Rare but precious: Microsaccades are highly informative about attentional allocation

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ABSTRACT

To clarify the relation between attention and microsaccades, we monitored microsaccades while observers performed tasks with different attentional demand. In four high-demand conditions, observers shifted attention covertly to a peripheral location, or focused attention at fixation. Three corresponding low-demand conditions on physically identical displays provided a basis for comparison. Our results revealed two distinct effects of attentional load: higher loads were associated consistently with lower microsaccade rates, but also with increased directional selectivity (up to 98% congruent). In short, when microsaccades were most rare, the direction of microsaccades proved most informative about the location of the attention focus. The detailed time-courses of the two effects differed, however, suggesting that they may reflect independent processes.

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1. Introduction

When our eyes fixate a visual target, they nevertheless perform a continual series of small and non-voluntary movements. These "fixational eye movements" have been categorized into tremor, drift and microsaccades (see (Martinez-Conde, Macknik, Troncoso, & Hubel, 2009) for a review). Microsaccades are fast, jerky displacements, with amplitude of typically less than 1°. Although long dismissed as serving little purpose (Kowler & Steinman, 1980), microsaccades are now thought to be highly relevant for vision and to fulfill several functions, such as counteracting visual fading, correcting eye position, and generating synchronous visual transients (Martinez-Conde et al., 2009; Rolfs, 2009).

One intriguing line of research suggests that microsaccades are affected by covert attention, and possibly by other high-level cognitive processes, when overt eye movements are suppressed. For example, microsaccade rate is reduced by the onset of a visual cue or stimulus (Engbert & Kliegl, 2003a, 2003b; Hafed & Clark, 2002), by the appearance of a visual or auditory oddball stimulus within a sequence of standard stimuli (Rolfs, Kliegl, & Engbert, 2008; Valsecchi, Betta, & Turatto, 2007; Valsecchi & Turatto, 2009), as well as during the preparation of a motor response (Betta & Turatto, 2006). Covert shifts of visual attention have been reported to affect the direction of microsaccades in a complex way, with microsaccades being initially directed towards the focus of attention (Engbert & Kliegl, 2003a, 2003b; Hafed & Clark, 2002) and subsequently being deflected away from the focus of attention

(Betta, Galfano, & Turatto, 2007; Galfano, Betta, & Turatto, 2004; Laubrock, Engbert, & Kliegl, 2005). In addition, there is a negative report that attention-demanding visual performance exerts no influence on automatic eye movements (Tse, Sheinberg, & Logothetis, 2002). This mixed set of findings raises the question as to how reliably attention and microsaccades are associated, and therefore, whether microsaccades provide useful information about the allocation of covert attention (Horowitz, Fencsik, Fine, Yurgenson, & Wolfe, 2007; Horowitz, Fine, Sergey, & Wolfe, 2007; Laubrock, Engbert, Rolfs, & Kliegl, 2007).

To clarify the relationship between microsaccades and covert attention, it would be helpful to have precise information about when and where attention is deployed. It is often taken for granted that observers focus attention on a target prior to reporting about this target. However, a voluntary report about a target does not guarantee that attention has been focused fully on this target. Indeed, the minimal allocation of attention that is necessary for a voluntary report differs greatly between different task situations (Braun, 1994; Braun & Julesz, 1998; Festman & Braun, in press; Houtkamp & Braun 2009; Li, VanRullen, Koch, & Perona, 2002; Morrone, Denti, & Spinelli, 2002; Reddy, Reddy, & Koch, 2006; Reddy, Wilken, & Koch, 2004). Fortunately, the attentional demand posed by a particular task situation can be quantified with the help of dual-task experiments, which force observers to divide attention between tasks and result in disproportionate performance losses on more demanding tasks (Lee, Koch, & Braun, 1999a, 1999b; Pastukhov, Fischer, & Braun, 2009). For example, a consistent finding by several groups is that the discrimination of rotated letter-shapes demands full attention while the discrimination of color or hue demands little or no attention (Braun & Julesz, 1998; Lee

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et al., 1999a, 1999b; Festman & Braun, in press; Houtkamp & Braun, 2009; Li et al., 2002; Pastukhov et al., 2009).

Taking advantage of the disparate attentional demands of different tasks, the present study investigated how such demands affect microsaccades. In three experiments, observers reported either the letter shape (high demand) or the color (low demand) of target stimuli that were physically identical. In Experiments 1 and 2, an array of target and distracter stimuli appeared in the visual periphery. Thus, when performing the more attention-demanding task (discriminating letter shape), observers were obliged to shift attention away from fixation and to focus it on a peripheral location. In Experiment 3, targets and distracters were presented serially at fixation, obviating the need to shift attention away from fixation. Instead, when performing the demanding task, observers had to focus attention at fixation.

The results showed that more attention-demanding tasks suppressed microsaccades more effectively than less attention-demanding tasks. Analyzing the timing of microsaccades relative to target appearance, we found that microsaccades were least frequent (most suppressed) when attention-demand peaked. In the situation in which attention had to be shifted away from fixation, the direction of microsaccades proved highly informative about target location. In some instances, 98% of microsaccades pointed towards the target hemifield. Taken together, our results show that attentional load reduces the number of microsaccades, but that the few microsaccades that remain are highly informative about attentional allocation. However, the effects on microsaccade rate and directionality exhibited distinct time-courses and therefore would seem to reflect independent processes.

2. General methods

2.1. Participants

Five observers (three female, two male) participated in all experiment reported here. Procedures were approved by the medical ethics board of the Otto-von-Guericke Universität, Magdeburg and informed consent was obtained from all observers. All observers had normal or corrected-to-normal vision. Observers were naïve as to the purpose of the experiment and were paid for participation.

2.2. Apparatus

Stimuli were generated online on a computer and displayed on a 21 in.CRT screen (Viewsonic P227fB, www.viewsonic.com), with a spatial resolution of 1024×768 pixels and a refresh rate of 150 Hz. The viewing distance was 70 cm, so that each pixel subtended approximately 0.02°. Background luminance was 32 cd/m². Eye movements were recorded binocularly with an Eyelink 2000 eye tracker (sr-research.com) with a sampling rate of 1000 Hz.

2.3. Statistical methods

As the most distributions were not normally distributed, significant differences reported were tested using Wilcoxon rank sum.

When applicable – microsaccade direction congruency and observers' performance – error bars represent a 95% confidence interval around mean based on a binomial distribution. In other cases – microsaccade rate and reaction times – error bars represent a standard error.

2.4. Microsaccades analysis

Microsaccades were parsed offline automatically, using an algorithm proposed by Engbert and Kliegl (2003a, 2003b), which was modified to accommodate for a higher sampling rate. Extracted microsaccades showed a strong correlation between their peak velocity and amplitude: dependence for microsaccades for Exp. 1 is shown in Fig. 1b, correlation coefficient $R = 0.903$ ($p < 0.001$).

