It has been suggested that subjective disappearance of visual stimuli results from a spontaneous reduction of microsaccade rate causing image stabilization, enhanced adaptation, and a consequent fading. In motion-induced blindness (MIB), salient visual targets disappear intermittently when surrounded by a moving pattern. We investigated whether changes in microsaccade rate can account for MIB. We first determined that the moving mask does not affect microsaccade metrics (rate, magnitude, and temporal distribution). We then compared the dynamics of microsaccades during reported illusory disappearance (MIB) and physical disappearance (Replay) of a salient peripheral target. We found large modulations of microsaccade rate following perceptual transitions, whether illusory (MIB) or real (Replay). For MIB, the rate also decreased prior to disappearance and increased prior to reappearance. Importantly, MIB persisted in the presence of microsaccades although sustained microsaccade rate was lower during invisible than visible periods. These results suggest that the microsaccade system reacts to changes in visibility, but microsaccades also modulate MIB. The latter modulation is well described by a Poisson model of the perceptual transitions assuming that the probability for reappearance and disappearance is modulated following a microsaccade. Our results show that microsaccades counteract disappearance but are neither necessary nor sufficient to account for MIB.

Keywords: eye movements, visual cognition, spatial vision

competition between the neural representations of the regarded as an instance of perceptual bistability of cortical MIB (New & Scholl, 2008). Alternatively, MIB could be Livingstone, 2009) and for a related functional account of mechanisms that discard functionally inappropriate stimuli with higher level perceptual interpretation Kramar, 2006), and motion streak suppression (Wallis & Hubel, 1987), a brighter target pattern disappears more suppression during its illusory disappearance in MIB, consistent with a central origin of MIB (Donner, Sagi, & Hubel, 1987), a brighter target pattern disappears more suppression or adaptation and is not caused by a shutdown of retinal input to the cortex, such as could arise for example from freezing of fixational eye movements. First, different patterns tend to disappear independently and in some cases, such as adjacent orthogonal patches, disappear in a rivalry-like alternation (Bonneh et al., 2001). This argues strongly against global underlying mechanisms, including retinal stabilization. Second, moving or dynamic patterns can also disappear, producing the striking phenomenon of a pattern that disappears at one position and reappears on the other side of the screen after a few seconds (Bonneh et al., 2001). Third, at least under certain conditions and unlike Troxler fading (Livingstone & Hubel, 1987), a brighter target pattern disappears more (Bonneh et al., 2001), ruling out a “gain control” or adaptation mechanism that attenuates responses to low-contrast stimuli in a cluttered environment. Fourth, there is evidence for residual subconscious processing of invisible stimuli, including the capacity to produce orientation-selective adaptation (Montaser-Kouhsari, Moradi, Zandvakili, & Esteky, 2004), negative afterimages (Hofstoetter, Koch, & Kiper, 2004), and Gestalt grouping (Mitroff & Scholl, 2005). Fifth, target-specific fMRI responses in human V1, showing robust suppression during physical removal of the target, exhibit only weak suppression during its illusory disappearance in MIB, consistent with a central origin of MIB (Donner, Sagi, Bonneh, & Heeger, 2008). Further, areas in extrastriate dorsal and ventral visual cortices show competitive dynamics specifically during MIB (Donner et al., 2008).

Instead, MIB could be caused by a combination of low-level mechanisms that trigger disappearance (such as adaptation (Gorea & Caetta, 2009), filling-in (Hsu, Yeh, & Kramer, 2006), and motion streak suppression (Wallis & Arnold, 2009)) with higher level perceptual interpretation mechanisms that discard functionally inappropriate stimuli (such as depth ordering and surface completion (Graf, Adams, & Lages, 2002)). Indirect physiological evidence was found for such a scheme (Libedinsky, Savage, & Livingstone, 2009) and for a related functional account of MIB (New & Scholl, 2008). Alternatively, MIB could be regarded as an instance of perceptual bistability of cortical visual processing at some level(s), which is a result of a competition between the neural representations of the static target and the moving mask (Bonneh et al., 2001; Graf et al., 2002; Keysers & Perrett, 2002). fMRI evidence for antagonistic interplay between human ventral and dorsal visual cortices during MIB supports this notion (Donner et al., 2008).

