

Motion-induced blindness and microsaccades: Cause and effect

Yoram S. Bonneh

Department of Human Biology, University of Haifa,
Mt. Carmel, Israel, &
Department of Neurobiology, Brain Research,
Weizmann Institute of Science, Rehovot, Israel



Tobias H. Donner

Department of Psychology, University of Amsterdam,
Amsterdam, The Netherlands, &
Department of Psychology and Center for Neural Science,
New York University, New York, NY, USA



Dov Sagi

Department of Neurobiology, Brain Research,
Weizmann Institute of Science, Rehovot, Israel



Moshe Fried

Goldschleger Eye Research Institute, Tel-Aviv University,
Sheba Medical Center, Tel Hashomer, Israel



Alexander Cooperman

Department of Neurobiology, Brain Research,
Weizmann Institute of Science, Rehovot, Israel



David J. Heeger

Department of Psychology and Center for Neural Science,
New York University, New York, NY, USA



Amos Arieli

Department of Neurobiology, Brain Research,
Weizmann Institute of Science, Rehovot, Israel



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

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Introduction

When a global moving pattern surrounds a high-contrast stationary or slowly moving target stimulus, the target disappears and reappears alternately for durations of

several seconds, a phenomenon called “motion-induced blindness” (MIB; Bonneh, Cooperman, & Sagi, 2001). MIB belongs to a class of “visual disappearance” phenomena, in which otherwise salient visible stimuli disappear explicitly from awareness, as if erased in front of the observer’s eyes. These include binocular rivalry

(Blake & Logothetis, 2002), “generalized flash suppression” (Wilke, Logothetis, & Leopold, 2003), artificial scotoma (Ramachandran & Gregory, 1991), Troxler fading (Troxler, 1804), and the related “scene fading” effect (Simons et al., 2006). The interest in MIB and the other disappearance effects stems from the all-or-none and explicit nature of the illusory disappearance in the face of constant physical stimulation, which could be useful for identifying the neural correlates of consciousness (Koch, 2007) and the intrinsic mechanisms underlying perceptual organization (Blake & Logothetis, 2002; Kim & Blake, 2005).

MIB is not solely determined by low-level sensory 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 ($\sigma = \lambda$), 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