3. Experiment 1: spatial cueing of peripheral target

The purpose of this experiment was to confirm the results of earlier studies (Engbert & Kliegl, 2003a, 2003b; Hafed & Clark, 2002; Horowitz, Fine, et al., 2007) and to extend these results by comparing task situations that place disparate demands on attention. The display and trial sequence is illustrated in Fig. 1a. Each trial began with a valid symbolic cue (one arm of the x-cross at fixation was highlighted briefly) that foretold the target location (500 ms). Following a delay period (1000 ms), the target appeared briefly in an array with three distracters (90 ms). After short delay
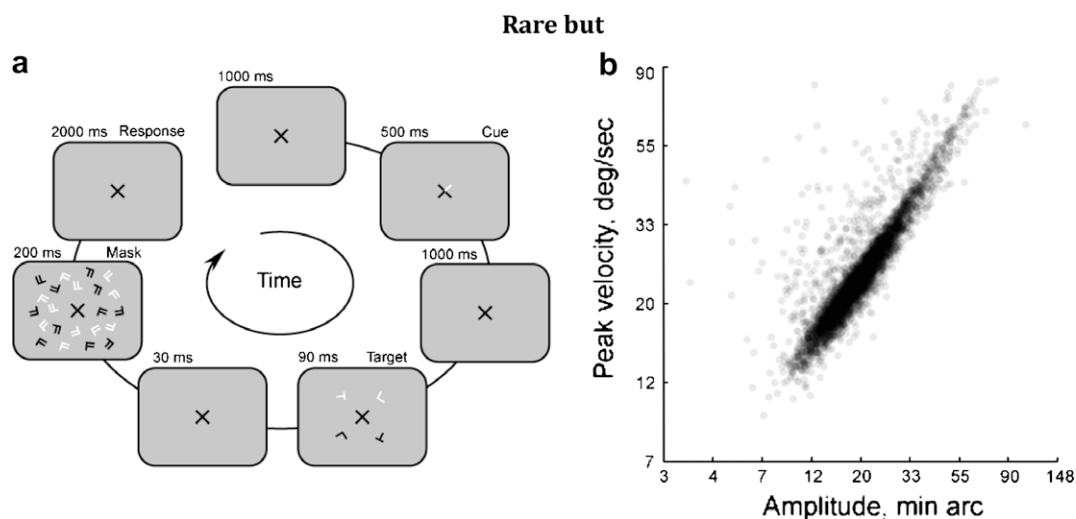
Rare but

Fig. 1. (a) Trial sequence with cue, target, mask, and response interval (Exp. 1). The cue (bright arm of fixation cross) was always valid. Observers reported either the letter shape (high-load) or the color (low-load) of the cued target. The mask limited visual persistence and created an acute attentional demand. (b) Maximum velocities of microsaccades as a function of their amplitude.

(30 ms), visual persistence was curtailed by a mask array (200 ms). Observers reported either the letter shape (rotated *T* or *L*) or the color (*red* or *green*) of the target. Shape discrimination is known to place a high, and color discrimination a low demand on attention (Lee et al., 1999a, 1999b; Li et al., 2002; Pastukhov et al., 2009).

3.1. Methods

3.1.1. Stimuli and procedure

Each trial consisted of a fixation interval (2.5 s) with cue presented during the middle 500 ms. Fixation (arm length 1°) was followed by a brief presentation of targets (90 ms), blank interval (30 ms), mask (200 ms) and response interval 2000, see also Fig. 1a. During the cue interval one of the crosses half-arm was presented in white, to indicate the quadrant of the target appearance. Targets were four randomly rotated letters (T or L, height 5.5°) presented at four quadrants (eccentricity 9.5°). Observers had to report either letter identity ("L" or "T", letter condition, pressing "F" or "J", respectively) or color of the target (red or green, color condition, pressing "F" or "J", respectively). In order to balance the presentation, during the *letter* condition two letters were "Ls" and other two letters were "Ts", while in *color* condition two targets were red and two targets were green. All possible combinations were presented four times, so that each letter was a target in turn. Total number of trials per block: 24. Color (during *letter* condition) and identity (during *color* condition) were randomized.

3.1.2. Data pre-processing

Eye movement data was checked for incorrect fixation, blinks and other errors. After pre-processing 8.1% were discarded: bad fixations – 1.4%, blinks – 6.4%, no response – 0.3%.

3.2. Results

In agreement with previous reports, the MR was reduced by both cue onset and target onset, but rebounded after both events (Figs. 2 and 3, top row). The rebound after the cue was modest (∼30% above average; white arrows in Figs. 2 and 3, top row) and was soon overwhelmed by a renewed suppression that continued until approximately 100 ms after the target onset (black arrows in Figs. 2 and 3, top row). The rebound after the target was larger (∼100% above average) and reached its peak approximately 1000 ms after target onset (Figs. 2 and 3, top row). Overall, the average MR remained slightly but significantly higher during the less attention-demanding task (0.47 ± 0.03 Hz for the color and 0.41 ± 0.025 Hz for the shape condition).

To examine the correlation between target location and microsaccade direction, we computed a mean 'congruency coefficient' for sliding time bins of 200 ms duration, starting every 2 ms. This coefficient was set to unity if (i) a microsaccade occurred during a time bin and (ii) the microsaccade direction pointed into the visual hemifield of the target (either upper-lower or left–right). Otherwise, the coefficient was set to zero. Accordingly, a congruency coefficient close to 1 implied that most microsaccades were directed towards the target hemifield and a value close to 0 implied that most microsaccades were directed towards the other hemifield.

Microsaccades' direction tended to point into the target hemifield immediately after the cue presentation and during the last 500 ms before the target onset (see Figs. 2 and 3, second row). Interestingly, the congruency between microsaccades and target location depended strongly on the task. For the color condition, microsaccades were only weakly predictive about target location in the left or right hemifield (62% congruency reached at −300 ms, p = 0.003; arrow in Fig. 2, second row) and unpredictive

about location in the upper or lower hemifield. For the shape condition, on the other hand, we observed significantly higher congruency values. The predictiveness of microsaccades about left vs. right target positions reached 66% and was significant from 450 ms to 350 ms before target onset (p < 0.05). The predictiveness about upper vs. lower target positions reached 75% and remained significant from 450 ms before up to target onset. This difference could not have been due to either differences in task difficulty – as both tasks were performed comparably well with 96.5 ± 2% for the color and 95.8 ± 1.1% for the shape task – or to differences in response preparation, as identical response buttons were used.

Previous studies examined the direction of microsaccades in the period following cue onset, in which microsaccades abound (Engbert & Kliegl, 2003a, 2003b). Our results suggest that this approach was less than optimal: while we find some predictiveness during the rebound following cue presentation, the most informative microsaccades consistently coincided with the most profound suppression (black arrows in Figs. 2 and 3). In other words, microsaccades were most informative just about when they were particularly rare.

The amplitude of microsaccades remained stable throughout the trial, with no significant increase following either cue or target presentation (Figs. 2 and 3, fourth row). A small increase in amplitude coincided with periods of negative congruency, suggesting that it reflected corrective eye movements back to the fixation mark.

We also investigated the influence of microsaccades on reaction times (RTs). To this end, we assigned trials to time bins based on the timing of microsaccades: all trials with a microsaccade during a given bin were assigned to this bin. In this way, we could compute the mean RT for all trials with a microsaccade in a particular bin (see Figs. 2 and 3, bottom row).

This analysis showed that microsaccades at or around the time of target onset tended to delay reaction times: 96 ± 38 ms slower than average for the color condition ($-200 \leqslant t < 200$, p = 0.007) and 124 ± 82 ms slower than average for the shape condition (p = 0.008). Conversely, microsaccades in the period from 200 ms to 700 ms after target onset did accelerate reaction times. The reduction was 26 ± 10 ms ($200 \leqslant t < 700$ ms, p = 0.002) for the color condition and 47 ± 8 ms ($200 \leqslant t < 700$ ms, p = 0.0006) for the shape condition.