Microsaccades have been in a focus of studies of visual awareness and attention (see review in Rolfs, 2009) because of their suggested role in active perception and because of their hypothesized role in counteracting visual fading (Martinez-Conde, Macknik, Troncoso, & Dyar, 2006; Troncoso, Macknik, & Martinez-Conde, 2008). It is generally known that stimulus transients reduce disappearance in MIB (Bonneh et al., 2001) and Troxler fading (Livingstone & Hubel, 1987) and increase dominance (terminate disappearance) in binocular rivalry (see review in Blake & Logothetis, 2002). Transients induced by microsaccades are effective and large enough to trigger reappearance and counteract fading. This was shown for Troxler fading (Martinez-Conde et al., 2006), artificial scotoma (Troncoso et al., 2008), and MIB (Hsieh & Tse, 2009). In these studies, the rate or probability of microsaccades was found to increase before reappearance and decrease before disappearance, suggesting that microsaccades cause reappearance and that the absence of microsaccades enables disappearance. These results ostensibly contradict the reasoning summarized above and support a solely low-level explanation of MIB, such as shutdown of retinal input due to adaptation in the absence of eye movements. These studies, however, did not include physical removal of the targets as a control condition to be compared with spontaneous, illusory disappearance. The need for such a condition stems from the accumulating evidence for rich spatiotemporal dynamics of microsaccade rate and direction in response to sensory and cognitive events (Engbert, 2006). Following such an event, microsaccade rate first decreases, then increases above baseline, before returning to baseline. This stereotypical time course of microsaccade rate (decrease–increase–baseline) is modulated by attention and expectation (see review in Rolfs, 2009). It is thus important to dissociate between cause and effect in studies linking microsaccade dynamics to perceptual transitions.

In the current study, we investigated whether fixational eye movements can account for MIB. Specifically, we addressed the hypothesis that the global motion of the MIB mask alters the normal pattern of fixational eye movements, which in turn reduces visual transients and, consequently, enhances fading (Troxler effect), making parafoveal targets disappear. This hypothesis stems from the classical literature on “stabilized images” demonstrating that visual targets fade after a few seconds in the absence of motion of the retinal image (Riggs, Ratliff, Cornsweet, & Cornsweet, 1953), depending on stimulus factors such as size, retinal eccentricity, spatial frequency, and contrast (Riggs et al., 1953; see review in Steinman & Levinson, 1990). This hypothesis makes the following predictions: (i) the moving mask should alter the fixational
eye movements, even in the absence of the targets; and (ii) changes in microsaccade rate (or other metrics) coincident with target disappearance should be specific to illusory disappearance in MIB and markedly/qualitatively different from changes in microsaccades evident during physical removal of the targets.

Our goal was to test the above hypothesis by determining (i) if the moving mask modulates microsaccade rate and (ii) if the modulation of microsaccade rate coincident with illusory target disappearance in MIB (Hsieh & Tse, 2009) is different from that coincident with physical target removal. In the first set of experiments, we measured eye movements while subjects were instructed to hold fixation, with and without the MIB mask, in the absence of MIB targets. In the second set of experiments, we computed the event-related modulations of eye movements when the observers reported the disappearance and reappearance of a target. Crucially, we measured eye movements during both MIB (illusory perceptual disappearance) and Replay (physical disappearance). Finally, to distinguish between a causal and a modulatory role of microsaccades in MIB, we implemented a simple Poisson model with the minimal assumptions sufficient to account for the results. Our results suggest that microsaccades counteract visual fading in MIB but are unlikely to be involved in causing it.

**Methods**

**Subjects**

Six observers (4 females, ages 25–48) with normal or corrected-to-normal vision including the first author participated in the experiments.

**Apparatus**

Stimuli were displayed on a 22” CRT monitor controlled by dedicated software running on a Windows PC. The video format was true color (RGB), at 100-Hz refresh rate, with 1280 × 1024 pixels resolution occupying a 25° × 20° area. Luminance values were gamma-corrected. The sitting distance was 1 m, and all experiments were administered in the dark.

Eye movements were recorded monocularly, with an iViewX Hi-Speed infrared eye tracker (SensoMotoric Instruments (SMI), Teltow, Germany), at a sampling rate of 240 Hz, which was used to test four of the observers. In addition, an Eyelink II infrared system (SR Research, Ontario, Canada) with a sampling rate of 1000 Hz and a spatial resolution of less than 0.01° was used to test 3 observers (one observer was tested on both systems). Movements of the head were limited by a chin and forehead rest. Recording was from the left eye, though viewing was binocular. A standard 9-point calibration was performed before each session, though the absolute position of the eyes was never used and had no importance in the study.

**Stimuli and procedure**

**Experiment 1: The effect of motion on microsaccades**

Six observers fixated a central dot and passively viewed a rotating mask (similar to Figure 1a, but without the peripheral patch) followed by a blank screen, for 4 min each. The 8-min mini-sessions were repeated twice. The mask consisted of an array of 7 × 7 gray crosses (half the background luminance) with spacing of 1.5 pattern diameter occupying 6° × 6° and rotated in a speed of 0.5 cycle/s. Background luminance was 30 cd/m².

