Title: Different fixational eye movements mediate the prevention and the reversal of visual fading

Running title: Fading prevention by fixational eye movements

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Key points summary:

- Fixational eye movements (microsaccades, drift, and tremor) are thought to improve visibility during fixation by thwarting neural adaptation to unchanging stimuli, but how the different fixational eye movements influence this process is a matter of debate.
- Prior studies confounded the reversal of fading (where vision is restored after fading) with its prevention (where fading is blocked before it happens). We found that, whereas microsaccades are most important to reversing fading, both microsaccades and drift help to prevent it.

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- Drift's contribution to preventing fading is potentially larger than that of microsaccades, but microsaccades prevent fading with higher efficacy than drift.

- Microsaccades prevent foveal and peripheral fading in an equivalent fashion, and microsaccadic efficacy does not depend on microsaccade size, number, or direction. Further, faster drift may prevent fading better than slower drift

- These combined findings help reconcile the long-standing controversy concerning the roles of microsaccades and drift in visibility during fixation

ABSTRACT

Fixational eye movements (FEMs; including microsaccades, drift and tremor) are thought to improve visibility during fixation by thwarting neural adaptation to unchanging stimuli, but how the different FEM types influence this process is a matter of debate. Attempts to answer this question have been hampered by the failure to distinguish between the prevention of fading (where fading is blocked before it happens in the first place) and the reversal of fading (where vision is restored after fading has already occurred). Because fading during fixation is a detriment to clear vision, the prevention of fading --which avoids visual degradation before it happens-- is a more desirable scenario than improving visibility after fading has occurred. Yet, previous studies have not examined the role of FEMs in the prevention of fading, but have focused on visual restoration instead. Here we set out to determine the differential contributions and efficacies of microsaccades and drift to preventing fading in human vision. Our results indicate that both microsaccades and drift mediate the prevention of visual fading. We also found that drift is a potentially larger contributor to preventing fading than microsaccades, although microsaccades are more effective than drift. Microsaccades moreover prevented foveal and peripheral fading in an equivalent fashion, and their efficacy was independent of their size, number, and direction. Our data also suggest that faster drift may prevent fading better than slower drift. These findings may help to reconcile the long-standing controversy concerning the comparative roles of microsaccades and drift in visibility during fixation.

INTRODUCTION

When eye movements are eliminated, stationary or unchanging objects fade from perception (Ditchburn and Ginsborg, 1952; Riggs and Ratliff, 1952 p.52; Yarbus, 1957). Outside of the laboratory, our eyes are never still, however: even when we attempt to fixate our gaze on an object of interest, small ocular motions, called fixational eye movements (FEMs: including microsaccades, drift and tremor) shift our eye position. FEMs are thought to help visibility during fixation by thwarting neural adaptation to unchanging stimuli (Martinez-Conde et al., 2004, 2013; Engbert and Mergenthaler, 2006), but how the different FEM types influence this process is a matter of debate. Attempts to answer this question have been hampered by the failure to distinguish between the prevention of fading (where fading is blocked *before* it happens in the first place) and the reversal of fading (where vision is restored *after* fading has already occurred). There has been a relative dearth of research to specify the oculomotor mechanisms underlying the prevention of fading.

Because fading during fixation is a detriment to clear vision, the prevention of fading --which avoids visual degradation before it happens during fading-- is a more desirable scenario than improving visibility after fading has occurred. Thus, determining how the different eye movement types prevent fading is more important than establishing how they restore visibility once fading has taken place. Yet, previous studies have not examined the role of FEMs in the prevention of fading , but have focused on restoration instead (Martinez-Conde et al., 2006; Troncoso et al., 2008; McCamy et al., 2012; Costela et al., 2013). It follows that no research to date has determined the differential effects of each individual FEM type on fading prevention, as we now do here. Recently, we developed a principled quantitative method to determine the contribution and efficacy of microsaccades and other eye movements to reversing fading during fixation (McCamy et al., 2012). Here we have enhanced the method to determine the differential contributions and efficacies of microsaccades and drift to *preventing* fading.

Our results indicate that both microsaccades and drift work to prevent fading. We also found that drift is a potentially larger contributor to fading prevention than microsaccades, although microsaccades are more effective than drift. Microsaccades moreover prevented foveal and peripheral fading in an equivalent fashion, and their efficacy was independent of their size, number, and direction. Our data also suggest that faster drift may prevent fading better than slower drift. These findings may help to reconcile the long-standing controversy concerning the comparative roles of microsaccades and drift in visibility during fixation.

METHODS

Ethics statement

Experiments were approved by the Barrow Neurological Institute Institutional Review Board (protocol number 04BN039) and conformed to the Declaration of Helsinki. Written informed consent was obtained from each participant.

Subjects

Seven subjects (5 males) with normal or corrected-to-normal vision participated in the experiments. Six subjects were naive and were paid $15/session. For one subject, 2 experimental sessions were discarded due to pupil occlusion (which made the data too noisy for accurate microsaccade detection). Three other subjects lost 5 or less trials of data, out of 256 trials, due to pupil occlusion (the eye position was lost by the eye tracker); these data losses did not significantly affect the results.

Experimental design

Subjects rested their forehead and chin on the EyeLink 1000 head/chin support ~57 cm away from a linearized video monitor (Barco Reference Calibrator V, 75 Hz refresh rate). The experiment consisted of 5 ~ 1-1.5 hours sessions, each including 64 randomly interleaved trials. The first session was counted as a training session and not included in the analyses.

Illusory fading condition. While fixating a small red spot (with a diameter of 0.05 degrees of visual angle (deg)) on the center of the screen, subjects continuously reported whether a stimulus was faded/fading (button press) or intensified/intensifying (button release) (Martinez-Conde et al., 2006) (**Fig. 1*A***). To start the trial, subjects pressed a key and the stimulus appeared on the screen. The stimulus was a two-lobe Gabor patch with a peak-to-trough width of 2.5 deg (Gaussian standard deviations of x = 1.5 deg and y = 1 deg; sine wave period of 5 deg; sine wave phase of 0 deg). The Gabor had a maximum contrast of 40% from peak-to-trough and the same average luminance (50%) as the background. The Gabor was presented at random eccentricities of 0 deg, 3 deg, 6 deg, 9 deg (measured from the center of the fixation point to the center of the Gabor). The position of the Gabor varied randomly across trials at one of the eight points of the compass, to control for possible contrast adaptation effects across trials. The orientation of the Gabor also varied randomly between 0º

(here, ° represents circular angle) and 360º in each trial, to control for orientation adaptation effects. After 30 seconds, the stimuli disappeared and the trial ended. To disregard the potential effect of the initial stimulus onset transient at the start of each trial, we conducted analyses only on data recorded after the first second of the trial. A minimum average of 2 transitions per 30 second trial was imposed to ensure that the subjects experienced the illusion; one subject was discontinued after the training session due to this restriction.

Real fading condition. Experimental details were as in the Illusory fading condition; however, the Gabor now *physically* faded and intensified (**Fig. 1*B***). The Gabor always started at 40% contrast. Then, according to the times of transitions reported by the subject in prior randomly chosen Illusory fading trials, the Gabor faded/intensified in step fashion to a lower/higher contrast randomly chosen from the set: 0%, 10%, 20%, 30%, 40%. To avoid perceptual transitions due to illusory fading which might interfere with the physical transitions, the Gabor moved at a constant speed (0.1 cycles/s) in a circular path of 1.25 deg radius. The parameters for the movement of the Gabor were the minimal values found to make the Gabor continuously visible at any given contrast.

Subjects performed this task well (95 ± 15% of real fadings detected; 97 ± 16% of reports of real fading were hits), and their reaction times provided tight estimates of reaction times in the Illusory fading condition, necessary for the contribution and efficacy analyses (**Fig. 3**). The data from the Real fading trials were not otherwise subjected to additional analyses.