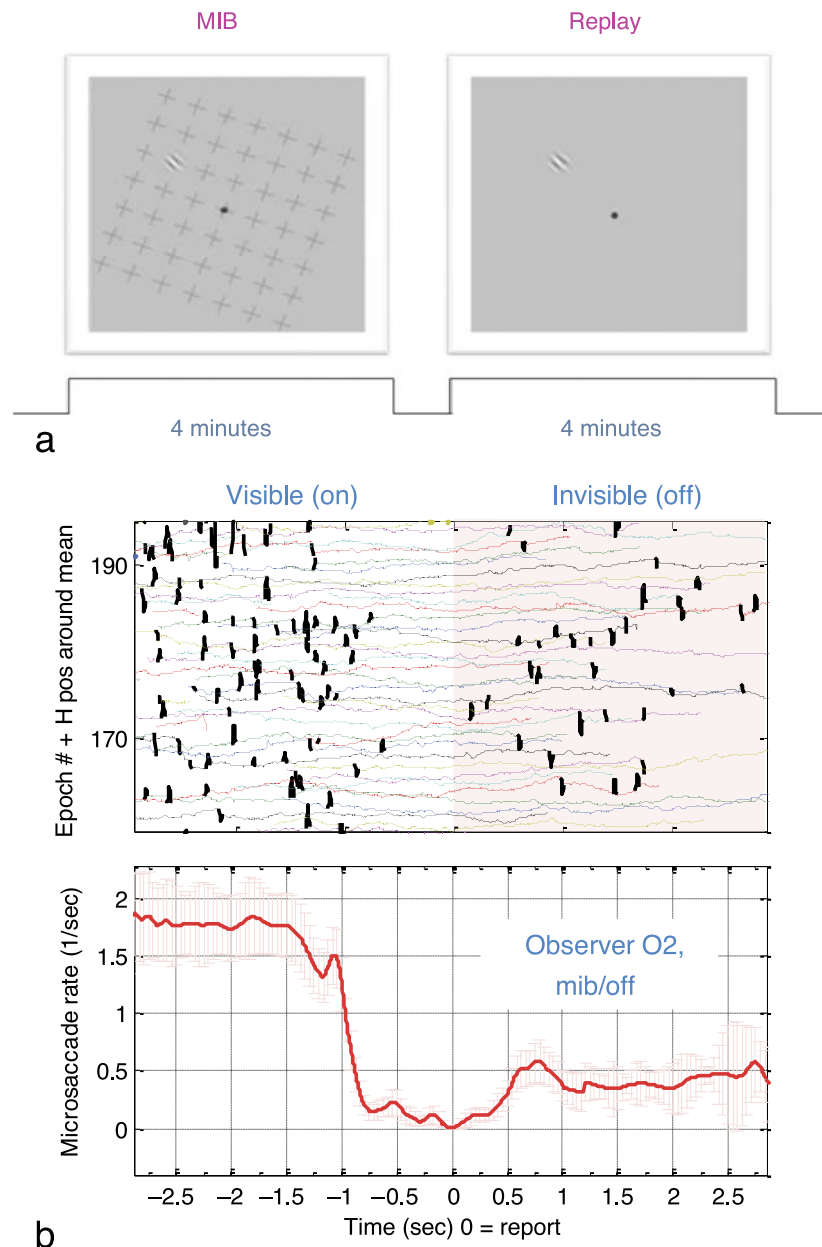


Figure 1. Experimental methods and data analysis. (a) Schematic illustration of MIB. In Experiment 2, observers viewed a 4-min MIB display (left) while reporting disappearance and reappearance with a button press. The observers then repeated the same task while viewing a 4-min “replay” of physical disappearance 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).

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.

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 ($\sigma = 0.5$ 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 ($\sigma = 0.5$ 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

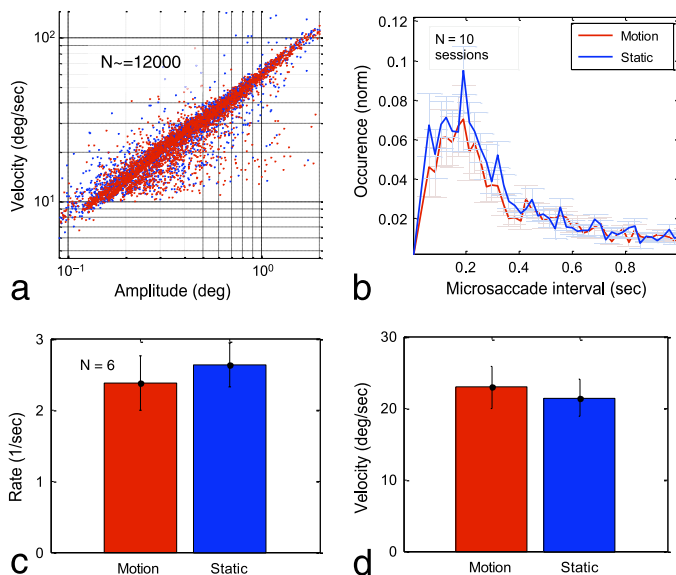


Figure 2. The effect of motion on the rate and temporal distribution of microsaccades (Experiment 1). Observers viewed passively a rotating mask (“motion” condition) or a fixation point (“static” condition). (a) Maximal speed vs. amplitude of over 12,000 microsaccades measured for 6 observers. Red and blue dots correspond to microsaccades in the “motion” and “static” conditions, respectively. The plot is used to validate the quality of microsaccade detection, showing the typical overlapping log–log linear relation for both conditions. (b) The distribution of inter-microsaccade intervals plotted as normalized occurrence histogram for the two conditions averaged across 10 mini-sessions (1–2 mini-sessions per observer for each of 6 observers). Error bars denote *SEM* ($N = 10$). Some observers showed fewer occurrences of short intervals in the motion condition, but this effect was not significant for the group. Group averages of (c) microsaccade rate and (d) microsaccade maximal velocity for the two conditions. The microsaccade rate for the motion condition (2.37/s) was slightly lower than the rate for the static condition (2.62/s), though this difference was not statistically significant.