**Experiment 2: Eye movements during disappearance and reappearance**

Observers reported the disappearance and reappearance of a salient target surrounded by a moving mask (Figure 1a). The target consisted of a single Gabor patch (σ = λ), 4 cpd, 80% contrast, presented in the upper left quadrant at 2 deg eccentricity. The mask was as in Experiment 1 described above. A circular patch of the background luminance (30 cd/m²), 1.5 deg in diameter, was used as a “protected zone,” which occluded the mask and was covered by the target.

While fixating a central dot, observers reported their perception of the Gabor target by depressing and releasing a button for reporting disappearance and reappearance, respectively. There were two experimental conditions, lasting 4 min each and tested successively: MIB in which observers reported perceptual disappearance and Replay in which the Gabor patch was physically erased according to the time course of the observer’s reports in the preceding period of the MIB condition. In half of the experiments, there was no mask in the replay condition, while in the other half the mask was the same as in the MIB condition except that it rotated very slowly (6 deg/s, 1 cycle/min). Each observer was tested on 6 to 9 pairs of successive MIB and Replay periods, with short breaks between the 8-min periods.

**Data analysis**

**Microsaccade detection**

Microsaccades were detected using the algorithm introduced by Engbert and Kliegl (2003). Raw data were first smoothed with a window of 15 ms to optimize microsaccade extraction. This smoothing was found critical for lower quality or noisy recordings. The permitted velocity range was 8–150°/s and the permitted...
amplitude range was 0.08°–2°, with minimum duration of 9 ms; microsaccades outside these ranges were rejected. The rejection rate varied across recordings and was typically 5–20%. Microsaccade rate was calculated by convolving a raw rate estimate of 1 microsaccade per sample duration at the time of microsaccade onset with a Gaussian window with a sigma of 50 ms. Data collected with the SMI tracker were analyzed with an alternative algorithm (developed by Moshe Fried) that yielded more accurate microsaccade detection than Engbert and Kliegl’s algorithm in some cases. This algorithm searched the horizontal and vertical pupil position vectors for a continuous sequence of data samples, which satisfied the velocity, amplitude, and duration restrictions defined above.

Figure 1. Experimental methods and data analysis. (a) Schematic illustration of MIB. In Experiment 2, observers viewed a 4-min MIB display (left) while reporting disappearance and reappearance with a button press. The observers then repeated the same task while viewing a 4-min “replay” of physical disappearance according to their previous reports. (b) Analysis of eye tracking data illustrated by example from one observer in one condition. Data were first segmented into epochs, time locked to the perceptual reports of disappearance. The upper panel shows the pupil horizontal position around its mean per epoch, with microsaccades marked in bold (not all of 190 epochs are shown). Note the variable length epochs, each corresponding to periods with a single perceptual transition from visible (on the left) to invisible (on the right). The lower panel shows the event-related microsaccade rate averaged across epochs. The event-related average is thus based on epochs with variable numbers of time points (N = 151 on average).
Total drift calculation

An estimate of the total retinal slip including drift and microsaccades was calculated for each axis as the range of positions (max minus min) within a sliding window of 0.15 s in steps of 10 ms. Drift estimates greater than 3° were discarded from further analysis similar to eye blinks (see below). The overall drift was calculated as the square root of the sum of squares (RMS) of the drift in the two axes.

Epoch extraction (second experiment)

Epochs were extracted time locked to observers’ reports of disappearance and reappearance events in a total range of 3 s before and 3 s after each event, with the following restriction. Epochs of the same kind did not overlap; they were terminated 0.5 s after or before the preceding and following events (values beyond these termination points were discarded from further analysis). This ensured that there was no mixing or averaging data from different perceptual states (visible, invisible), while taking into account a response time (RT) of about 0.5 s. Periods of missing data, such as during eye blinks, were locally discarded from further analysis, with additional margin of 0.25 s, without discarding the whole epoch. Epochs shorter than 0.5 s (24% of epochs across all observers and conditions) were discarded since they could reflect button press errors. An example of the variable length epochs appears in Figure 1b (top panel).

Epoch averaging

The microsaccade rate and total drift were averaged across epochs to compute the event-related modulation of eye movements (ERE). Because some samples were excluded from the analysis (see above), there was a variable number of samples per ERE data point (N specifies the average of this number across all data points). In order to emphasize the tonic differences between microsaccade rates in non-transient regions of different conditions, we applied smoothing (0.4 s moving average window) beyond a ±1 s time range. This smoothing appears in all plots of microsaccade rate time courses. An example for epoch averaging from one observer in one condition appears in Figure 1b (bottom panel), showing microsaccade rate averaged across trials. The group (all observers) average and standard error of the microsaccade rate were obtained by normalizing (subtracting individual means) and rescaling the average (adding the group mean rate). An alternative group average was computed by averaging all epochs from all observers together without normalization, thus taking into account the variation in the number of disappearance events across observers.