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Eye movement analyses

Microsaccade and blink detection. Eye position was acquired noninvasively with a fast video-based eye tracker at 500 Hz (EyeLink 1000, SR Research). EyeLink 1000 records eye movements simultaneously in both eyes (instrument noise 0.01 deg RMS). We identified and removed blink periods as portions of the raw data where pupil information was missing. We also removed portions of data where very fast decreases and increases in pupil area occurred (> 50 units/sample, such periods are probably semi-blinks where the pupil is never fully occluded) (Troncoso et al., 2008). We added 200 ms before and after each blink/semi-blink to eliminate the initial and final parts where the pupil was still partially occluded (Troncoso et al., 2008). Saccades were identified with a modified version of the algorithm

developed by Engbert & Kliegl (Engbert and Kliegl, 2003; Laubrock et al., 2005; Engbert, 2006; Engbert and Mergenthaler, 2006; Rolfs et al., 2006) with $\lambda = 4$ (used to obtain the velocity threshold) and a minimum saccadic duration of 6 ms. To reduce the amount of potential noise, we considered only binocular saccades, that is, saccades with a minimum overlap of one data sample in both eyes (Laubrock et al., 2005; Engbert, 2006; Engbert and Mergenthaler, 2006; Rolfs et al., 2006).

Some saccades are followed by a fast and small saccadic eye movement in the opposite direction, called dynamic overshoot, which is often more prominent in the eye that moves in the abducting direction (Kapoula et al., 1986). Unlike the return saccade in a square-wave jerk, a dynamic overshoot follows a saccade with very short latency between the two movements. We identified dynamic overshoots as saccades that occurred less than 20 ms after a preceding saccade (Møller et al., 2002) and we did not regard them as new saccades. Instead, we added the duration of the overshoot into the duration of the saccade, thus considering it part of the saccade. Microsaccades were defined as saccades with magnitude < 1 deg in each eye (Martinez-Conde et al., 2004). To calculate (micro)saccade properties such as magnitude and peak velocity we averaged the values for the right and left eyes. The mean of the median intersaccadic interval (including saccades and microsaccades) across subjects was 285 ms (± 27 s.e.m.).

Drift periods. Drift periods were defined as the eye-position epochs between (micro)saccades and blinks. We removed 10 ms from the start and end of each of these epochs (because of imperfect detection of blinks and (micro)saccades), and we filtered the remaining eye-position data with a low-pass Butterworth filter of order 13 and a cut-off frequency of 30 Hz (Di Stasi et al., 2013). Because drifts are not generally conjugate (Krauskopf et al., 1960; Yarbus, 1967; Martinez-Conde et al., 2004), we used data from both the left and right eye. For instance, any given drift period had a unique maximum (mean, standard deviation) drift speed for each eye. The values reported in **Figs. 6-7** were found by averaging all data from both eyes. The average duration of drifts across subjects was 1.11 s (± 0.19 s.e.m.). The mean maximum drift duration across subjects was 11.24 s (± 1.40 s.e.m.).

Removing filter edge effects. Before calculating drift properties (such as the mean and maximum speed), we removed an additional 34 ms from the beginning and 110 ms from the end of each drift period as defined above, to reduce edge effects due to the filter. We determined that filter edge effects caused artificial increases/decreases in drift speed before

microsaccades (**Fig. 6*A***) because we observed increases/decreases seen in the drift speed correlation with random microsaccades (**Fig. 6*B***). The values (34 and 110 ms) chosen were determined by finding when the drift speed around random microsaccades (black solid line in **Fig. 6*B***) was first within 5% of the average drift speed (dotted horizontal line **Fig. 6*B***). This choice resulted in a flat correlation of drift speed with random microsaccades; thus it removed any detectable edge effects (**Fig. 6*D***). The removal of the edge effects due to the filter was especially important in our analyses because microsaccade rates differ between the two regions compared in **Fig.** 7. If filter edge effects had remained, we would have obtained artificial results because the increased numbers of microsaccades would have resulted in more instances of higher drift speeds. Finally, because we had to remove 144 ms from each drift's duration (34 ms from the beginning and 110 ms from the end), drifts shorter than 300 ms were not analyzed in **Fig. 7*A***.

Removing post-saccadic drift effects. After we removed the edge effects due to the filter, we still observed increases in drift speed after microsaccades (**Fig. 6*C***). These are real increases as opposed to artificial ones caused by the filter because these increases are not seen for the correlation with random microsaccades (**Fig. 6*D***). This agrees with recent research reporting increased post-saccadic drift (Chen and Hafed, 2013). To analyze drift properties without the effects of post-saccadic drift (**Fig. 7*B***), we removed 380 ms from the beginning of each drift (and still the 110 ms from the end for the filter edge effects) before calculating drift properties. This value was determined by finding where the drift speed after a microsaccade (black solid line in **Fig. 6*C***) first equaled the average drift speed (dotted horizontal line **Fig. 6*C***). The correlation of drift speed with microsaccades becomes completely flat with this choice (**Fig. 6*A***). Finally, because we had to remove 490 ms from each drift's duration (380 ms from the beginning for post-saccadic drift and 110 ms from the end for the filter edge effects), drifts shorter than 600 ms were not analyzed in **Fig. 7*B***.

<<<PLEASE INSERT FIGURE 2 AROUND HERE>>>

Contribution and efficacy

Correlograms and notation. Let X_M, X_S, X_B, and X_F denote the microsaccade, saccade, blink, and fading report (*F*) stochastic onset processes, and $X_A = X_M + X_S + X_B$ of all eye movements. Let N_* be the number of times $*$ occurs. Let $\xi_{AF}(t) = \sum_{j \in I(t)} X_A(j+t) X_F(j)$

(where $I(t)$ is as above), be the correlation of X_A with X_F, and $\tilde{\xi}_{AF}(n) = \sum_{t=wn}^{t=w(n+1)-1} \xi_{AF}(t)$ the correlogram of X_A with X_F (bin width w = 50 ms). We take the convention that $\tilde{\xi}_{AF}(n)$ refers to the bin value of $\tilde{\xi}_{AF}$ at bin n, and $\tilde{\xi}_{AF}(t)$ refers to the bin value of bin n, where $wn \leq t \leq w(n + 1) - 1$ (we adopt the same convention for any other function that is binned in time, such as B_{AF}, defined below).

Contribution and efficacy development. The concepts of contribution and efficacy have been used to measure the strength of connection between two neurons (Levick et al., 1972; Mastronarde, 1987; Aertsen et al., 1989; Reid and Alonso, 1995; Alonso et al., 1996, 2001; Usrey et al., 1998, 1999), and recently in determining the impact of microsaccades in restoring faded vision (McCamy et al., 2012). Here we are concerned with the impact of microsaccades in the prevention of fading. Thus, we include no analyses concerning the efficacy and contribution of different eye movement types to the reversal of fading (previously reported by (McCamy et al., 2012), using this dataset). The present analyses do not overlap with the previous analyses unless otherwise noted.

We defined the contribution of microsaccades to the prevention of fading, $\mathcal{C}_R(M)$, as the percentage of fading prevention reports (*R*; to be defined below) caused by microsaccades, and the efficacy of microsaccades in preventing fading, $\mathcal{E}_R(M)$, as the percentage of microsaccades which caused a prevented fading report. That is:

$$\mathcal{C}_R(M) = \frac{\text{number of } R\text{s caused by microsaccades}}{\text{total number of } R\text{s}}, \text{ and}$$

$$\mathcal{E}_R(M) = \frac{\text{number of microsaccades which caused a } R}{\text{number of microsaccades eligible to cause a } R}.$$

To calculate the contribution and efficacy of microsaccades in preventing fading, along with those of other eye movements, we estimated the number of *R*s caused by microsaccades, as well as those caused by saccades, blinks, and combinations thereof. Because we did not ask subjects (nor could we have asked them) to report when the stimulus was prevented from fading, we first had to take some steps to define what a report of fading prevention was. The most crucial step to this was to find the microsaccades (and other eye movements) that we know did not prevent fading (i.e. did not prevent an *F*). Importantly, only eye movements occurring during a specific window of time in the "intensified region" (i.e. the time in which the stimulus was reported as intensified/intensifying) did not prevent

an *F*. We call this window of time the "trough interval" because it corresponds to the trough of the correlogram between eye movements and *F*s, and we denote it by τ.

