Kliegl, in preparation). There, we reproduced the characteristic modulation of the microsaccade rate, even in the condition with auditory cues and auditory targets, i.e. in the absence of any visual display change. In perspective microsaccade rate and mean orientation may prove useful for the study of the dynamics of attention allocation in complex tasks such as reading (Engbert & Kliegl, 2001; Engbert, Longtin, & Kliegl, 2002; Reichle, Pollatsek, Fisher, & Rayner, 1998).

In our experiments, trials without eye movements were run as part of an experimental session with eye movement blocks interleaved. From a methodological point of view, the interleaved saccade blocks could have increased the probability (or biased the direction) of microsaccades in the non-saccade blocks due to learning or habits. Effects of context and prior trials on saccades have been noted before (Kapoula & Robinson, 1986; Kowler, Martins, & Pavel, 1984). To investigate this issue, we analyzed data of first-block trials for those participants who started with key-press responses. In these trial, an impact from saccadic responses can be ruled out. The effect of microsaccadic inhibition and enhancement was still present, while an analysis of the orientation effect could not be performed due to insufficient statistical power. Therefore, we ran a control experiment [3] with key-press responses only. We reproduced the orientation effect in the directional distributions ($K(29) = 0.063$, $p < 0.01$). We conclude that the effects we report here are also present in a task without saccades.

In summary, we propose a new algorithm for the detection of microsaccades. We observed characteristic modulations of the statistics of microsaccades. Most importantly, our results suggest that microsaccades can be exploited to map the orientation of covert visual attention by analyzing their directional distributions—as a new measure to study the dynamics of allocation of visual attention.

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[3] Using arrow cues to the left and to the right like in Experiment 1, 12 naive participants were tested in 180 trials each.

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