Statistical significance assessment

For each observer, we performed a series of t-tests comparing the frequency of microsaccades in all combinations of MIB, Replay, ON, and OFF in 100-ms steps across the −3 s to 3 s time range, yielding 60 p-values per comparison. We then combined the computed p-values across observers, using Fisher’s inverse chi-square method (see Hedges & Olkin, 1985). False Discovery Rate (alpha < 0.05) was used to assess the statistical significance of the 60 combined p-values (Benjamini & Yekutieli, 2001). We also performed a similar analysis, averaging epochs across all observers, but without combining p-values.

Model

The model used a Poisson process to determine transitions from invisible to visible and from visible to invisible during MIB (Figure 7a). The Poisson rate was modulated by microsaccade onsets. The time series of microsaccades was sampled from the measured microsaccade times acquired for one observer during about 10 min of passive viewing of a fixation point (without a mask). We used a time step of 1/240 s to match the sample rate of the eye tracking data. The probability of a transition in the absence of microsaccades was \( p_0 = 0.0008 \) per 1-ms step, for both the transitions from invisible to visible and from visible to invisible, consistent due to symmetry with 50% invisibility. Immediately after a microsaccade, the probability for switching from OFF (invisible) to ON (visible) increased to \( p_1 = 0.0035 \) and the increase decayed gradually with time, with a Gaussian weighting \( (\sigma = 0.5 \text{ s}) \). Similarly, following a microsaccade, the probability for switching from ON to OFF decreased to \( p_2 = 0.0004 \) and the decrease decayed gradually with time, with a Gaussian weighting \( (\sigma = 0.5 \text{ s}) \). An example of the simulated Poisson rate is shown in Figure 7a (upper right box). The Poisson rate was used to simulate a time series of switch events assuming a response time of 450 ms (as measured in the Replay condition, see Psychophysical results section). The simulation was repeated and data accumulated to obtain over 1000 switching events of each type (ON, OFF). These events were used as triggers for extracting a similar number of epochs of the simulated observer from the passive fixation eye movement data to match the total number of epochs of the MIB experimental data. We then computed event-related modulations of eye movement time courses from the simulated data for comparison with the results obtained from real observers (Figure 7b). The 3 probability parameters of the model were manually selected to yield about 40% disappearance and produce event-related microsaccade time courses that matched the experimental group average as much as possible.
Results

Experiment 1: The effect of motion on microsaccades

The experiment tested the effect of motion on the rate and temporal distribution of microsaccades during passive viewing. The results are summarized in Figure 2. No significant differences across observers between the “static” condition (fixating a dot on a gray blank screen) and the “motion” condition (additional rotating mask) were found for the average rate (Figure 2c), the average velocity (Figure 2d), nor for the interval distribution (Figure 2b). A tendency for a lower rate as well as lower occurrence of short temporal intervals was observed in the motion condition, but it was not statistically significant in the group average. A further analysis of the microsaccade rate changes across time in 10-s epochs revealed fluctuations in the static condition that were comparable to the difference in rate between conditions. For all observers, there were long periods in which the microsaccade rate without the mask was lower than other periods with the mask. We conclude that changes in microsaccade rate, velocity, or temporal distribution evoked by the moving mask could not account for MIB, at least not in conditions of passive viewing without a disappearing pattern.

Experiment 2: Eye movements during MIB and replay

The second experiment examined the pattern of eye movements with a disappearing target and observers’ report.

Psychophysical results

The psychophysical results, not shown in the figures, were typical of MIB: disappearance rate across observers of 18–55%, mean of 39%, an average disappearance period of 0.9–2.8 s (mean 1.75 s), and a gamma shape distribution of both disappearance and reappearance periods. When the short disappearance periods were excluded (<0.5 s, see Methods section), the disappearance durations across observers were in the range of 1.2–3.1 s with a mean of 2.1 s. These periods were long enough to measure eye movements during a perceptual event, which typically takes about half a second (reviewed in Rolfs, 2009). Individual observers had occasionally much longer disappearance periods, and there were overall more than 40 disappearance episodes longer than 5 s and 7 disappearance episodes longer than 8 s. Overall, there was almost no perceptual disappearance in the Replay condition as we conclude from the small difference (2%) we found in the number of report events in the two conditions.

The response times (RTs) were measured in the Replay condition relative to the physical onsets and offsets of the stimuli, and the RT histogram peaks were computed for each observer. These peaks were in the range of 443–531 ms with a mean of 469 ms for disappearance and 323–463 ms with a mean of 400 ms for reappearance. The response times for MIB are unknown and are likely to be longer than for Replay, as according to subjective reports by several subjects under these conditions, it takes more time to judge the illusory disappearance of the target as compared to its physical removal. On the other hand, the MIB response times for reappearance are likely to be similar to those of the Replay, as indicated by the similar latency of the event-related microsaccade time courses (see Figure 3, compare blue and green, and below).
Event-related microsaccade rate modulations

Figure 3 summarizes the event-related modulations of microsaccade rate for the two experimental conditions, MIB and Replay, and for the two types of perceptual events, disappearance (OFF) and reappearance (ON). The figure shows the group averages. Individual data are shown in Supplementary Figure S1. The modulations during MIB-OFF and Replay-OFF were similar in shape but less strongly pronounced during Replay (compare red and pink curves). Before MIB-OFF (red curve), the microsaccade rate was high, and around 0.5 s before report, it decreased close to zero, and finally increased again. Before Replay-OFF (pink curve), the rate also dropped and increased again, now remaining at a higher sustained level than during MIB. Nevertheless, the decrease before the OFF report started earlier during MIB than during Replay.