Defining the trough interval τ. We estimated τ in two steps: 1) First, we used the distribution of the subjects' reaction times to target fading in the Real fading condition (which we denote by *Frt*) to estimate the reaction times in the Illusory fading condition. We required τ to be contained within the interval $\omega_F = [-b, -a]$ (where the interval [*a*, *b*] contains 98% of the data from *Frt*, discarding the top and bottom 1%; **Fig. 3*A***); we restricted τ to be contained in ω_F because eye movements in ω_F are the only ones which did not prevent an *F*, as these are the only eye movements which occurred within the reaction times of the subject. 2) We further refined τ's limits as follows. Let $\tilde{\xi}_{AF}$ be the correlogram of all eye movement onsets (microsaccades, saccades, and blinks) with *F*s. Also, let the baseline, B_{AF}, be the expected value of $\tilde{\xi}_{AF}$ assuming that the eye movements and *F*s were independent (Mastronarde, 1987; McCamy et al., 2012) (see the "Correlogram baseline and trough interval" section below for an exact definition of the baseline; **Fig. 3*B***). We took τ as the interval of time inside of ω_F where $\tilde{\xi}_{AF}$ was below B_{AF} (Levick et al., 1972; Mastronarde, 1987; Palm et al., 1988; Aertsen et al., 1989; Alonso et al., 1996; Usrey et al., 1998, 1999; Grun, 2009; McCamy et al., 2012) and contiguous with the minimum bin closest to the *F*s (see the "Correlogram baseline and trough interval" section below for an exact definition of τ; **Fig. 3*B***). If no bin of $\tilde{\xi}_{AF}$ within ω_F was significantly below B_{AF}, we took τ as nonexistent and the contribution and efficacy as zero for that subject.

Defining prevented fading reports. Having defined τ, we defined a report of the prevention of fading (*R*) as follows. If for a given interval of time [*x*, *y*], whose duration equals τ's duration, and which is contained in the intensified region, the stimulus was not subsequently reported as fading at some point during the interval [*y*, *y* + *a*], we equated that to a subjects report, at time *t* = *y* + *a*, that the stimulus was prevented from fading. This means that any given interval with τ's duration inside of the intensified region occurring before τ satisfies this criterion. Any τ interval or any interval after τ does not satisfy this criterion by definition. We call the intensified region before τ the prevention region and denote it by $\wp$ (**Fig. 3*B***). To obtain distinct reports of fading prevention with corresponding distinct prevention intervals, we divided the prevention region into disjoint "prevention intervals," which we denote by $\wp_i$, of the same duration as τ. See "Prevention and eligible

intervals" section for more details. Each $\wp_i$ corresponds to exactly one report of fading prevention (i.e. one *R*). Our goal was to estimate the number of microsaccades in the $\wp_i$ that caused an *R*.

Contribution and efficacy definitions To calculate the number of *R*s caused by microsaccades, one cannot simply add the number of microsaccades that occurred within the $\wp_i$, for two reasons: 1) Some $\wp_i$ may have contained multiple microsaccades or combinations of microsaccades and other eye movements (i.e. blinks or saccades) (**Fig. 4**). The simple addition of the number of microsaccades in all the $\wp_i$ could thus result in some *R*s being counted as caused more than once, leading to an overestimate of microsaccadic contribution and efficacy. 2) Some microsaccades that occurred within a $\wp_i$ may not have caused an *R*; thus, counting them as causal would overestimate their contribution and efficacy.

<<<PLEASE INSERT FIGURE 3 AROUND HERE>>>

Multiple eye movements To account for the possibility that multiple eye movements may have led to an *R* (reason 1 above), we defined the event: *M* = event that only microsaccades (one or more) occurred over a time interval of duration equal to τ's duration (**Fig. 4**). We defined analogous events for saccades (*S*), blinks (*B*), microsaccades and saccades (MS), microsaccades and blinks (MB), saccades and blinks (SB), and microsaccades, saccades, and blinks (MSB) and calculated the contribution, $\mathcal{C}_R(E)$, and efficacy, $\mathcal{E}_R(E)$, of each event *E* = *M*, *S*, *B*, MS, MB, SB, and MSB. That is, for each *E*, we calculated:

$$\mathcal{C}_R(E) = \frac{\text{number of } R\text{s caused by } E}{\text{total number of } R\text{s}}, \text{ and } \mathcal{E}_R(E) = \frac{\text{number of } E \text{ which caused a } R}{\text{number of } E \text{ eligible to cause a } R}.$$

The definitions of the ocular events *E* ensure a one-to-one correspondence between the caused *R*s and the causal ocular events within the $\wp_i$; thus, the numerators of $\mathcal{E}_R(E)$ and $\mathcal{C}_R(E)$ represent the same quantity even though their semantics differ.

Control level To account for the possibility that some of the *E*s occurring within the $\wp_i$ may not have caused a *R* (reason 2 above), we estimated the number of non-causal *E*s within the $\wp_i$ from the trough interval τ. *E*s in τ did not prevent fading, but they were

nevertheless eligible to prevent fading because they occurred in the intensified region. We call the probability of an *E* occurring within the τ, $P(E \mid \tau)$, the control level. If N_R was the total number of *R*s, then the expected number of non-causal *E*s that occurred within the $\wp_i$ was estimated, using the control level, as $P(E \mid \tau)N_R$.

Definitions The total number of *E*s that occurred is $P(E \mid \wp_i)N_R$, thus we took the difference between $P(E \mid \wp_i)N_R$ and $P(E \mid \tau)N_R$ as our estimate of the causal number of *E*s, i.e. the numerator of both $\mathcal{C}_R(E)$ and $\mathcal{E}_R(E)$. Therefore, the contribution and efficacy of an ocular event *E* are:

$$\mathcal{C}_R(E) = \frac{P(E \mid \wp_i)N_R - P(E \mid \tau)N_R}{N_R} = P(E \mid \wp_i) - P(E \mid \tau), \text{ and}$$

$$\mathcal{E}_R(E) = \frac{P(E \mid \wp_i)N_R - P(E \mid \tau)N_R}{N_E} = [P(E \mid \wp_i) - P(E \mid \tau)]\frac{N_R}{N_E},$$

where N_E is the number of *E*s that were eligible to cause an *R* (**Fig. 5**). Eligible *E*s are those that occurred in the intensified region before the termination of τ (we call this the "eligible region" and denote it by Ψ); *E*s that occurred after τ cannot be counted as eligible because the subject's perception had already changed at some point during the τ interval and so those *E*s were not in the intensified region and were thus unable to prevent fading. We took $N_E = P(E \mid \Psi)T_\Psi / d_\tau$, where d_τ is the duration of τ, $P(E \mid \Psi)$ was estimated using "eligible intervals" in the same way $P(E \mid \wp_i)$ was found (see the "Prevention and eligible intervals" section below; **Fig. 3*B***), and T_Ψ is the amount of time spent in Ψ by the subject.

<<<PLEASE INSERT FIGURE 4 AROUND HERE>>>

Correlogram baseline and trough interval. We estimated the baseline, B_{AF}, using the data from the intensified region before ω_F. We chose this region because microsaccades and other eye movements in this region are completely independent of the *F*s as they occurred outside of the reaction time window in both directions of time. If $J \in \{0,1\}^\infty$ indexes when X_A is in the intensified region before ω_F, then we took the baseline rate to be

$$r_A = \frac{\sum_{t=-\infty}^{\infty} X_A(t)J(t)}{\sum_{t=-\infty}^{\infty} J(t)}.$$

r_A is the rate at which eye movements occurred during the intensified region before ω_F. If s_n was the amount of time in bin *n*, the baseline value for bin *n* was $B_{AF}(n) = s_n r_A$. Let $H = \min_{n \in \omega_F} \tilde{\xi}_{AF}(n)$ (where $n \in \omega_F$ if bin *n* contains some time in ω_F) be the minimum of $\tilde{\xi}_{AF}$ within ω_F. If *H* was significantly below B_{AF} (Levick et al., 1972; Mastronarde, 1987; Palm et al., 1988; Aertsen et al., 1989; Alonso et al., 1996; Usrey et al., 1998, 1999; Grun, 2009; McCamy et al., 2012) (significance defined in the "Significance level" section below and shown in **Fig. 3*B***), we let $n_0 = \min\{n : n \in \omega_F$ and $\tilde{\xi}_{AF}(n) = H\}$. We defined the trough interval as all time, $t \in \omega_F$, contiguous with n_0, such that $\tilde{\xi}_{AF}(t)$ was below $B_{AF}(t)$ and we denote it by τ. If no bin achieved significance, τ did not exist, and the contribution and efficacy were taken as 0.