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.

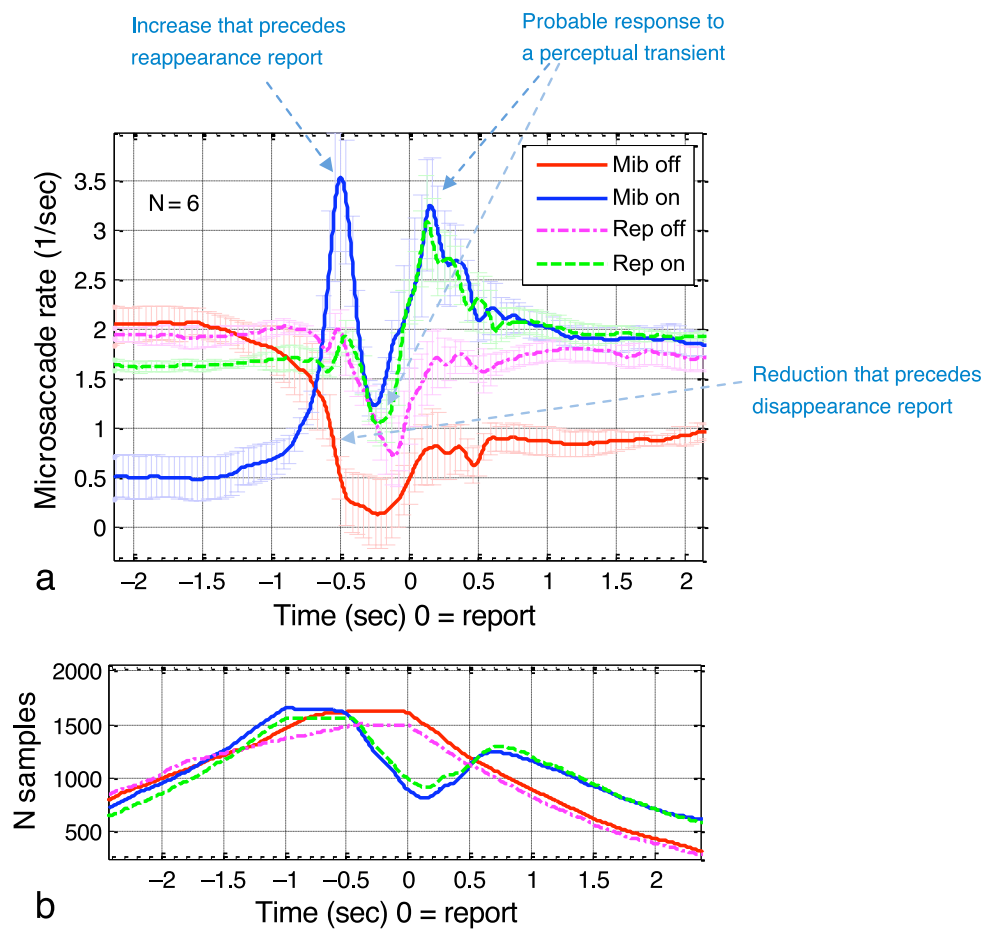


Figure 3. Eye movements during MIB and replay (Experiment 2). (a) Event-related modulations of microsaccade rate for each of the four conditions: MIB and Replay (rep), reappearance (on), and disappearance (off). Data were averaged across epochs within observer, normalized per observer and then averaged 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.