The modulations around ON events showed the opposite trend as the ones around OFF events, but they were again similar between MIB and Replay (compare blue and green curves). However, there was a tonic difference in microsaccade rate between MIB-ON and MIB-OFF (red vs. blue curve). In addition, MIB-ON exhibited one additional early and sharp increase before reappearance. During MIB, the rate rose sharply to a first peak (about −0.5 s) and then decreased again (about −0.25 s) before the ON report. This transient did not have an analogue in Replay; it thus constitutes the main qualitative difference between modulations observed during MIB and Replay.

![Figure 3. Eye movements during MIB and replay (Experiment 2). (a) Event-related modulations of microsaccade rate for each of the four conditions: MIB and Replay (rep), reappearance (on), and disappearance (off). Data were averaged across epochs within observer, normalized per observer and then averaged and rescaled by the group mean (results were similar when averaging across all epochs without normalization as well as when normalizing per epoch). The resulting event-related time courses were smoothed beyond ±1 s time range to emphasize the tonic differences (see Methods section). Error bars, indicating SEM across observers, were down-sampled for clarity. All visible differences (without error bar overlap) between the curves were highly significant, except for the difference between “rep off” and “rep on” before report (see text for details). (b) The accumulated number of samples per data point (summed across observers) for the different conditions. The number decreases as a function of the time from the report because longer epochs were less frequent. The additional modulation around report for reappearance (on) reflects a tendency to blink about 0.5 s after reappearance.](image-url)
During both MIB and Replay, the rate decreased and then increased around the time of the report, and then decreased again, typical of microsaccade rate modulations in response to stimulus or perceptual transients (Rolfs, 2009).

All differences between the curves that are evident (without error bar overlap) in Figure 3 were statistically significant ($p < 0.05$, FDR corrected, see Methods section), except for the difference between Replay ON and Replay OFF in the time range of $-3$ s to 0.5 s (compare green and pink curves), which was only intermittently significant. The $p$-values were typically $p < 0.0001$. We also performed a similar analysis for data obtained by averaging all epochs of all observers (Figure 5, see below and Methods section), yielding a significant difference between Replay ON and OFF ($p < 0.0002$).

The latency between a perceptual transition and report is unknown for MIB. As the second peak of the ON response for MIB and Replay is almost identical (compare blue and green curves, $\sim 50$ ms delay for MIB), we estimated MIB response latency to be $\sim 450$ ms for reappearance. The analogous estimate of $\sim 500$ ms for disappearance (based on Replay) is less certain. Accordingly, the peak that precedes the reappearance report by 0.5 s could reflect microsaccades triggering reappearance. Likewise, the reduction to almost zero rate 0.5 s prior to disappearance reports might reflect an enabling condition for disappearance, provided that response latencies for disappearance during MIB and Replay were equal. If these latencies were longer during MIB, the decrease 0.5 s prior to MIB-OFF may have simply reflected the decrease occurring $\sim 0.25$ ms prior to Replay-OFF in reaction to the perceptual transient (see Supplementary Figure S2).

Regardless, we show below that this time course of microsaccade modulations before perceptual transitions can be fully accounted for by a simple model in which microsaccades merely modulate the probabilities of perceptual transitions, rather than instigating the bistable perceptual process per se.

**Persistence of MIB in the presence of microsaccades**

The transient peak observed before reappearance (MIB-ON) shows, as expected from the consequent visual transient (see above), that microsaccades increase the probability of reappearance during MIB. However, do microsaccades necessarily cause reappearance? In other words, can MIB persist even in the presence of visual transients induced by microsaccades?

We extracted a small subset of the data, which included 108 epochs of invisibility longer than 4 s. The average microsaccade rate for these epochs was around 1/s. Since microsaccades were well within the long periods of invisibility and thus are unlikely to arise from delayed or erroneous reporting, this shows that microsaccades did indeed occur without necessarily causing reappearance.