Significance level. We define here what it means for $\tilde{\xi}_{AF}(n)$ to be significantly different from $B_{AF}(n)$. Let *V* be the deviations of $\tilde{\xi}_{AF}(n)$ from $B_{AF}(n)$, $B_{AF}(n) - \tilde{\xi}_{AF}(n)$, in the intensified region before ω_F where at least 10 *F*s had data going back the same duration of time before the prior intensification occurred (this prevents the use of outliers and makes the definition of significance more stable). Let μ_V and σ_V be the mean and standard deviation of *V*. We declared $\tilde{\xi}_{AF}(n)$ as significantly different from $B_{AF}(n)$ if $B_{AF}(n) - \tilde{\xi}_{AF}(n)$ was at least 2.5 standard deviations (σ_V) below the mean (μ_V) (Levick et al., 1972; Mastronarde, 1987; Palm et al., 1988; Aertsen et al., 1989; Alonso et al., 1996; Usrey et al., 1998, 1999; Grun, 2009; McCamy et al., 2012) (**Fig. 3*B***).

Prevention and eligible intervals. To obtain the prevention intervals $\wp_i$, we divided $\wp$ into disjoint intervals of the same duration as τ (**Figs. 3*B*, 4**). For each *F*, we divided the interval of data which began at the prior intensification onset and ended at the start of τ into as many disjoint adjacent segments with τ's duration as possible. The prevention interval which was closest in time relative to a given *F* was always adjacent to τ. To avoid any bias, if there was more than one prevention interval for a given *F*, the prevention interval furthest in time from the *F* was randomly chosen as being adjacent to the prior intensification onset or adjacent to the prior prevention interval. The same principle was used to find the eligible

intervals used to calculate $P(M \mid \Psi)$, only in this case, the interval which was closest in time relative to a given *F* was always τ (**Fig. 3*B***).

Partitioning the microsaccadic event M. We partitioned the event *M* in different ways to investigate its efficacy as a function of microsaccade magnitude, number of microsaccades, and microsaccade direction (**Fig. 8**). For example, in the case of microsaccade magnitude we defined M_i as the microsaccadic event with magnitude in the interval $[0.25(i-1), 0.25i)$ degrees, for $i = 1, \ldots, 4$. Notice then, $M_i \cap M_j = \varnothing$ for $i \neq j$, and $M = \bigcup_{i=1}^{4} M_i$, hence the M_i partition *M*. We also compared the efficacy of microsaccadic events *M* with two or more microsaccades (denoted by $M^{\geq 2}$) to those with one microsaccade (M^1). Furthermore, we compared two aspects of microsaccade direction with respect to the fading target: 1) The angle, θ_{C}, between the compass position of the Gabor patch and the direction of the microsaccade, with θ_{C} varying between 0º (towards the Gabor) and 180º (away from the Gabor). 2) The angle, θ_{O}, between the orientation of the Gabor and the direction of the microsaccade with θ_{O} varying between 0º (parallel) and 90º (orthogonal). See (McCamy et al., 2012) for an illustration of each. M_{Ci} denotes the microsaccadic event *M* whose θ_{C} falls in the interval $[10(i-1), 10i)$ degrees, for $i = 1, \ldots, 18$. $M_{\mathrm{O}i}$ denotes the microsaccadic event *M* whose θ_{O} falls in the interval $[10(i-1), 10i)$ degrees, for $i = 1, \ldots, 9$. Note, $\{M^1, M^{\geq 2}\}$, $\{M_{\mathrm{O}i}\}_{i=1}^{9}$, and $\{M_{\mathrm{C}i}\}_{i=1}^{18}$ also form partitions of *M*. To calculate the contribution and efficacy of any event *E* of a given partition, we used the same τ from the main analysis and applied the contribution and efficacy formulas to *E*. For a discussion on how the contribution and efficacy of *M* relate to the contributions and efficacies of events which partition *M*, see (McCamy et al., 2012).

Contribution and efficacy notes. For the contribution and efficacy analyses, we discarded *F*s when the duration of the prior intensified period was too short to contain the entire ω_F period (15% ± 6% *F*s discarded). In the Illusory fading condition, the average number of *F*s (N_F) for the contribution and efficacy analyses was 334 ± 64 *F*s. For all Illusory fading trials combined, each subject had a sufficient number of *R*s to perform the contribution and efficacy analyses; the average number of *R*s (N_R) was (2999 ± 285). To

carry out the analyses on Illusory fading trials subject to a specific condition (for instance, only trials with the Gabor in the fovea), we required that at least 15 *F*s occurred for this condition, otherwise the measurement became noisy due to insufficient data; in that case we took both the contribution and efficacy as nonexistent (as opposed to 0). We also included a restriction on the number of ocular events (i.e. *M*, *S*, *B* etc.). That is, to measure the efficacy of a particular ocular event *E*, we required that *E* occurred at least 12 times in the eligible region; otherwise we took the efficacy of *E* as nonexistent. See Table 1 for the amount of eligible events across subjects. Finally, because we did not consider the significance of any ocular event *E* alone, we were not guaranteed that $P(E \mid \wp_i) > P(E \mid \tau)$ for each type of event *E* and so in all cases (*E* = *M*, *S*, *B*, MS, MB, SB, MSB, M_1, M_2, etc.) we took $\mathcal{C}_R(E) = \max\{P(E \mid \wp_i) - P(E \mid \tau), 0\}$ and $\mathcal{E}_R(E) = \max\{P(E \mid \wp_i) - P(E \mid \tau), 0\} N_R / N_E$ for each *E* because a negative contribution/efficacy has no meaning.

Statistical analyses

All statistical tests were two-tailed, paired *t*-tests. Significance levels were set at $\alpha = 0.05$ and every test was corrected for multiple comparisons (where necessary) using Bonferroni correction.

RESULTS

<<<PLEASE INSERT FIGURE 5 AROUND HERE>>>

Subjects fixated a small target on the center of a computer screen and continuously reported, via button press, whether an unchanging visual stimulus (a 2-lobe Gabor patch with 40% contrast), presented either foveally or peripherally, was faded (or in the process of fading) versus intensified (or intensifying) (Martinez-Conde et al., 2006; McCamy et al., 2012) (**Fig. 1*A***). We set out to determine the role of fixational microsaccades and drift in the *prevention* of visual fading. Although previous studies have studied the roles of different eye movement types on the *restoration* to visibility of *already faded* targets (Martinez-Conde et al., 2006; Troncoso et al., 2008; McCamy et al., 2012; Costela et al., 2013), no research to date has determined the relationship between the different eye movement types and the prevention of fading (Martinez-Conde et al., 2013). One simplistic and indirect way to determine whether microsaccades may help to prevent fading is to look at microsaccade rates as a function of how long it took for the stimulus to fade. Here we found that microsaccade

rates increased with longer times to fading (**Fig. 2**). To take this a step further, and to principally quantify the impacts of each FEM type in preventing fading, we will calculate the contribution and efficacy of microsaccades to preventing fading, as well as the potential contribution of drift to preventing fading.

Approach to calculating contribution and efficacy

To calculate the contribution and efficacy of microsaccades to preventing fading, we first defined the contribution of microsaccades as the percentage of fading preventions due to microsaccades, and the efficacy of microsaccades as the percentage of microsaccades that prevented fading. Because we did not ask subjects (nor could we have asked them) to report when the stimulus was prevented from fading, we first defined what a report of fading prevention (*R*) was. The first step to do this was to note that if a subject's perceptual report was in the "intensified region" (i.e. the time in which the stimulus was reported as intensified/intensifying) and the subject did not subsequently report fading within his/her reaction times, then fading was prevented. The next and most crucial step was to then find the microsaccades (and any other eye movements) that we know did not prevent fading. Importantly, only eye movements occurring during a specific window of time in the intensified region did not prevent fading. We call this window of time the "trough interval", and denote it by τ, because it corresponds to the trough of the correlogram between eye movements and reports of fading (**Fig. 3**). The subjects' reaction times to physical fadings from the Real fading trials (**Fig. 1*B***) were crucial to defining the trough interval (see Methods for the technical definition of the trough interval) (**Fig. 3**). We then used the trough interval to define reports of fading prevention in the intensified region before the trough interval. Fading was prevented during a period in the intensified region that we call the prevention region and denote by $\wp$. The eye movements that prevented fading occurred during time intervals of the same duration as τ inside the prevention region we term "prevention intervals", and denote by $\wp_i$ (**Fig. 4**). Determining these regions allowed us to estimate the contribution and efficacy of FEMs to preventing fading.