4. Experiment 2: color cueing of peripheral target

The previous experiment confirmed earlier reports (Engbert & Kliegl, 2003a, 2003b; Hafed & Clark, 2002; Horowitz, Fine, et al., 2007) that microsaccades tend to point towards a task-relevant target. However, the magnitude of this effect was fairly small, as noted by others (Horowitz, Fencsik, et al., 2007). It seemed possible that the relative weakness of the effect might have been due to the long pre-target interval of 1500 ms. Even if microsaccades associated with an attention shift were to faithfully indicate the direction of such a shift, this could have occurred at any time during the pre-target interval, so that "shift-related" microsaccades would have statistically overlapped in time with other, unrelated microsaccades. To investigate this possibility, we modified the experiment in such a way as to force observers to shift attention within a brief window of time.

To this end, observers always reported the letter shape (T/L) of a target item, which again appeared in an array together with three distracter items. Target identity was defined by the color of the fixation cross, rather than by a spatial cue. Accordingly, as soon as the cue appeared, observers could anticipate the color of the target item, but not its location. The display and trial sequence is shown
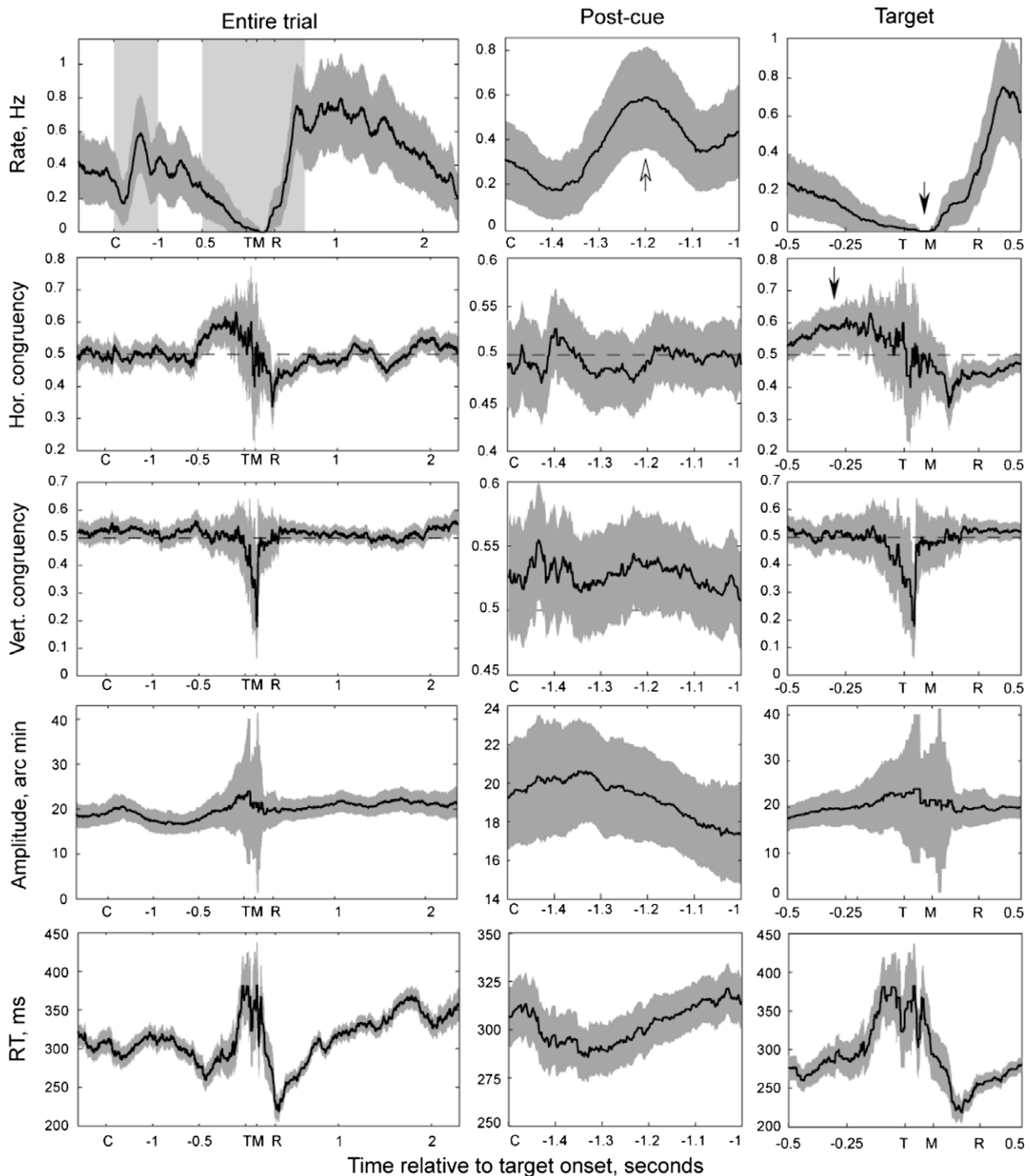
Fig. 2. Rate, congruency, amplitude, and effect on reaction time of microsaccades for the low-load (color) condition of Exp. 1. Each graph depicts a time course, either over the entire trial (left column), after cue onset (middle column), or around target onset (right column). The top row shows instantaneous microsaccade rate (mean ± standard error in Hz). The second and third rows show congruency between microsaccade direction and target location (2nd row: left vs. right hemifields; 3rd row: top vs. bottom hemifields; mean ± 95% confidence interval). The fourth row shows microsaccade amplitude (mean ± standard error in arc min). The bottom row shows reaction times for all trials with at least one microsaccade in each time bin (mean ± standard error in ms).Time axis legend: C – cue onset, T – target onset, M – mask onset, R – start of the response interval.

in Fig. 4. After the cue that foretold target color (2000 ms), target and distracters appeared briefly (90 ms) and, after a short delay (30 ms), were followed a mask array (200 ms). Thus observers had available a target-mask SOA of 120 ms for locating the target, shifting attention there, and encoding the letter shape. As expected, the forced delay in any attention shift lowered performance significantly: with this color cueing procedure, observers performed at 81.5 ± 1.1%, compared to the spatial cueing used in Experiment 1 (95.8 ± 1.1%).