### The temporal relation between microsaccades and perceptual transitions

To further investigate the possible causal relations between microsaccades and the perceptual transitions, we computed histograms of the intervals between a microsaccade and the perceptual transition that followed it. The results appear in Figure 4, separately for each of the six observers. The right panels show that for some observers (e.g., blue curve) a microsaccade can precede disappearance by less than 500 ms, very close to the presumed perceptual event, thus ruling out a significant stabilization period. Other observers (e.g., see red curve) show longer intervals up to 900 ms, which may imply a delay in reporting or a longer stabilization period necessary for disappearance. The left panels show a high frequency of reappearance about 500 ms after a microsaccade, presumably just before the perceptual switch, but this is not true for all observers (e.g., see red curve), which implies that a microsaccade is not necessary for reappearance.

### The effect of microsaccade amplitude and direction

We also investigated the relation between the amplitude of the microsaccade and the perceptual state and transitions. The microsaccade amplitude distributions for time periods around the two perceptual transitions as well as the sustained states are plotted in Figure 6. The data show that larger amplitude microsaccades were more frequent around the time of reappearance, but the sustained states of visible and invisible did not show any evidence for a reduction in microsaccade amplitude during invisibility, including long invisibility periods.

Further analysis of microsaccade directionality (Supplementary Figure S4) revealed that the microsaccade peak 0.5 s prior to the reappearance report had an average direction downward to the left, orthogonal to the Gabor orientation and thus maximized its stimulating effect; testing other configurations is required to verify this apparent functional tendency.

### The dependency of the results on the microsaccade detection method

The results presented so far were based on microsaccades extracted with a commonly used algorithm and parameters, with maximum microsaccade amplitude of 2 deg. However, historical definitions of microsaccades limit their size to 12' (0.2 deg) or 20' (0.33 deg) at most (Collewijn & Kowler, 2008), with larger eye movements considered to be saccades. We investigated the dependency of our results on the choice of microsaccade amplitude limit and algorithm. The results appear in
Figure 5, showing the normalized (z-score) microsaccade rates for MIB reappearance (Figure 5a) and disappearance (Figure 5b), for microsaccade amplitude limits of 2, 0.33, and 0.2 deg. Overall, the pattern of results was similar for all 3 amplitude limits, with the modulation effects decreasing in magnitude for smaller microsaccades. However, a specific dependency on microsaccade amplitude limits was found for reappearance, as the peak that typically occurred \(\approx 500\) ms before reappearance was almost invisible for the smallest microsaccade amplitude limit. This suggests that reappearance was primarily triggered by larger microsaccades or small saccades.

The pattern of results did not depend on the choice of microsaccade detection algorithm (Figure 5c). We obtained similar results using a simple quantification of the total drift or retinal slip (including microsaccades), taking the horizontal/vertical position range within a sliding window of 150 ms (see Methods section). The data for the total horizontal drift alone were very similar, while the data for the total vertical drift alone showed a very similar shape except for a missing peak at 500 ms before reappearance in the MIB condition (see Supplementary Figure S3). We note that the vast majority of microsaccades were roughly horizontal, consistent with previous findings (Liang et al., 2005).

We conclude that the event-related modulation of eye movements measured in our experiment is robust, largely independent of the choice of parameters and algorithms. The total drift calculation, which we presented here for the first time, is particularly simple and robust and may be useful for future studies (Figure 6).

A simple model helps understand the role of microsaccades in MIB

The results of Experiment 2 showed that the microsaccade rate decreased prior to disappearance and increased prior to reappearance reports. However, is this effect due to the moving mask that somehow altered the pattern of microsaccades in the presence of a target, or is it the outcome of the known tendency for transients to prevent or terminate fading regardless of a specific configuration? To address this issue, we developed a simple Poisson model of the perceptual transitions in MIB that incorporates a weak probabilistic form of a modulatory relation between microsaccades and disappearance. The model receives a time series of microsaccades and simulates the perceptual transitions to produce an artificial observer's perceptual reports, which are then used to extract event-related microsaccade rate time courses (see Methods section). Using the model with microsaccade data collected during passive fixation in the absence of the mask allowed us to examine the role of the mask in modulating the microsaccades and producing the observed pattern of results. The model details and simulation results appear in Figure 7. Overall, model results are remarkably similar to the experimental data, including the tonic
difference between visible and invisible states, the increase in microsaccade rate ~0.5 s before reappearance, and the decrease 0.5 s before disappearance. As expected, the model does not account for the microsaccade rate changes in response to the perceptual transition, i.e., the wave-shape pattern that normally follows any perceptual transient (marked by arrows in Figure 7b). The stronger and longer reduction in the experimental data during offsets (see “magenta” vs. “red” curves) could also reflect microsaccade inhibition in response to a perceptual event.