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, ~ 50 ms delay for MIB), we estimated MIB response latency to be ~ 450 ms for reappearance. The analogous estimate of ~ 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 ~ 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 small saccades. We investigated the dependency of our results on the choice of microsaccade amplitude limit and algorithm. The results appear in

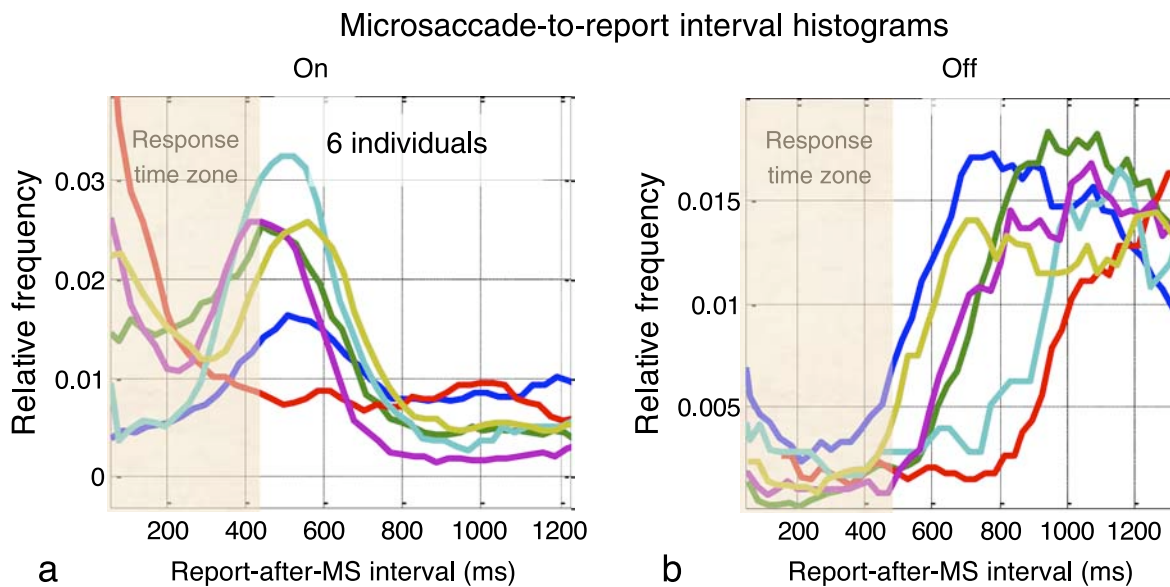


Figure 4. The dependence of MIB reappearance and disappearance on the time interval since the preceding microsaccade. (a) Reappearance (“on”). (b) Disappearance (“off”). Intervals were obtained from all epochs of the MIB condition for each observer and were used to compute normalized histograms (dividing by the total count). Colors correspond to different observers. Shaded regions denote an interval equivalent to 450 ms (the approximate response time) prior to report. Note, however, that although report occurs with a delay of approximately 450 ms, disappearance (b) may occur a short time after a microsaccade for some observers (e.g., dark blue trace, within 400 ms) while for other observers the time interval can be as long as 700 ms (e.g., red curve). Note also that the reappearance report (a) occurs typically about 500 ms following a microsaccade (red is the only exception), which implies a high probability for occurrence immediately after a microsaccade assuming ~ 450 ms response time.

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 ~ 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