4.1. Methods

4.1.1. Stimuli and procedure

Each trial consisted of a fixation period (2 s), followed by a brief targets presentation (90 ms), blank (30 ms), mask (200 ms) and response interval (2000 ms). Targets (height 5.5°) were four randomly rotated letters (T or L) presented at four quadrants (eccentricity 9.5°), each letter uniquely colored (red, green, blue or white), for schematic procedure see Fig. 4. Color
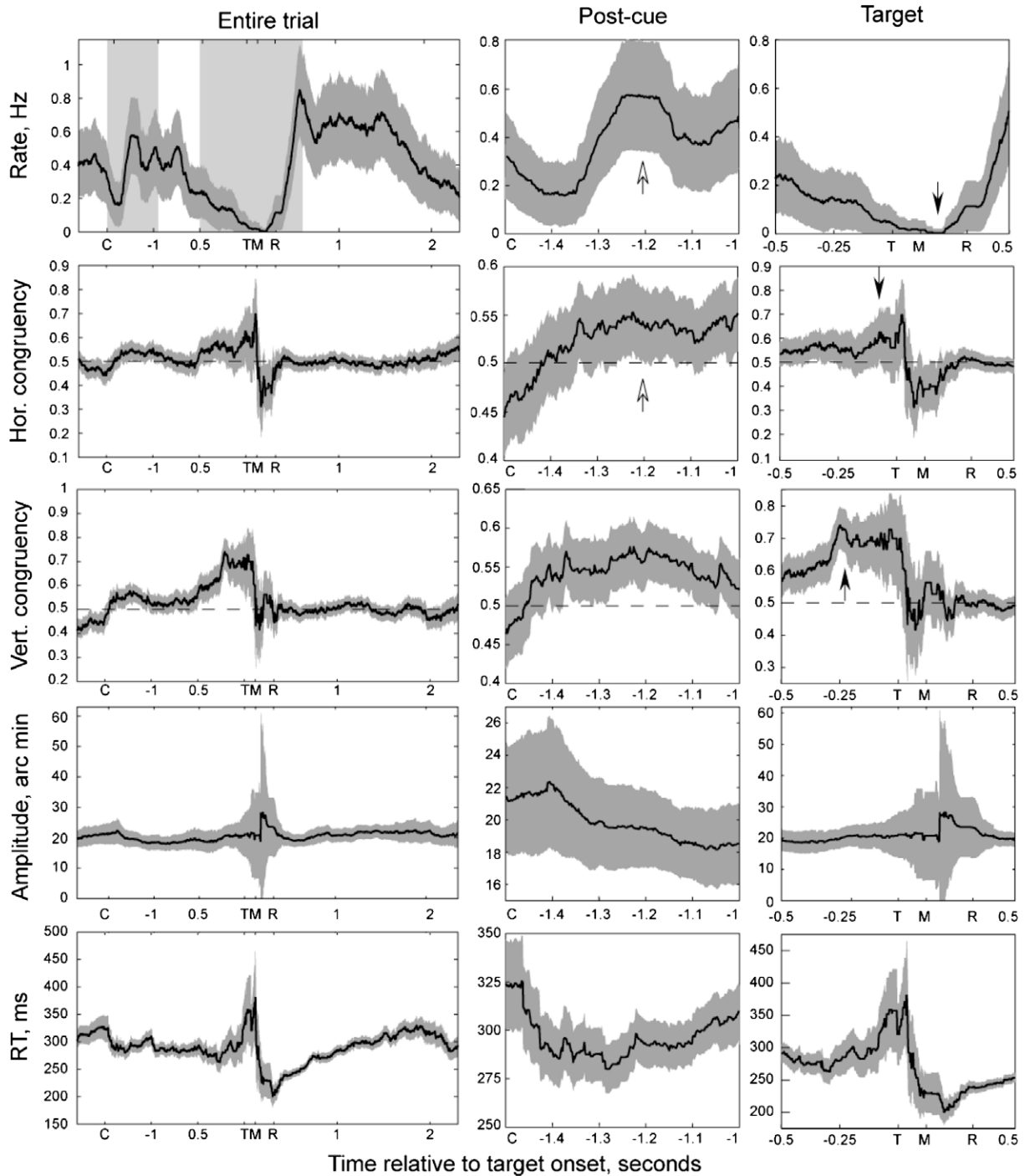
Fig. 3. Rate, congruency, amplitude, and effect on reaction time of microsaccades for the high-load (letter shape) condition of Exp. 1. Each graph depicts a time course, either over the entire trial (left column), or after cue onset (middle column), or around target onset (right column). The top row shows instantaneous microsaccade rate (mean ± standard error in Hz). The second and third rows show congruency between microsaccade direction and target location (2nd row: left vs. right hemifields; 3rd row: top vs. bottom hemifields; mean ± 95% confidence interval). The fourth row shows microsaccade amplitude (mean ± standard error in arc min). The bottom row shows reaction times for all trials with at least one microsaccade in each time bin (mean ± standard error in ms). Time axis legend: C – cue onset, T – target onset, M – mask onset, R – start of the response interval.

of the fixation (arm length 1°), which remained constant throughout the entire trial, identified which letter was the target. Observer's task was to report whether the target letter was 'L' or 'T' by means of key presses (keys "F" and "J", respectively). If observer failed to responds within 2 s interval, the trial was discarded (0.3% of the trials). Mask consisted of four randomly rotated letters 'F' presented at the same location and in

the same colors as targets. Conditions were balanced to ensure that each ordered combination of colors were presented 4 times in each block and each letter was designated to be a target in turn. Total number of trials was 64. Trials order was randomized, so that prior to the onset of targets cue color was completely non-informative about the quadrant where the target will appear.
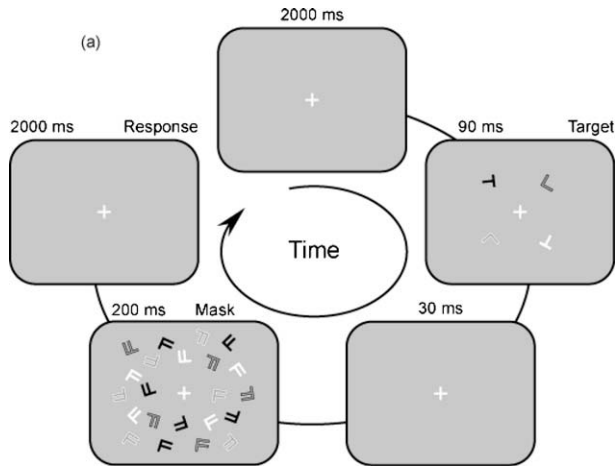
Fig. 4. Trial sequence with fixation, target, mask, and response interval (Exp. 2). The target was identified by color of the fixation cross and observers reported the letter shape of the target (high-load only). Attention had to be shifted during the interval from target to mask onset in order to affect performance.

4.1.2. Data pre-processing

Eye movement data was checked for incorrect fixation, blinks and other errors. After pre-processing 10.5% were discarded: bad fixations – 2.7%, blinks – 7.5%, no response – 0.3%.

4.2. Results

The overall MR and the pattern of suppression and rebound following each onset resembled that observed in Experiment 1 (see Fig. 5, top row). Microsaccade suppression deepened and became virtually complete approximately 200 ms after target onset ($100 \leqslant t < 300$), with a residual rate of 0.005 ± 0.002 Hz. The following rebound peaked approximately 1100 s after target onset with a rate of 1.12 ± 0.03 Hz ($1000 \leqslant t < 1200$).

The direction of microsaccades was tightly correlated with the target location (see Fig. 5, second and third rows). Comparing left vs. right hemifields, the congruency between microsaccade direction and target location peaked at 98% shortly after target onset ($160 \leqslant t < 360$ ms, $p < 0.001$; white arrows in second row of Fig. 5) and remained above 75% during a period of approximately 430 ms ($120 \leqslant t < 550$ ms, $p < 0.05$). Comparing top vs. bottom hemifields, congruence was less pronounced, reaching merely 65% approximately 330 ms after target onset ($330 \leqslant t < 530$ ms, $p < 0.001$; white arrows in third row of Fig. 5).

As in the previous experiment, microsaccades were most informative when they were also most scarce, that is, at the end of the suppression and the beginning of the rebound (white arrows in Fig. 5). Only 9% of trials contained a microsaccade during the informative time period ($120 \leqslant t < 550$ ms, when congruency exceeded 75%). However, a closer look reveals some differences between the respective time-profiles of informativeness and scarcity. Whereas MR starts to wane before the target onset in the absence of any visual events (black arrow in top row of Fig. 5), maximal informativeness peaked only ~200 ms after target onset (white arrows in Fig. 5). This may suggest that the suppression and the directional selectivity of microsaccades are caused by different underlying processes.

As in Exp. 1, the amplitude of microsaccades did not change significantly throughout the trial (Fig. 5, fifth row), except for slightly larger amplitudes during periods with negative congruency.