The model accounts well for the microsaccade rate changes prior to the perceptual transition, by specifying the non-deterministic effect of microsaccades on these transitions. The probability for reappearance/disappearance to occur spontaneously after 0.5 s of invisibility/visibility (respectively) in the model was calculated to be 0.33, while 0.5 s after a microsaccade, these probabilities changed to 0.7 for reappearance and 0.25 for disappearance. This shows that the effect of microsaccades on disappearance in the model is relatively small (decrease...
from 0.33 to 0.25), while their effect on reappearance is much larger (increase from 0.33 to 0.7). Most importantly, within this short time window of 0.5 s, microsaccades do not necessarily cause reappearance ($p = 0.7 < 1$) and do not prevent disappearance ($p = 0.25 > 0$), thus invisibility cannot be explained by extended retinal stabilization. Microsaccades are assumed to modulate the Poisson process via a multiplicative process thus having a smaller effect when the base rate is reduced, such as in the absence of the mask. The critical role of the stimulus (mask) in the visibility modulation, which corresponds to the basic (unmodulated) Poisson process in the model, remains unexplained.

Discussion

We investigated the properties of microsaccades under conditions of MIB, exploring their possible role in causing or modulating visual disappearance. We discuss below several aspects of the results and their theoretical implications.

An oculomotor response to illusory perceptual transitions

Our results suggest that the oculomotor system generating microsaccades responds to intrinsic, illusory perceptual transitions in a similar fashion as to physical perceptual transitions. First, we found that physical disappearance/reappearance caused a stereotypical change in microsaccade rate, consistent with other studies on microsaccades reacting to stimulus onsets (Valsecchi, Betta, & Turatto, 2007). This stereotypical response was likely to reflect the perceptual transition and not the report itself since time locking to the stimulus did not alter the response (Supplementary Figure S2) and since a similar response occurred with and without reporting (2 observers in a Replay condition, data not shown). Second, we observed a very similar stereotypical change in microsaccade rate during illusory reappearance in MIB compared to Replay (Figure 3, compare “mib on” and “rep on,” green and blue curves). A somewhat similar stereotypical response could also be observed during disappearance, but it was much smaller perhaps because the baseline rate was attenuated and the rebound part of the response had thus a smaller dynamic range. Third, the Poisson model that accounted well for most of the experimental results, including the tonic difference between visible and invisible states and the modulation of microsaccade rate prior to the perceptual transitions, did not account for the modulation that followed the perceptual transitions, which thus appears to reflect the stereotypical response of the microsaccade system to perceptual transients, real or illusory (Figure 7). We conclude that the microsaccade system reacts to changes in visibility and that it is the perceptual transients, rather than the stimulus transients per se that trigger the stereotyped response. This conclusion may seem surprising in light of the involuntary
Figure 7. A Poisson model of MIB that incorporates the effect of microsaccades on perceptual transitions. (a) A schematic illustration of the model. The model receives a time series of microsaccades collected during passive fixation without a mask (upper left box). It simulates the perceptual transitions with a Poisson process whose probability parameter is altered by the onsets of microsaccades (upper right box). A microsaccade is assumed to increase probability for a switch when the MIB target is invisible (upper right box, bottom panel) and to decrease probability of a switch when it is visible (upper panel, different scale). This change in switch probability decays within 0.5 s following each microsaccade. The output of this process is a series of reports of a simulated observer that mimics human observers with a typical distribution of invisibility periods and durations (bottom right box). The series of reports is then applied to the original microsaccade time series to produce the event-related microsaccade rate curves assuming 450-ms response times (bottom left box). (b) Simulation results (solid curves) repeated several times to produce over 1000 epochs of each condition. Blue, reappearance (“on”). Red, disappearance (“off”). Error bars indicate SEM across simulated epochs. Dashed curves show the experimental results (similar to Figure 3, but averaged across all epochs of all observers) superimposed for comparison.
nature of microsaccades, but it is consistent with a
growing body of evidence linking microsaccades to higher
level visual processes such as selective attention and
visibility (Pastukhov & Braun, 2010; Valsecchi et al.,
2007).

Similar findings of an oculomotor modulation related to
illusory transitions were reported for binocular rivalry
(van Dam & van Ee, 2006) and MIB (Hsieh & Tse, 2009).
This previous MIB study showed a similar reduction in
microsaccade rate before disappearance and increase
before reappearance, but with less temporal precision,
and without the critical comparison to physical transitions
shown here in the Replay control condition. Another
related study measured the microsaccades following the
onset of a surround mask in a generalized flash suppression
(GFS) protocol in monkeys (Cui, Wilke, Logothetis,
Leopold, & Liang, 2009). In this study, the perceptual
event was neither illusory nor spontaneous as in our case,
but the microsaccade rate for illusory disappearance
following mask onset showed a slow recovery similar to
our data on disappearance (Figure 3a, “mib off” condition).