Contribution

Our results indicate that both drift and microsaccades contribute to preventing fading. Microsaccadic events occurred in 44% of the prevention intervals (i.e. $\wp_i$, the intervals without reported transitions to decreased visibility within the subjects' reaction times; **Fig.**

5*A*), and in only 3% of the trough intervals (i.e. τ, intervals preceding reports of decreased visibility within the reaction times of the subjects). The difference between these two quantities (41%) provides a lower bound on the contribution of microsaccades, $\mathcal{C}_R(M)$, to preventing fading (**Fig. 5*B***). That is, microsaccades caused a minimum of 41% and a maximum of 44% of all fading preventions.

Drift is ever-present (Cornsweet, 1956), thus drift occurred in essentially every prevention interval and every trough interval. Due to the continuous nature of drift, one cannot determine its contribution and efficacy in the same manner as with transient eye movements such as microsaccades, saccades, and blinks. We defined drift alone (*D*) as the event that only drift occurred over an interval of time with duration equal to τ's duration. The probability of drift alone in a prevention interval $\wp_i$, was 52%, placing an upper bound on the contribution of drift alone to preventing visual fading (this upper bound did not vary significantly with eccentricity; data not shown). In other words, drift alone caused a maximum of 52% of all fading preventions (**Fig. 5*A***). This suggests that, whereas the contribution of drift to the reversal of fading is small (McCamy et al., 2012), drift alone is a large contributor to preventing fading. Thus, the low contribution of drifts to the reversal of fading does not preclude its playing a larger role in the prevention of fading; indeed, it is possible that drift is more important than microsaccades to preventing fading.

Efficacy

The efficacy of microsaccades, $\mathcal{E}_R(M)$, was 88%; that is, 88% of the microsaccadic events that occurred during a period of intensification prevented fading (**Fig. 5*C***). Saccadic efficacy , $\mathcal{E}_R(S)$, (89%) and microsaccadic efficacy were similar (**Fig. 5*C***). The efficacy of any combination of microsaccades, saccades, and blinks (i.e. *M*, *S*, *B*, MS, MB) ranged from 87-92%, indicating that fading is rare in the presence of abrupt eye movements.

Neither the contribution nor the efficacy of microsaccades varied significantly as a function of stimulus eccentricity (data not shown).

The efficacy of drift alone is difficult to get at, because of drift's continuous nature. If we simply applied our efficacy formula to drift alone, then we would get an efficacy of zero. It could be that some drifts are better than others for preventing fading, and so it is not appropriate to equate all drift alone events. It is important to remember that only the ocular events that occurred within the prevention region $\wp$ -- but not the ocular events that occurred within the trough interval τ-- prevented fading. Our results show that 97% of trough intervals

contained drift alone (i.e. 97% of fading reports were preceded by drift alone in the trough interval), whereas only 52% of the prevention intervals contained drift alone. Thus, drift alone was able to prevent fading in some cases, but not in others. Because of this, we wondered whether drift alone in trough intervals was different (i.e. possibly slower) from drift alone in the prevention intervals.

<<<PLEASE INSERT FIGURE 6 AROUND HERE>>>

Drift and microsaccades in the trough intervals vs. prevention intervals

Drift .To compare drift inside the trough to drift in the prevention region, we compared the mean, maximum, and standard deviation of the instantaneous drift speed inside of trough intervals to those in the prevention intervals. We analyzed only drifts that occurred in trough/prevention intervals without microsaccades/saccades or blinks. Furthermore, because there are higher microsaccade rates in the prevention region than in the trough interval (**Fig. 3*B***), edge effects due to filtering can artificially change drift speeds between the two regions (**Fig. 6*B***), so we made comparisons after removing the edge effects due to the filter (see Methods; **Fig. 6*C*-*D***). We found that all three parameters (i.e. mean, maximum, and standard deviation) of instantaneous drift speed were larger on average inside the prevention intervals than in the trough intervals (**Fig. 7*A***), suggesting that faster drifts and drifts with more variation in speed are better at preventing fading.

We wondered whether this result might be mainly due to increased post-saccadic drift speeds after (micro)saccades (Chen and Hafed, 2013); **Fig. 6*C***), To find out, we increased the window after the beginning of the drift to get rid of the correlation of (micro)saccades (i.e. post-saccadic drift; see Methods) and we analyzed only drift in prevention/trough intervals that did not contain (micro)saccades or blinks. This approach ensured that the results would not be explained by increased post-saccadic drift in the prevention region (**Fig. 6*C*-*D***). In this case, only the mean speed of drift was significantly, although moderately, faster in the prevention intervals than in the trough intervals (**Fig. 7*B***).

We note that removing the edge effects due to the filter was critical to our analyses, because microsaccade rates differed between prevention and trough regions compared in **Fig 7**. If filter edge effects had remained, we would have obtained artificial results, because the increased numbers of microsaccades in the prevention region would have resulted in more instances of higher drift speeds. A similar argument applies to the post-saccadic drift. Given

that drifts seem to be faster in prevention intervals compared to the trough intervals, we wondered whether microsaccade properties also differed between the two regions.

<<<PLEASE INSERT FIGURE 7 AROUND HERE>>>

Microsaccade magnitude, number, and direction. Because the probability of a microsaccade occurring in the trough interval is so low (3% of trough intervals had one or more microsaccades) we suspected that the efficacy of microsaccades would not change with different types of microsaccadic events. Upon doing the calculations, this is mostly what we found; that is, microsaccades were equally effective at preventing fading independent of their size and direction (**Fig. 8*A*,*C*-*D***). In fact, the smallest microsaccades were just as effective as large saccades at preventing fading. This is in extreme contrast to the role of microsaccades in reversing fading, where microsaccadic efficacy increased linearly with microsaccade magnitude, and multiple microsaccades were more effective at reversing fading than isolated microsaccades (McCamy et al., 2012). Here, microsaccadic events with two or more microsaccades were slightly, but significantly, more effective than microsaccadic events with just one microsaccade (**Fig. 8*B***).

<<<PLEASE INSERT FIGURE 8 AROUND HERE>>>

DISCUSSION

Even when we attempt to fixate our gaze, small eye movements, called fixational eye movements (FEMs: including microsaccades, drift and tremor) continue to shift our eye position. Here we determined the role of FEMs in the prevention of visual fading during fixation, for the first time, and found that both drift and microsaccades contribute to preventing fading. Our results indicate that the contribution of drift to preventing fading is potentially higher than that of microsaccades, but that microsaccades of any size prevent fading with higher efficacy than drift, both in the visual periphery and in the fovea. Microsaccades of all directions were equally effective at preventing fading, but two or more microsaccades occurring in close succession were slightly (5%) more efficacious than single microsaccades. We also found that drift was faster and had more variation in prevention intervals (i.e. intervals without reported transitions to decreased visibility within the subjects' reaction times) compared to trough intervals (i.e. intervals preceding reports of decreased visibility within the subjects' reaction times), but most of these differences were due to the combination of increased post-saccadic drift speeds and higher microsaccade rates in prevention intervals compared to trough intervals.

Our findings are compatible with a pioneering study by Gerrits and Vendrick, where simulated drift and/or microsaccadic motions were imposed on parafoveal stimuli otherwise stabilized on the retina (Gerrits and Vendrik, 1974). Based on qualitative analyses, the authors concluded that "[…] the most effective eye movement to preserve vision is better characterized by its qualities (irregularity and continuity) than by its name (drift or saccade)" and that "[…] both the irregularity (the continuous change of direction) and the continuity of the movement of a stimulus with respect to the retina are very important for the preservation of perception." Gerrits and Vendrick stressed that microsaccades were of minor importance to visibility, however, in light of previous (albeit qualitative) work suggesting that microsaccades were not needed to preserve foveal vision during maintained fixation. Gerrits and Vendrick also proposed that Gaussian noise (drift) interspersed with binary noise (microsaccades) resulted in very long periods of visibility, suggesting that the combination of drift and microsaccades could optimize visibility during fixation, as indeed our present data indicates. Our conclusion that microsaccades and drift both prevent fading is also consistent with the finding (Engbert and Kliegl, 2004) that microsaccades and drift together provide motion that is continuous (persistent on a short time scale) and irregular (anti-persistent on a long time scale), also in line with Gerrits and Vendrick's predictions.