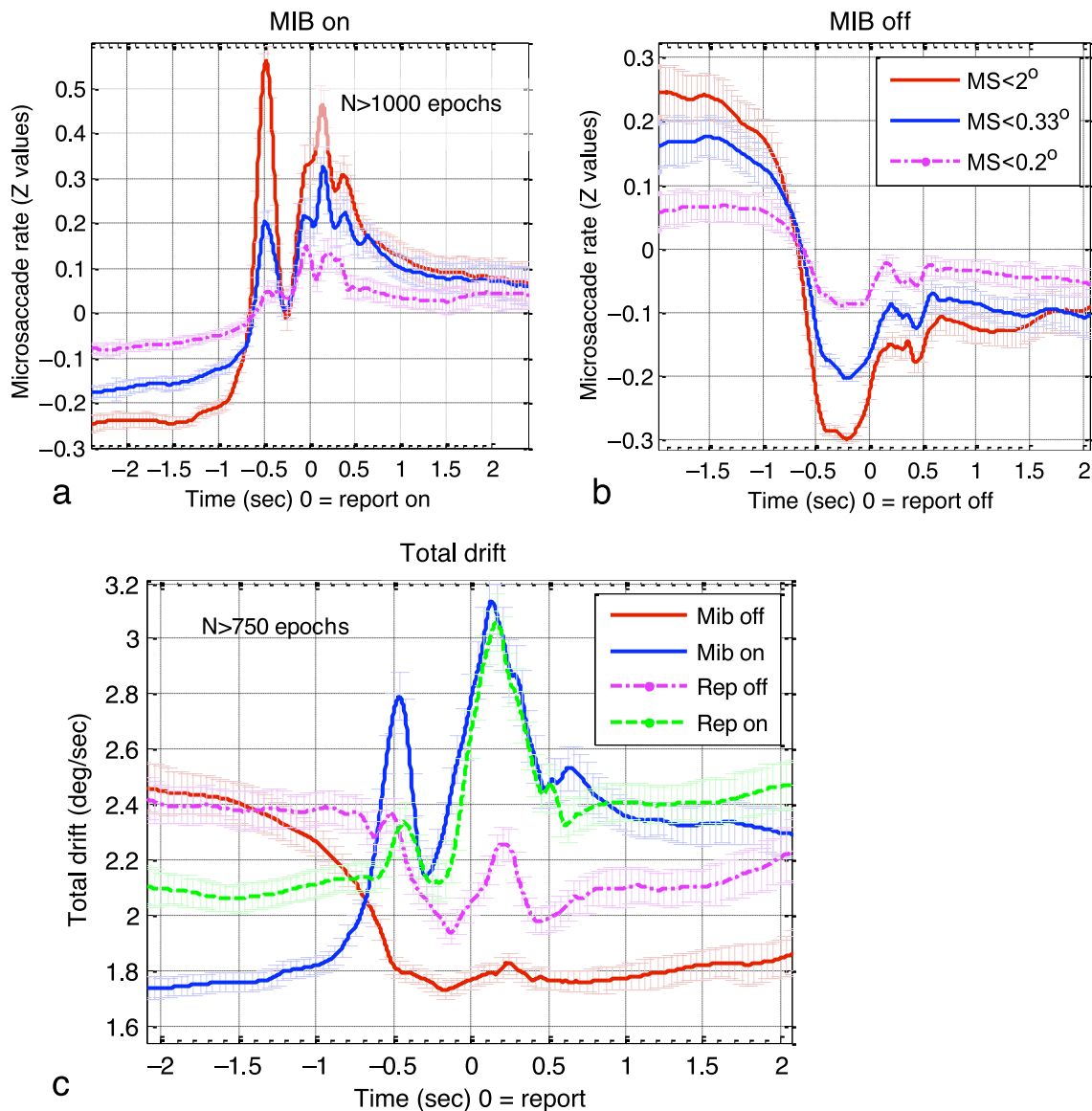


Figure 5. Comparison of methods for detecting and quantifying fixational eye movements (Experiment 2). (a, b) Event-related microsaccade rate time courses were computed for three microsaccade amplitude limits: 2 deg (standard), 0.33 deg (20'), and 0.2 deg (12'). (a) Reappearance (“on”). (b) Disappearance (“off”). The baseline microsaccade rates are similar for all three, although the peak prior to reappearance is smaller with smaller amplitude limits. (c) An alternative quantification of the fixational eye movements via a measure of the total drift (or retinal slip), including microsaccades. This measure yielded similar results to those obtained with the event-related microsaccade rate analysis but with a somewhat different weighting for the different effects. All visible effects are highly significant, including the tonic difference between Replay “on” and “off.” In all three plots, data were averaged per condition and event type across all epochs from all observers, yielding a variable number of samples per point. Error bars indicate *SEM* across epochs ($N > 750$), down-sampled for clarity.