As before, the timing of microsaccades affected reaction times (Fig. 5, bottom row). When they occurred immediately after target onset ($100 \leqslant t < 300$ ms), microsaccades lengthened reaction times

by $2.1–1044 \pm 238$ ms, whereas later microsaccades shortened reaction times by 0.9: 435 ± 4 ms, compared to an average value of 490 ± 4 ms, $p < 0.001$. A similar trend was evident in the response accuracy (Fig. 5, fourth row): microsaccades just before target onset ($-200 \leqslant t < 50$ ms) reduced performance significantly to $72 \pm 5\%$ ($p = 0.04$), while subsequent microsaccades ($50 \leqslant t < 800$ ms) increased performance to $85 \pm 1\%$ ($p = 0.007$), compared to the average performance of $81 \pm 5\%$.

5. Experiment 3: RSVP

Our previous experiments established that attentional load influences both the frequency and the directional selectivity of microsaccades. However, in both experiments, the high-load condition entailed shifting the attention focus away from fixation to a peripheral target location. In the low-load condition, the task did not require such a shift. Accordingly, the observed differences may not have been a consequence of attentional load *per se*, but rather a consequence of whether or not the attention focus was shifted. To resolve this ambiguity, our third experiment examined the effect of attentional load in the absence of confounding attention shifts.

To this end, we employed a rapid serial visual presentation (RSVP) paradigm in which both targets and distracters were presented sequentially at fixation (Fig. 6a). Rotated letter-shapes appeared at fixation at a rate of 90 ms per shape (11 Hz). The sequence comprised a total of 21 shapes and lasted for 2190 ms. At the beginning of a block of trials, observers were instructed to report the presence or absence of either a particular letter (letter condition) or of an oddly-colored item (color condition). Shape targets and color targets occurred independently in half the trials (i.e., 25% of the trials had two targets, 25% had only the color target, 25% had only the shape target, and 25% had zero targets). Performance in the shape condition was significantly lower $83 \pm 4\%$ than in the color condition $99 \pm 1\%$ (binomial distribution, $p < 0.01$).

5.1. Methods

5.1.1. Stimuli and procedure

Each trial consisted of a set of successively presented randomly rotated upper case letters, for schematic procedure see Fig. 6a. Each letter was presented for either 500 ms (2 Hz condition) or 90 ms (11 Hz condition) and had a height of 2° of visual angle. In a 2 Hz condition, first four and last four letters were distracters. In the middle part of the stream, two out of four letters were randomly picked to be color and letter target (same letter was both color and letter target in 6.25% of the trials for 2 Hz condition and in 2% of the trials for 11 Hz condition). For 11 Hz condition each portion of the stream consisted of seven rather than four letters. Conditions were balanced in a 2-by-2 design – both targets present, both targets absent, only color target and only letter target – so that each combination was present in 25% of the trials. Each block consisted of 20 trials. Each set was preceded by a 2 s fixation interval and followed by an unlimited response interval. Observers had to respond whether the specified target (opposite color or specific letter) were present (by pressing 'J') or absent (by pressing 'F').

5.1.2. Data pre-processing

Eye movement data was checked for incorrect fixation, blinks and other errors. Total fraction of discarded trials for 11 Hz condition 8.6%: bad fixations – 7.5%, blinks – 1.1%, no response – 0.0%. Total fraction of discarded trials for 2 Hz condition 11.6%: bad fixations – 3.3%, blinks – 8.3%, no response – 0.0%.
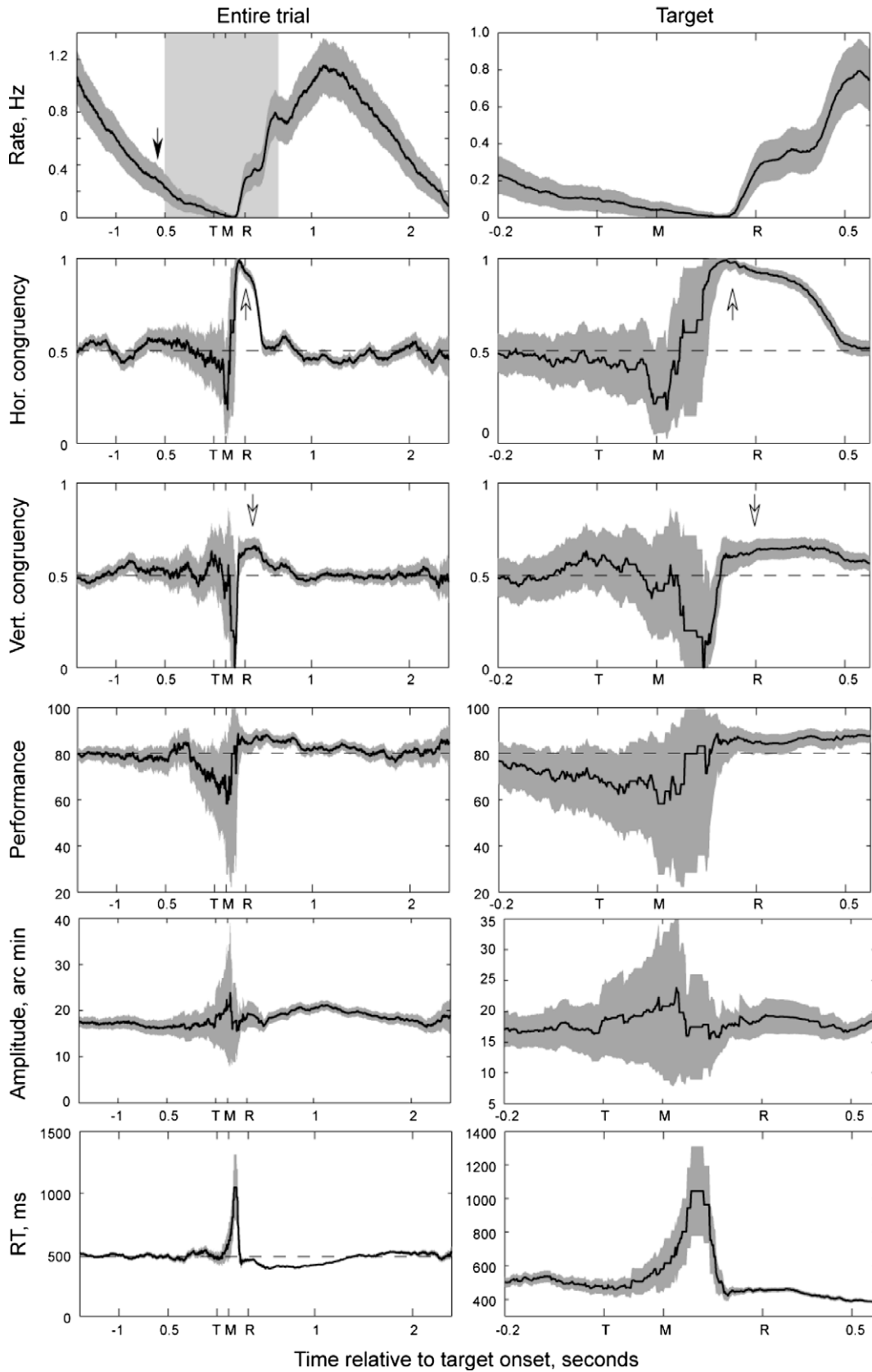
Fig. 5. Rate, congruency, amplitude, and effect on reaction time of microsaccades for Exp. 2 (high-load only). Each graph depicts a time course, either over the entire trial (left column), or around target onset (right column). The top row shows instantaneous microsaccade rate (mean ± standard error in Hz). The second and third rows show congruency between microsaccade direction and target location (2nd row: left vs. right hemifields; 3rd row: top vs. bottom hemifields). The fourth row shows performance for all trials with at least one microsaccade in each time bin (mean ± 95% confidence interval). The fifth row shows microsaccade amplitude (mean ± standard error in arc min). The bottom row shows reaction times for all trials with at least one microsaccade in each time bin (mean ± standard error in ms). Time axis legend: T – target onset, M – mask onset, R – start of the response interval.
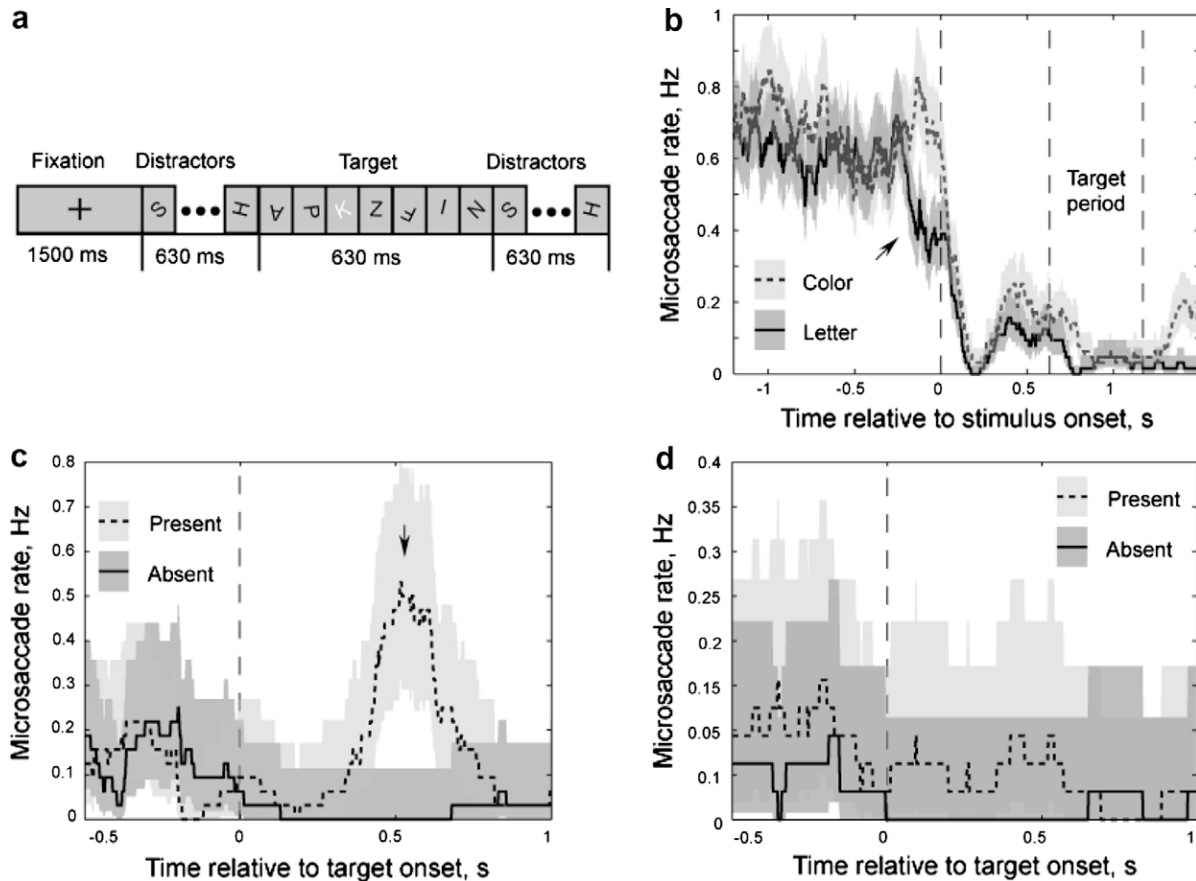
Fig. 6. Trial sequence and results for RSVP experiment with 11 Hz presentation rate. (a) A series of 21 rotated letters was presented at fixation. Up to two target letters exhibited an odd shape or color. Observers reported the presence of either an oddly-colored (low-load) or a specific letter (high-load). (b) Mean ± standard error of instantaneous microsaccade rates aligned to sequence onset for the color (dotted line, light gray) and letter conditions (solid line, dark gray). (c) Instantaneous microsaccade rate for target present (dotted line, light gray) and target-absent trials (solid line, dark gray) in the color condition. (d) Same for the letter condition.