Preventing vs. restoring faded vision

There has been much confusion about, and misuse of, the concepts of preventing and reversing visual fading in the literature. Indeed, many previous papers have used both terms as synonyms (Poletti and Rucci, 2010; Kagan, 2012) or failed to differentiate one from the other (Nachmias, 1961; Sharpe, 1972; Kowler and Steinman, 1979). The present research indicates that different constellations of eye movements mediate the prevention and the reversal of visual fading during fixation. The combined results from the current study and our previous research on the contribution and efficacy of FEMs to restoring faded vision (McCamy et al., 2012) suggest that, whereas microsaccades are critical to counteracting fading once it has happened, both drift and microsaccades synergistically prevent fading from occurring. It may be that drift effectively prevents fading for a limited time only: that is, that if a saccade, microsaccade, or blink does not interrupt the drift, then fading will occur eventually. This notion is supported by the fact that drift alone occurred in 97% of trough intervals: intervals preceding reports of decreased visibility within the reaction times of the subjects. These findings may help to reconcile the long-standing controversy concerning the comparative roles of microsaccades and drift in visibility during fixation.

Underlying physiology. Neural adaptation has been shown to occur at fast and slow time scales (Sanchez-Vives et al., 2000a, 2000b; Wang et al., 2003) in the primary visual cortex. One possible physiological explanation of the present perceptual results (as well as those reported by (McCamy et al., 2012)) is that microsaccades reverse fast adaptation and reverse/prevent slow adaptation, while drifts prevent/reverse slow adaptation. Because drift moves visual receptive fields slowly over a small region of space, it may be that drift does not work fast enough to reverse fast adaptation. In other words, because natural scenes are highly correlated in space (Simoncelli and Olshausen, 2001), it follows that new stimuli brought into receptive fields of visual neurons by drift are highly correlated to recent previous stimuli in those same receptive fields. Conversely, because of the larger distance covered by microsaccades, new stimuli entering the receptive fields of visual neurons will be less likely correlated to recent stimuli. Future research should investigate the possibility that transient signals due to microsaccades combine with sustained signals due to drifts to produce optimal visual stimulation.

Enhancement vs. suppression. It is widely believed that microsaccades come with elevated perceptual thresholds (Zuber and Stark, 1966; Beeler, 1967), but see (Krauskopf et al., 1966). This elevation does not preclude a perceptual benefit of microsaccades, however. Microsaccades act to move a visual stimulus to a new location on the retina. Once suppression has occurred, that act can still be beneficial to perception by causing transient stimulation, followed by increased sustained responses (enhanced by drift). Even square-wave jerks (SWJs), which are consecutive microsaccades that occur in opposite directions (Martinez-Conde, 2006; Chen et al., 2010; Otero-Millan et al., 2011, 2013; McCamy et al., 2013), may be perceptually advantageous; for instance if the brief movement caused by the first saccade, followed by the quick return to the initial position by the second saccade of the SWJ (usually within ~200 ms), provides enough time for a brief recovery from neural adaptation.

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ADDITIONAL INFORMATION

Competing interests

The authors declare no competing interests**.**

Author contributions

MBM, SLM, and SMC contributed to the conception and design of the study and to drafting the article or revising it critically for important intellectual content. MBM conducted the data analyses.

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TABLES

Table 1. Number of eligible microsaccadic events of a given type.

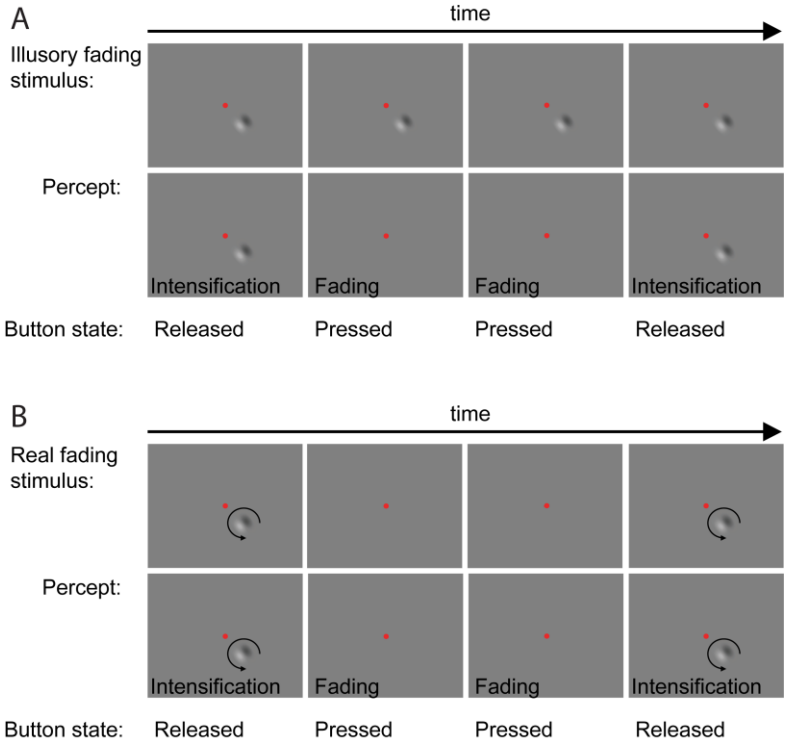
Ocular event (*E*)	**Number of subjects with ≥ 12 eligible events**	**Average number (± s.e.m.) of eligible events**
M	7	1424 ± 223
S	5	37 ± 21
B	6	64 ± 14
MS	6	26 ± 4
MB	6	42 ± 6

M_1 (magnitude in [0, 0.25) deg)	6	295 ± 73
M_2 (magnitude in [0.25, 0.5) deg)	7	860 ± 161
M_3 (magnitude in [0.5, 0.75) deg)	7	296 ± 68
M_4 (magnitude in [0.75, 1) deg)	6	64 ± 14
M^1 (one microsaccade)	7	1034 ± 143
$M^{\geq 2}$ (two or more microsaccades)	7	391 ± 112
D (drift alone)	7	1932 ± 309
M_{C1} (θ_C in [0 10) degrees)	7	62 ± 10
M_{C2} (θ_C in [10 20) degrees)	7	76 ± 14
M_{C3} (θ_C in [20 30) degrees)	7	71 ± 12
M_{C4} (θ_C in [30 40) degrees)	7	88 ± 15
M_{C5} (θ_C in [40 50) degrees)	7	90 ± 13
M_{C6} (θ_C in [50 60) degrees)	7	85 ± 14
M_{C7} (θ_C in [60 70) degrees)	7	74 ± 13
M_{C8} (θ_C in [70 80) degrees)	7	78 ± 16
M_{C9} (θ_C in [80 90) degrees)	7	93 ± 13
M_{C10} (θ_C in [90 100) degrees)	7	93 ± 13
M_{C11} (θ_C in [100 110) degrees)	7	71 ± 13
M_{C12} (θ_C in [110 120) degrees)	7	71 ± 12
M_{C13} (θ_C in [120 130) degrees)	7	86 ± 14
M_{C14} (θ_C in [130 140) degrees)	7	108 ± 18
M_{C15} (θ_C in [140 150) degrees)	7	90 ± 12
M_{C16} (θ_C in [150 160) degrees)	7	82 ± 12
M_{C17} (θ_C in [160 170) degrees)	7	85 ± 13

M_{C18} (θ_C in [170 180) degrees)	7	71 ± 10
M_{O1} (θ_O in [0 10) degrees)	7	68 ± 10
M_{O2} (θ_O in [10 20) degrees)	7	134 ± 20
M_{O3} (θ_O in [20 30) degrees)	7	166 ± 26
M_{O4} (θ_O in [30 40) degrees)	7	221 ± 36
M_{O5} (θ_O in [40 50) degrees)	7	283 ± 43
M_{O6} (θ_O in [50 60) degrees)	7	220 ± 36
M_{O7} (θ_O in [60 70) degrees)	7	171 ± 26
M_{O8} (θ_O in [70 80) degrees)	7	142 ± 23
M_{O9} (θ_O in [80 90) degrees)	7	60 ± 15

The efficacy calculations in **Figs. 5C, 8** required that each subject had a minimum of twelve occurrences per ocular event type.