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

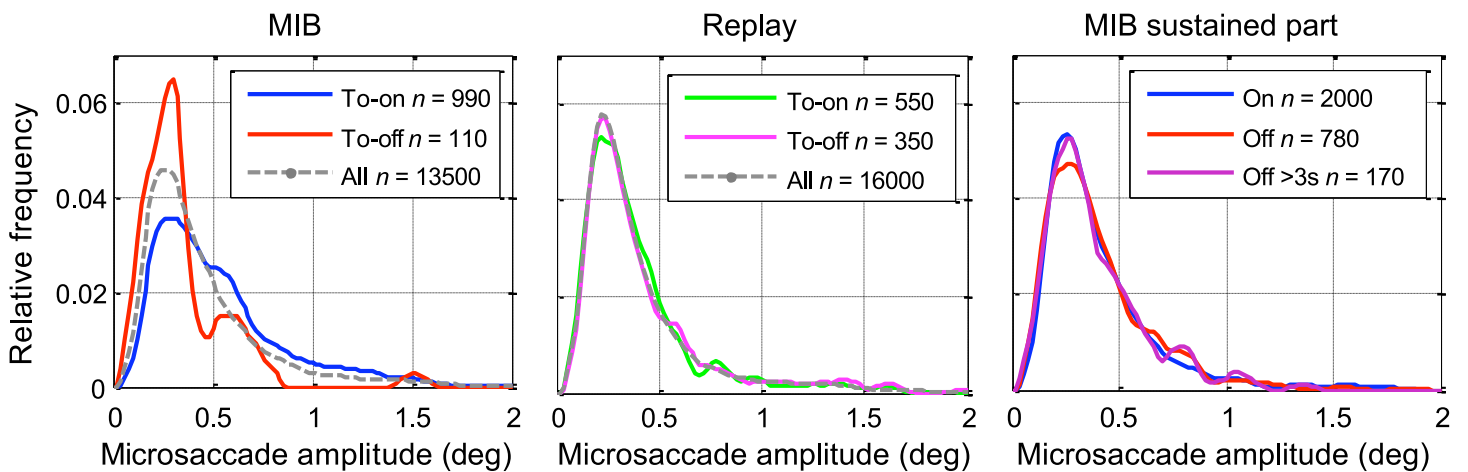


Figure 6. Relation between microsaccade amplitude (displacement) and the perceptual state and transitions. Microsaccade amplitude histograms were compiled across observers for different time windows and conditions. (a) The amplitude of microsaccades in a time window of ± 0.1 s around 0.5 s prior to report of either reappearance (blue, “on”) or disappearance (red, “off”) in comparison to the amplitude of microsaccades during the whole epoch period (dashed gray). Note the higher occurrence of larger microsaccades for reappearance (blue trace; smaller peak and longer tail) and shorter microsaccades for disappearance (red trace; larger peak and shorter tail). (b) The same for the Replay data showing no significant difference between the different transitions. (c) Comparison of the sustained states in MIB more than 1 s away from transition. There is no significant difference in microsaccade amplitude between the visible (blue, “on”) and invisible (red, “off”) conditions. Data selected for epochs longer than 3 s (purple, off >3) demonstrate the occurrence of typical size microsaccades well within the invisibility period.