5.2. Results

The serial visual onsets of the display greatly reduced the average frequency of microsaccades (Fig. 6b). There remained, however, a highly significant difference between the two load conditions, with a microsaccade frequency consistently higher under the low-load (color) than under the high-load (letter shape) condition. The average MR (average taken over the entire stimulus presentation sequence) was 0.26 ± 0.07 Hz during the low-load (color) condition and 0.12 ± 0.05 Hz during the high-load (letter) condition (significance of difference $p = 0.0001$). Even prior to the beginning of the trial sequence, microsaccade frequency significantly differed between the two conditions ($-200 \leqslant t < 0$, 0.4 ± 0.1 Hz for the shape and 0.75 ± 0.13 Hz for the color condition, $p = 0.015$; arrow in Fig. 6b).

Comparing trials with and without a target, we examined fixational eye movements immediately preceding and following a target presentation (target-present trials) and a distracter presentation (target-absent trials). In the low-load (color) condition, the instantaneous microsaccade frequency exhibits a dramatic and selective rebound following a target presentation ($420 \leqslant t < 620$, 0.53 ± 0.2 Hz; arrow in Fig. 6c), but not a distracter presentation ($420 \leqslant t < 620$, 0.02 ± 0.1 Hz). This difference is highly significant ($p < 0.001$). No such effect was observed in the high-load (letter shape) condition, where the microsaccade rate rose to 0.06 ± 0.12 Hz ($420 \leqslant t < 620$) after a target and to 0.01 ± 0.07 Hz after a distracter. The difference was not significant ($p = 0.08$).

To examine this target-related effect in greater detail, we slowed the presentation rate from 11 Hz to 2 Hz, also limiting number of presented items to 12, such as to allow fixational eye movements more time to recover from each visual onset. As a result of this change, task performance was now comparably high for both conditions ($98 \pm 2\%$ for color and $98 \pm 2\%$ for letters). In this modified situation, the instantaneous microsaccade frequency followed a periodic evolution, reaching a minimum approximately 130 ms and a maximum approximately 250 ms after each onset (Fig. 7a). Once again, the average MR was slightly but significantly higher under low-load (0.93 ± 0.08 Hz) than under high-load (0.85 ± 0.07 Hz; $p = 0.0005$) conditions.