Microsaccades modulate MIB but are neither
necessary nor sufficient to account for it

Our results indicate that microsaccades tend to counter-
act visual fading in MIB and terminate invisibility
periods, albeit not necessarily. This could be concluded
from the reappearance pattern of the microsaccade rate in
Experiment 2 (Figure 3a, “mib on” condition), where a
high rate was found ~0.5 s before the reappearance
report. These results and conclusion are consistent with a
study on microsaccades during Troxler fading (Martinez-
Conde et al., 2006). However, microsaccades seem neither
necessary nor sufficient for causing reappearance. First,
one of our observers did not show any significant increase
in microsaccade rate prior to reappearance (see Figure 4a,
red curve). Second, microsaccades were found well within
the invisibility periods when long periods (>4 s) were
investigated (see Results section). Since any visual transient
(stimulus-driven or generated by retinal image
shifts due to microsaccades) is known to induce reappearance
of a faded image (e.g., see Collewijn & Kowler,
2008), this role of microsaccades in terminating perceptual
suppression is hardly surprising.

The central question is whether the microsaccades
instigate the enigmatic process leading to target disap-
ppearance in MIB, or whether they play a secondary,
modulatory role. In our second experiment, we found that
the microsaccade rate changed in relation to the visibility
of the target and was specifically low for an invisible
target starting ~0.5 s prior to the disappearance report.
Using a simple Poisson model of the perceptual transitions
(based on microsaccade time courses measured in the
absence of the mask), we show that these results can be
explained by a modulatory effect of microsaccades on the
disappearance/reappearance probability, while the process
culminating in disappearance is instigated by an inde-
pendent factor that we presume is triggered by the
presence of the moving mask. This conclusion is in
perfect agreement with the data from the first experiment,
which revealed no interaction between the mask and the
pattern of microsaccades (the moving mask does not alter
microsaccades during passive viewing without a target).
The conclusion is also corroborated by two previous
findings. First, two separate patterns such as orthogonal
peripheral patches tend to disappear in alternation (Bonneh
et al., 2001), which implies an impossible dual role for
microsaccades to suppress one pattern and revive the other
at roughly the same time. Second, disappearance in MIB
is accompanied by small target-specific modulation of fMRI responses in human V1 but robust suppression in
extrastriate area V4 with opposite modulations in the
dorsal visual pathway (Donner et al., 2008). Again, this
suggests that the perceptual suppression that involves
representations of the moving mask has cortical origin.

The disappearance in MIB can be further illuminated by
comparing MIB with Troxler fading. Our results seem
consistent with Martinez-Conde et al. (2006) in clearly
establishing a counter-fading effect of microsaccades.
Martinez-Conde et al. (2006) further suggested that
Troxler fading occurs when microsaccades are sponta-
nearously suppressed because receptive fields in the periph-
ery could be considerably larger than the amplitudes of
drifts and tremor, which are thus ineffective in prevent-
ing fading of low-contrast stimuli. This is unlikely the
case in MIB, which occurs even for high-contrast stimuli
(sometimes even more strongly than for low-contrast
stimuli) as close as 1 deg off fixation (Bonneh et al.,
2001). Moreover, our results do not provide evidence for
a stabilization period during which microsaccades were
suppressed, which would have allowed for neuronal
adaptation and consequent perceptual fading. The micro-
saccade rate was reduced just a few hundred milliseconds
before observers’ disappearance reports, an order of magni-
tude shorter than the latencies described in studies of
perceptual fading, such as few seconds in Riggs et al.’s
(1953) study of stabilized images, or 2 s in a more recent
study of induced image fading (Simons et al., 2006). Thus,
MIB seems to differ from Troxler fading with respect to the
mechanism underlying disappearance and specifically with
respect to the moving mask; we showed that the critical
role of the moving mask in inducing disappearance does
not involve microsaccades and thus remains to be found.

Finally, it has been suggested that microsaccades are
triggered dynamically to counteract a reduction in retinal
image slip and perhaps even a reduction in cortical
activation (Engbert & Mergenthaler, 2006). If motion
disrupts the dynamic triggering of microsaccades in MIB,
it may prevent microsaccades from counteracting retinal
and cortical adaptation and thus cause disappearance.
Although our results cannot be used to rule out this
possibility, we find it unlikely because of the evidence
against a closed-loop feedback control of microsaccades: Microsaccades were found to be paradoxically less frequent when an image was stabilized and faded (Cornsweet, 1956, see also Poletti & Rucci, 2007). In addition, as noted above, microsaccades are a global mechanism, while disappearance occurs locally and largely independently across space.

We have shown that microsaccades modulate target disappearance and reappearance during MIB, as they do for several other bistable visual illusions. However, our current (and previous) results strongly suggest that MIB is instigated by a central mechanism, strongly influenced by the moving mask, rather than by a reduction of visual transients due to a spontaneous reduction in microsaccades. We conclude that microsaccades counteract visual fading and contribute in absence to disappearance but are neither necessary nor sufficient to account for motion-induced blindness.

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