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

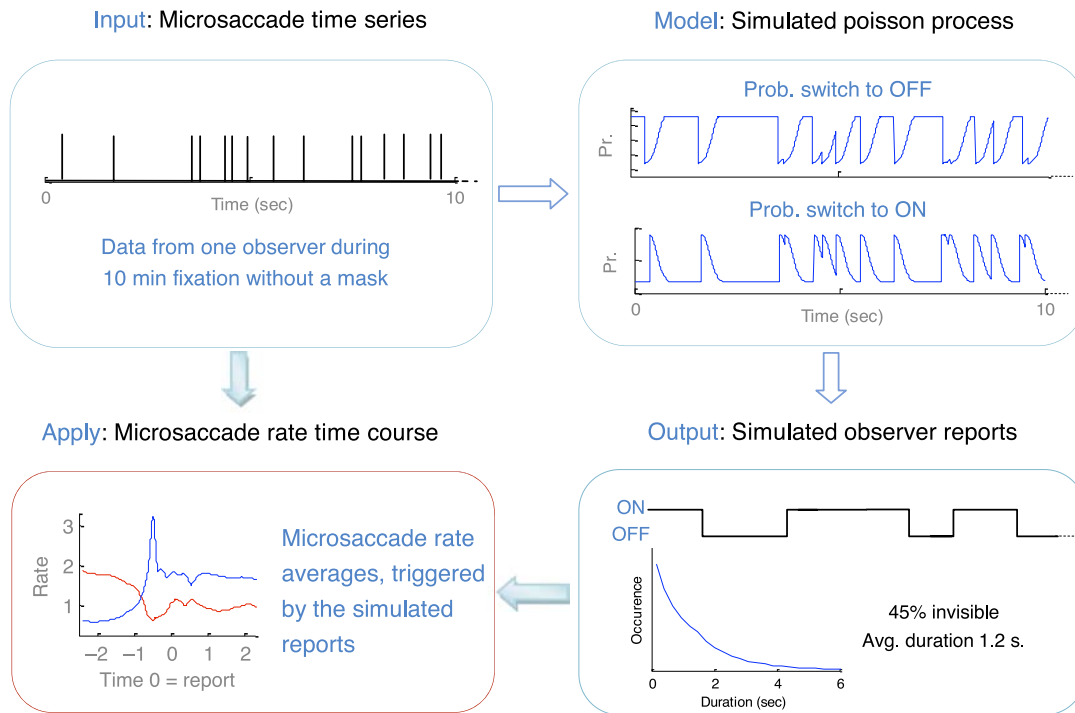
We investigated the properties of microsaccades under conditions of MIB, exploring their possible role in causing or modulating visual disappearance. We discuss below several aspects of the results and their theoretical implications.

An oculomotor response to illusory perceptual transitions

Our results suggest that the oculomotor system generating microsaccades responds to intrinsic, illusory perceptual

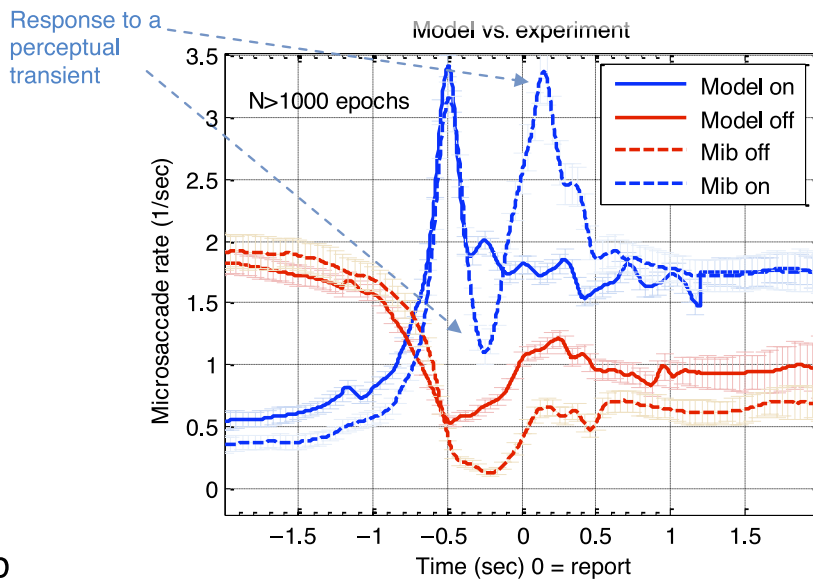
transitions in a similar fashion as to physical perceptual transitions. First, we found that physical disappearance/reappearance caused a stereotypical change in microsaccade rate, consistent with other studies on microsaccades reacting to stimulus onsets (Valsecchi, Betta, & Turatto, 2007). This stereotypical 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

Schematic illustration of the model



a

Model simulation results



b

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 counteract 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 disappearance 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 independent 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 spontaneously suppressed because receptive fields in the periphery could be considerably larger than the amplitudes of drifts and tremor, which are thus ineffective in preventing 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 microsaccade rate was reduced just a few hundred milliseconds before observers' disappearance reports, an order of magnitude 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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Corresponding author: Yoram S. Bonneh.

Email: yoram.bonneh@gmail.com.

Address: Department of Human Biology, University of Haifa, Mt. Carmel 31905, Israel.

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