The analysis of the instantaneous microsaccade rate revealed further target-related effects. Fig. 7b–d shows the respective effects of target and distracter presentation on instantaneous microsaccade frequency. All comparisons involve corresponding times in target-present and target-absent trials. In the low-load (color) condition, there were differential effects on the first rebound (which directly followed the target) and on further rebounds (which followed the subsequent distracters), see Fig. 7c. Specifically, the first rebound peaked with 1.15 ± 0.15 Hz at a *lower* level (black arrows in Fig. 7c) than in target-absent trials (1.7 ± 0.2 Hz; $p < 0.001$), whereas the second rebound peaked with 2.13 ± 0.21 Hz at a *higher* level (white arrows in Fig. 7c) than in target-absent trials (vs. 1.5 ± 0.19 Hz; $p < 0.001$). In the high-load (letter shape) condition, only the latter difference was observed (Fig. 7d). Specifically, the first peak was comparable for target-present and target-absent trials (1.32 ± 0.2 Hz, 1.49 ± 0.21 Hz, respectively; black arrow in
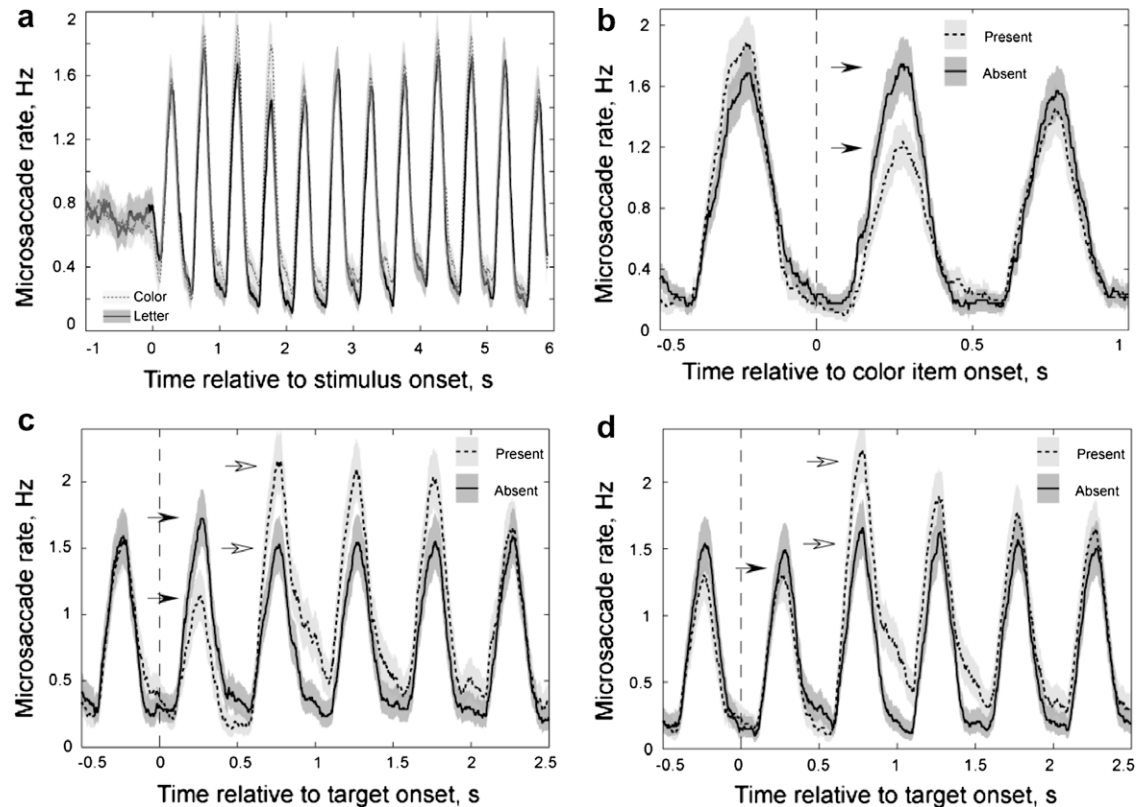
Fig. 7. Results for RSVP experiment with 2 Hz presentation rate. All graphs depict time evolutions of instantaneous microsaccade rates (mean ± standard error). (a) First half of RSVP sequence, aligned to sequence onset. (b) Interval of 1.5 s around the color target, letter trials only, aligned to color target onset. (c) Interval of 2.5 s following color target onset, color trials only, aligned to target onset. (d) Interval of 2.5 s following letter target onset, letter trials only, aligned to target onset.

Fig. 7d), but the second rebound peaked with 2.235 ± 0.25 Hz at a *higher* level (white arrows in Fig. 7d) than in target-absent trials (1.66 ± 0.18 Hz, $p < 0.001$).

The reduced frequency of microsaccades during the first rebound (Fig. 7c and d, filled arrows) following a color, but not a letter target presumably reflected the higher saliency of color targets, which attracted attention automatically. This is consistent with previous reports that visual oddball items transiently inhibit microsaccade rates (Rolfs et al., 2008; Valsecchi & Turatto, 2009; Valsecchi et al., 2007). The increased frequency of microsaccades on subsequent rebounds (Fig. 7c and d, open arrows) presumably reflected a relaxation of attention following the target. This transient increase was more pronounced after color targets, presumably once again due to the higher salience of such targets. This interpretation is not inconsistent with observers' subjective reports that the appearance of a color target effectively signaled the end of the trial, whereas the appearance of a letter target did not register sufficiently prominently to do the same.

To confirm the suspected saliency of color targets, we compared trials with and without a color target under the letter condition (i.e., when observers reported letter targets and ignored color targets), and indeed found the expected, transient reduction of instantaneous microsaccade rate after the (task-irrelevant) color target (arrows in Fig. 7b). Specifically, the frequency peaked with 1.24 ± 0.11 Hz well below the reference level of 1.47 ± 0.12 Hz ($p = 0.036$).

6. Discussion

We have examined the effect of attentional load on microsaccades. Observers performed tasks posing different attention de-

mands on physically identical displays. In the high-demand conditions, observers either shifted attention covertly to a peripheral location or focused attention at fixation. Corresponding low-demand conditions provided a comparison. In general terms, we found that microsaccades grew less frequent with higher attentional load, but were directed more consistently towards the attention focus. In short, microsaccades were most informative about the attended location just about when they were most rare.

Our detailed findings may be summarized as follows. Comparing the discrimination of a peripheral target under low and high attentional load (spatially cued color and letter discrimination in Exp. 1), we found that microsaccades grew less frequent (rate 0.47 Hz and 0.41 Hz, respectively) with increasing load, but were directed more consistently towards the attention focus (congruency 62% and 74%, respectively). Comparing target discrimination at an expected and an unexpected peripheral location (spatially cued letter discrimination in Exp. 1 and color-cued letter discrimination in Exp. 2) we found that microsaccades were directed even more consistently towards the attended location (congruency 74% and 98%, respectively).

When attention was engaged by a serial presentation at fixation, we observed both sustained and transient effects of attentional load (Exp. 3). The sustained microsaccade rate was more than halved under high-load (0.12 ± 0.05 Hz compared to 0.26 ± 0.07 Hz under low-load, 11 Hz condition).

6.1. An almost perfect correlation

Our main finding was that, under certain conditions, microsaccades were directed consistently towards the attended hemifield (approximately 100% congruency), revealing an almost perfect correlation between microsaccade direction and attended location.

This attested also to the high degree of attention control achieved by our experimental design. Two aspects of our design are likely to have contributed: (i) we used a visual discrimination of known attention demand (Braun & Julesz, 1998; Lee et al., 1999a, 1999b; Houtkamp & Braun, 2009; Li et al., 2002; Pastukhov et al., 2009), instead of a visual detection or hue discrimination task of low to moderate attention demand, as employed by previous studies (Engbert & Kliegl, 2003a, 2003b; Hafed & Clark, 2002; Rolfs, Engbert, & Kliegl, 2004). (ii) We obliged observers to shift attention at a particular moment in time (i.e., immediately after target onset), instead of allowing a long interval for such shifts (i.e., the 1100–2600 ms between cue and target onset; (Engbert & Kliegl, 2003a, 2003b; Gowen, Abadi, Poliakoff, Hansen, & Miall, 2007; Hafed & Clark, 2002; Laubrock et al., 2005; Rolfs et al., 2004)). Previous studies with endogenous spatial cues have encountered congruencies up to 80% (Hafed & Clark, 2002; Laubrock et al., 2005, 2007), while studies with exogenous cues have observed similar levels of congruency for microsaccades directed away from the cued location (Laubrock et al., 2005; Turatto, Valsecchi, Tame, & Betta, 2007; Valsecchi et al., 2007). Taken together, the available evidence seems to suggest that there may exist an essentially perfect correlation between microsaccade direction and attended location, which becomes experimentally evident when the attended location is known with sufficient certainty.