1. **Experimental tasks.** An epoch from ***A***, an Illusory fading trial and ***B***, a Real fading trial. Both panels show the physical stimulus (top row; fixation dot not to scale), the subject's perception of the Gabor stimulus (second row), and the subject's report (third row). The circular arrow around the Gabor stimulus in (B) condition indicates that the stimulus is moving in a small circle (see Methods). Panel (A) modified from (McCamy et al., 2012).



2.

Figure 2. Time-to-fading. Microsaccade rates (i.e microsaccades per second; N/s) as a function of how long the stimulus took to fade, i.e. microsaccade rates for intensification periods of varying duration. Shadow indicates the s.e.m. across subjects (n = 7).

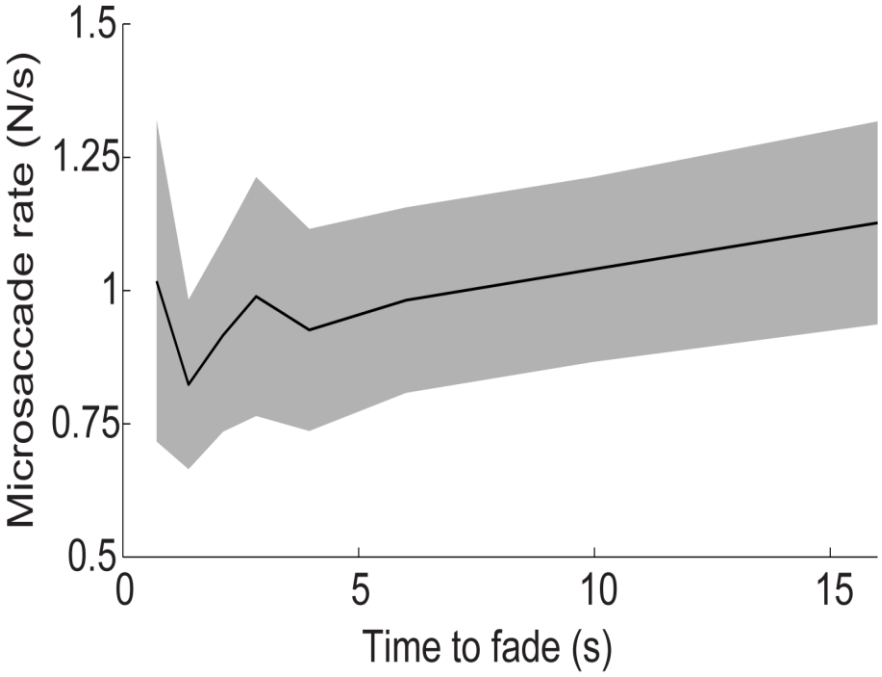


Figure 3. The definition of the trough interval and the prevention and eligible regions. ***A***, One subject's reaction time distribution to physical fadings during the Real fading condition, and ω_F (first approximation of the trough interval) for that subject. The average ω_F across subjects was [−828, −289] ± [33, 10] ms. ***B***, $\tilde{\xi}_{AF}$ is the correlogram of all eye movements with *F*s for the same subject from (*A*), B_{AF} is the baseline, and the purple interval contained inside of ω_F is the trough interval. See Methods for the criteria used to determine the trough interval, as a function of the reaction times, baseline, and significance level.

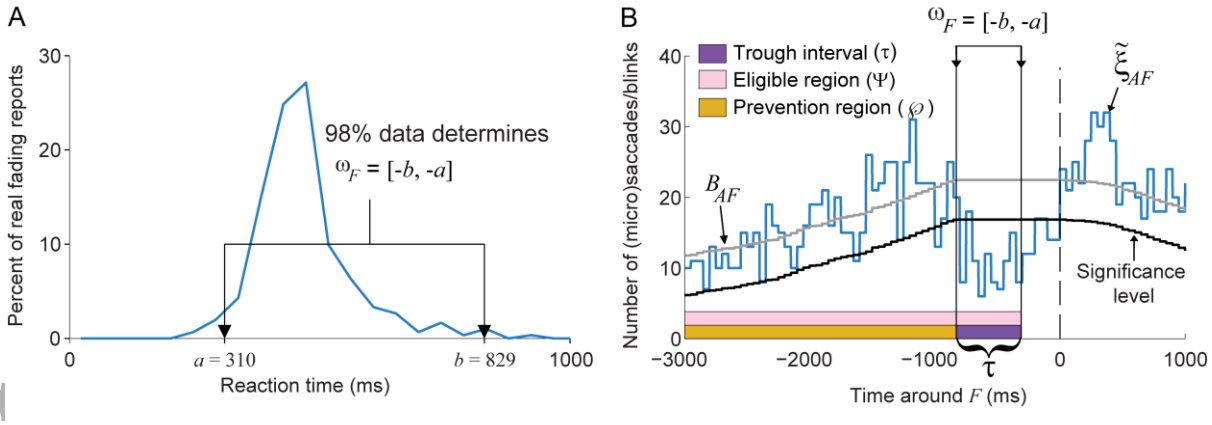


Figure 4. Ocular events. Each row shows two 3-second epochs during the Illusory fading condition from one subject. The black trace is the eye's horizontal position. The blue and red pulses represent the subject's perceptual reports. The purple pulse indicates the location of the trough interval, in which ocular events did not prevent fading. The golden pulses are prevention intervals, where fading was prevented. A green pulse indicates a detected microsaccade, a brown pulse a saccade, and a yellow pulse a blink. Several types of ocular events are indicated above their trough/prevention interval. *M* = event that only microsaccades (one or more) occurred over a time interval of duration equal to τ's duration. Analogous events are defined similarly for saccades (*S*), blinks (*B*), microsaccades and saccades (MS), microsaccades and blinks (MB), and ocular drift alone (*D*).

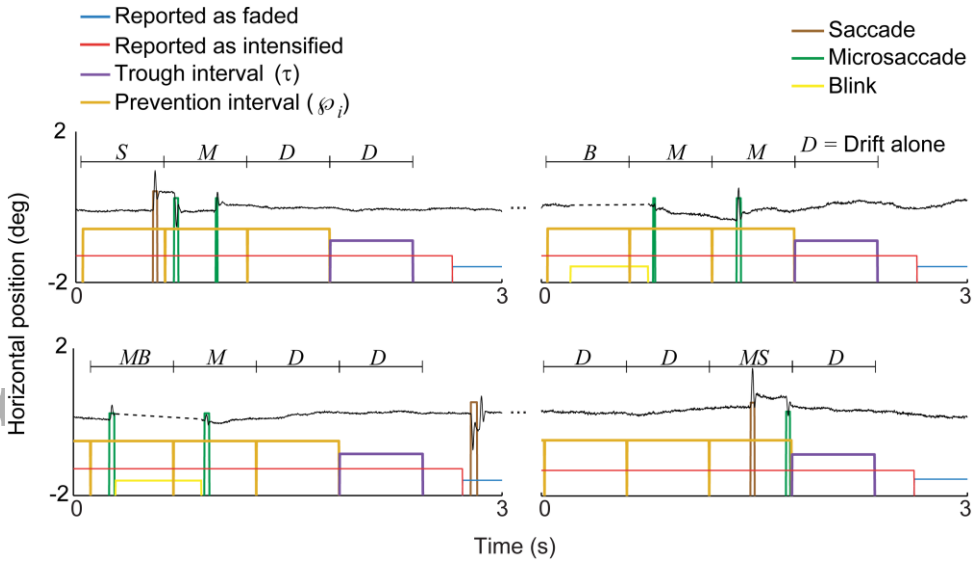


Figure 5. Contribution and efficacy of different ocular events to preventing fading. ***A***, The bars and pie chart show $P(E \mid \wp)$, the probability of an event E occurring within a prevention interval, for each event E. Because $P(D \mid \wp) = 52\%$, the upper bound on the contribution of drift alone (D) is 52%. ***B***, The contribution, $\mathcal{C}_R(E)$, of each ocular event E. ***C***, The efficacy, $\mathcal{E}_R(E)$, of each ocular event E. Error bars indicate the s.e.m. across subjects (n = 7 for (*A-B*), see Table 1 for the number of subjects in each type of event in (*C*)). M = event that only microsaccades (one or more) occurred over a time interval of duration equal to τ's duration (**Fig. 3**). Analogous events are defined similarly for saccades (S), blinks (B), microsaccades and saccades (MS), microsaccades and blinks (MB), and ocular drift alone (D).