Turatto and colleagues (Turatto et al., 2007) conducted an experiment that was superficially similar to ours, but produced quite different results. In their case, observers performed a visual search for an odd item, which was distinguished by either color or shape, on a continuously presented array. During the visual search, microsaccades were not directed consistently towards the target. However, it seems likely that multiple attention shifts, to both targets and non-targets, occurred during the search. If so, this would have obscured any association between microsaccade direction and target position. Some 500 ms after array onset, Turatto and colleagues observed microsaccades directed away from the target (congruency ∼0.35%). This may have reflected either attention shifting back towards fixation or an "inhibition-of-return" effect (Betta et al., 2007; Galfano et al., 2004; Laubrock et al., 2005).

6.2. An inverse relation with load

Our second main finding was that microsaccade rate correlated inversely with attentional load.

In our experiments with a single target presentation (Exps. 1 and 2), the microsaccade rate dipped around the time of target appearance, due to the inhibitory effect of visual onsets (Engbert, 2006; Engbert & Kliegl, 2003a, 2003b; Rolfs et al., 2008) and perhaps also due to voluntary control (see below). Although this pronounced modulation complicates comparison, average microsaccade rates were significantly lower under high-load than under low-load conditions. In our experiments with serial presentations (Exp. 3, 11 Hz and 2 Hz conditions), average microsaccade rates were more than halved by higher attentional load. Both observations are consistent with the possibility that the focusing of attention on the expected target location reduces microsaccade frequency.

In addition, we confirmed the previously reported inhibition of microsaccade by a visual "oddball" target (Valsecchi & Turatto, 2007, 2009; Valsecchi et al., 2007). As the "oddball" effect depends on the target stream being attended, it is thought to reflect cognitive/attentional levels of processing (Valsecchi & Turatto, 2009). Presumably, microsaccades are suppressed when attention is attracted to the "oddball" target and recover when the attentional focus subsequently relaxes.

Taken together, these observations suggest the following tentative working hypothesis: focusing attention causes a decrease, and dispersing attention causes an increase in the frequency of microsaccades.

6.3. Voluntary modulation of microsaccades

As saccades and microsaccades are partially under voluntary control (Bridgeman & Palca, 1980; Haddad & Steinman, 1973; Steinman, Cunitz, Timberlake, & Herman, 1967; Winterson & Collewijn, 1976), observers may learn the perceptual cost or benefit of microsaccades in any given situation and modulate microsaccade rates accordingly. It is not known whether this voluntary control over microsaccades is exerted directly, is mediated by attention, or both.

In the present experiments, which involved briefly presented and masked displays, perceptual performance was limited by viewing time. Accordingly, any microsaccades coinciding with target presentation should have been perceptually costly, due to the transient suppression of visual responsiveness (Herrington et al., 2009) and the attendant loss of visual sensitivity (Beeler, 1967; Ditchburn, 1955; Latour, 1962) while microsaccades were "in flight". Indeed, we found that microsaccades coinciding with target presentation significantly decreased performance and increased response time. Accordingly, we suspect that our observers voluntarily suppressed microsaccades in anticipation of the target presentation. Consistent with this possibility, we found that microsaccade frequency waned well before target onset and in the absence of any visual events. Interestingly, this was true under both low- and high-load conditions. This may be an indication that voluntary control was exerted directly, without involving attention.

In a recent related study, visual scenes were viewed continuously for 45 s and microsaccade rate was found to increase with the complexity of the scene (Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, & Martinez-Conde, 2008). Specifically, while viewing complex scenes (natural images, picture puzzles, "Where is Waldo?" cartoons), microsaccades were several times more frequent than while viewing a blank screen. Most intriguingly, microsaccades were particularly frequent in the spatial vicinity of identified targets (e.g., "Waldo" or "Wenda"), where attention was presumably focused. The authors concluded that "increased microsaccade production [may have been] due to increased attentional load" (Otero-Millan et al., 2008), which would be at variance with our observations.

An alternative possibility is that the number of microsaccades was increased by direct voluntary control (Haddad & Steinman, 1973). When viewing time is unlimited, microsaccades may benefit perceptual performance by counteracting visual fading (Cui, Wilke, Logothetis, Leopold, & Liang, 2009; Hsieh & Tse, 2009; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006; Troncoso, Macknik, & Martinez-Conde, 2008), by foveating attended parts of the visual scene more precisely (Cornsweet, 1956; Engbert & Kliegl, 2004; Liang, Moshel, Zivotofsky, Caspi, Engbert, & Kliegl, 2005), and/or by generally enhancing the responsiveness of the visual pathway (Dimigen, Valsecchi, Sommer, & Kliegl, 2009; Donner & Hemila, 2007; Martinez-Conde, Macknik, & Hubel, 2000, 2002; Tse, Baumgartner, & Greenlee, 2010). Accordingly, it seems likely that additional microsaccades would have benefitted perceptual performance in the situation investigated by Otero-Millan and colleagues.

6.4. Possible neural basis

There is compelling evidence that the brain structures that initiate and control eye movements, also guide and control the allocation of attention (Awh, Armstrong, & Moore, 2006; Corbetta, 1998; de Haan, Morgan, & Rorden, 2008; Grosbras, Laird, & Paus, 2005;

Krauzlis, 2005; Nobre, Gitelman, Dias, & Mesulam, 2000). As the same neural mechanisms mediate both saccades and microsaccades (Hafed, Goffart, & Krauzlis, 2009; Otero-Millan et al., 2008; Rolfs, Laubrock, & Kliegl, 2006; Rolfs et al., 2008), it is no surprise that microsaccades should also exhibit some relation to attention.

It has recently been shown that microsaccades reflect activity in the superior colliculus (Hafed et al., 2009), which contains a retinotopically organized motor map for eye movements of all amplitudes (e.g.,(Krauzlis, Basso, & Wurtz, 1997; Munoz, Dorris, Pare, & Everling, 2000)). According to a computational model developed to account for these results, map activity is elevated in the vicinity of both the fixated and the attended location (Hafed et al., 2009). In addition, activity fluctuates independently at every location. Microsaccades are triggered when the *center of mass* of the entire activity distribution deviates sufficiently far from zero. Several predictions of this model are consistent with our observations: attending at fixation sharpens the activity profile and reduces the number of microsaccades, while attending to the periphery distorts the profile asymmetrically and triggers microsaccades directed towards the attended site.

A similar model for microsaccade generation has been proposed by Rolfs and colleagues (Rolfs et al., 2008). In this model, the activity distribution is smoothed by center-surround interactions and microsaccades are triggered by displacements of the most active location (not the *center of mass* location). If one assumes that attention elevates map activity, this model correctly predicts that peripheral attention triggers microsaccades towards the attended location.

However, both models also predict that peripheral attention should increase microsaccade rates, which is contrary to our observations. A tentative explanation for this discrepancy lies in the observers' ability to voluntary suppress eye movements to avoid disruptive effects of microsaccades, as we have outlined above.

In conclusion, our observations are broadly consistent with recent accounts of microsaccades in terms of spontaneous fluctuations in a retinotopic activity map (Hafed et al., 2009; Rolfs et al., 2008).

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