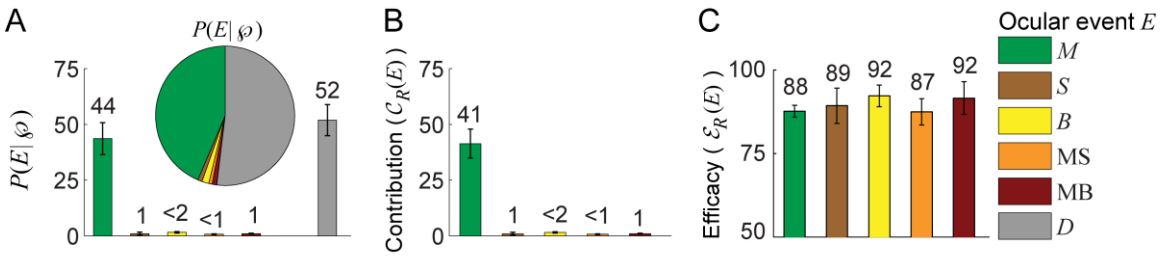


Figure 6. Instant drift speed correlations with microsaccades and random microsaccades. ***A-B***, Instant drift speed around microsaccades (*A*) and random microsaccades (*B*) with 10 ms windows removed from the beginning and end of each drift. The changes in drift speed around the time of random microsaccades (decreases prior to and increases after) are due to the edge effects of the filter. ***C-D***, Instant drift speed around microsaccades (*C*) and random microsaccades (*D*) with 34 ms removed from the beginning and 110 ms removed from the end of each drift; thus removing the edge effects due to the filter. Shadows indicate the s.e.m. across subjects ($n = 7$).

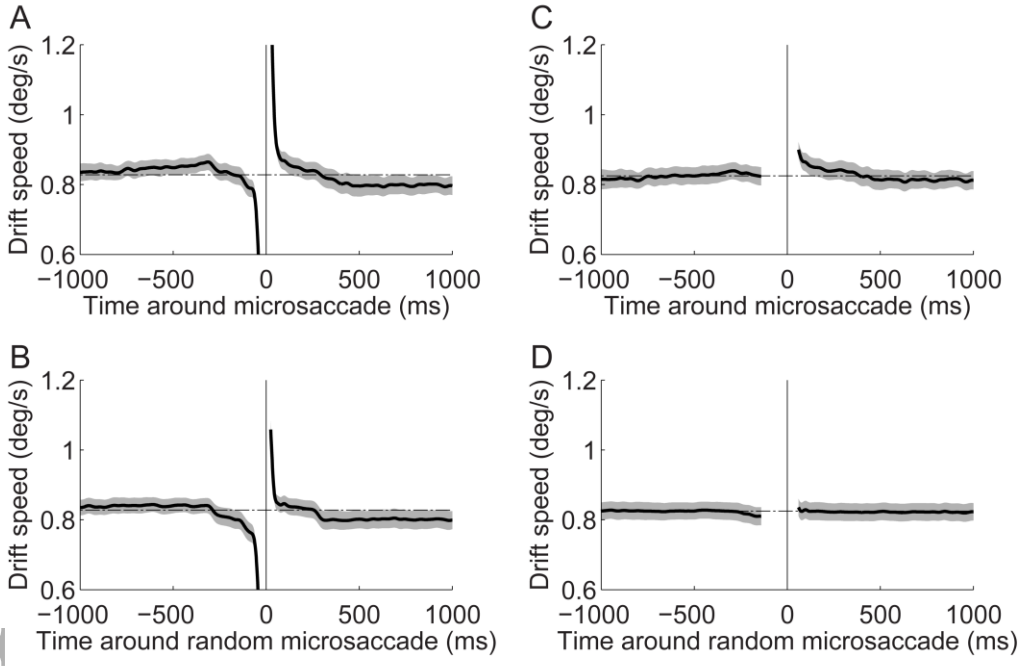


Figure 7. Drift properties inside prevention vs. trough intervals, with and without the effects of post-saccadic drift. Drift speed properties in prevention vs. trough intervals, ***A***, with, and ***B***, without, the effects of post-saccadic drift. Shadows and error bars indicate the s.e.m. across subjects ($n = 7$). * indicates statistical significance with $p < 0.05$ and ** indicates statistical significance with $p < 0.01$ (two-tailed, paired t-test). Error bars indicate the s.e.m. across subjects ($n = 7$).

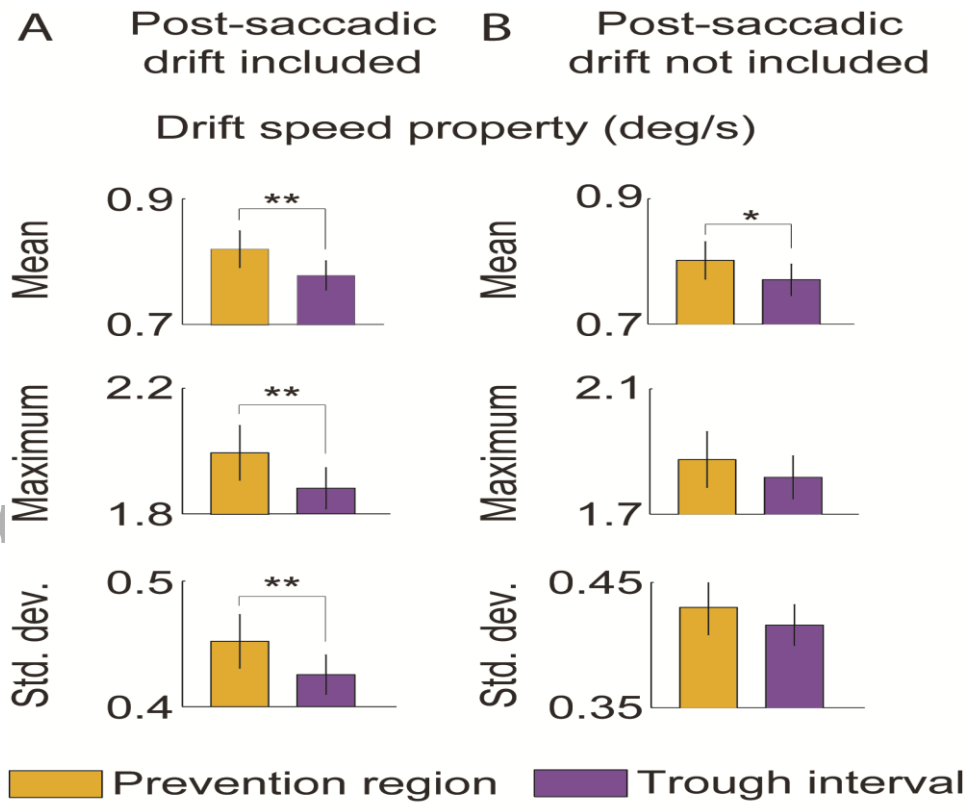


Figure 8. Microsaccade magnitude, number, and direction. ***A***, The efficacy of microsaccadic and saccadic events did not vary significantly with magnitude. M_i denotes the microsaccadic event *M* whose magnitude falls in the interval $[0.25(i-1), 0.25i)$ degrees, for $i = 1, \ldots, 4$. ***B***, Microsaccadic events *M* with two or more microsaccades $(M^{\geq 2})$ were slightly, but significantly, more efficacious than events with one microsaccade (M^1). ***C***, The efficacy of microsaccades did not vary as a function of their direction relative to the compass position of the Gabor. θ_C is the angle between the microsaccade direction and the compass position of the Gabor. M_{Ci} denotes the microsaccadic event *M* whose θ_C falls in the interval $[10(i-1), 10i)$ degrees, for $i = 1, \ldots, 18$. ***D***, The efficacy of microsaccades did not vary as a function of their direction relative to the orientation of the Gabor. θ_O is the angle between the microsaccade direction and the orientation of the Gabor. M_{Oi} denotes the microsaccadic event *M* whose θ_O falls in the interval $[10(i-1), 10i)$ degrees, for $i = 1, \ldots, 9$. Error bars indicate the s.e.m. across subjects; see Table 1 for the number of subjects in each type of event. * indicates statistical significance with $p < 0.05$ (two-tailed, paired *t*-test).