EJN European Journal of Neuroscience

FENS Federation of European Neuroscience Societies

European Journal of Neuroscience, pp. 1–7, 2017 doi:10.1111/ejn.13487

Changes in visibility as a function of spatial frequency and microsaccade occurrence

Francisco M. Costela,[1,2,3,*] Michael B. McCamy,[4,3,*] Mary Coffelt,[3,5] Jorge Otero-Millan,[6,3] Stephen L. Macknik[7,3] and Susana Martinez-Conde[7,3]

[1]Harvard Medical School, Schepens Eye Research Institute, Boston, MA, USA
[2]Interdisciplinary Graduate program in Neuroscience, Arizona State University, Tempe, AZ, USA
[3]Barrow Neurological Institute, Phoenix, AZ, USA
[4]Grand Canyon University, Phoenix, AZ, USA
[5]Department of Biomedical Engineering, University of Arizona, Tucson, AZ, USA
[6]Department of Neurology, Johns Hopkins University, Baltimore, MD, USA
[7]Downstate Medical Center, State University of New York, Brooklyn, NY 11203, USA

Keywords: fading, fixation, fovea, illusion, troxler fading

Edited by Doug Munoz
Received 2 March 2016, revised 7 November 2016, accepted 21 November 2016

Abstract

Fixational eye movements (FEMs), including microsaccades, drift, and tremor, shift our eye position during ocular fixation, producing retinal motion that is thought to help visibility by counteracting neural adaptation to unchanging stimulation. Yet, how each FEM type influences this process is still debated. Recent studies found little to no relationship between microsaccades and visual perception of spatial frequencies (SF). However, these conclusions were based on coarse analyses that make it hard to appreciate the actual effects of microsaccades on target visibility as a function of SF. Thus, how microsaccades contribute to the visibility of stimuli of different SFs remains unclear. Here, we asked how the visibility of targets of various SFs changed over time, in relationship with concurrent microsaccade production. Participants continuously reported on changes in target visibility, allowing us to time-lock ongoing changes in microsaccade parameters to perceptual transitions in visibility. Microsaccades restored/increased the visibility of low SF targets more efficiently than that of high SF targets. Yet, microsaccade rates rose before periods of increased visibility, and dropped before periods of diminished visibility, for all the SFs tested, suggesting that microsaccades boosted target visibility across a wide range of SFs. Our data also indicate that visual stimuli fade/become harder to see less often in the presence of microsaccades. In addition, larger microsaccades restored/increased target visibility more effectively than smaller microsaccades. These combined results support the proposal that microsaccades enhance visibility across a broad variety of SFs.

Introduction

Objects that are completely stationary on the retina fade from perception (Ditchburn & Ginsborg, 1952; Riggs & Ratliff, 1952, p. 52; Yarbus, 1957). Human eyes are never still, however. Even when we try to fixate our gaze on an object of interest, small ocular motions, known as fixational eye movements (FEMs: including microsaccades, drift, and tremor) shift our eye position. Retinal motion from FEMs is thought to help visibility during fixation by acting against neural adaptation to unchanging stimuli (Martinez-Conde *et al.*, 2004, 2006, 2013; Engbert & Mergenthaler, 2006). Yet, how each FEM type influences this process is still debated.

Previous work showed that microsaccades improve target visibility, both by reversing perceptual fading (Martinez-Conde *et al.*, 2006; McCamy *et al.*, 2012), and by preventing its incidence (McCamy *et al.*, 2014), even in the case of minute targets contained entirely within the fovea (Costela *et al.*, 2013). This research tested only targets with a single spatial frequency (SF), however. Thus, it did not address how microsaccades may contribute to modulations in target visibility as a function of SF.

Two recent studies set out to investigate how microsaccades might influence the perception of SF, and found their effects to be absent or negligible. However, these conclusions were based on coarse analyses that make it hard to appreciate the actual effects of microsaccades on target visibility as a function of SF.

Mostofi *et al.* (2016) concluded that microsaccades (defined as saccades < 0.5°) had little impact on contrast sensitivity (a similar, but not identical concept to visibility) at both low [0.8 cycles per

Correspondence: Susana Martinez-Conde, [7]Downstate Medical Center, as above.
E-mail: smart@neuralcorrelate.com

*Equal contributors to this study.

degree (cpd)] and high SFs (10 cpd); yet, spectral analyses suggested a microsaccadic contribution to enhancing low-frequency vision. Spotorno *et al.* (2016) similarly found no effect of microsaccade sizes or numbers in a grating detection task conducted at different SFs (0.5, 1, and 2.5 cpd). These two studies tested a limited range of SFs. More importantly, neither of them time-locked transient changes in microsaccade occurrence to perceptual changes in target visibility. Specifically, Spotorno *et al.* (2016) asked subjects to indicate which of two briefly presented sequential images (one with a grating embedded in noise, and one with noise only) contained a grating. They obtained a single subject report at the end of each 6.5 s trial, and likewise considered microsaccade production as a single parameter per trial. Mostofi *et al.* (2016) presented an oriented Gabor for 1 s, and asked participants to indicate its orientation (left or right) at the end of each trial; to determine whether microsaccades were beneficial, they compared subject performance on trials with vs. without microsaccades. Thus, how microsaccades contribute to the ongoing visibility of stimuli of different SFs remains unclear.

Here, we asked how the visibility of targets of various SFs (0.375, 0.75, 1.5, 3, and 6 cpd) changed over time, in relationship with concurrent changes in microsaccade production.

Participants continuously reported on changes in target visibility throughout the experiments, allowing us to time-lock ongoing, transient changes in microsaccade parameters (such as rate and magnitude) to perceptual transitions in visibility (increases and decreases), which occurred at multiple and variable times during each trial.

We found microsaccade production to restore/increase the visibility of low SF targets more efficiently than that of high SF targets. Yet, microsaccade rates transiently rose before periods of increased visibility, and dropped before periods of diminished visibility, for all the target SFs tested, indicating an association between microsaccades occurrence and target visibility across a wide range of SFs. In addition, larger microsaccades were more strongly associated with restored/increased target visibility than smaller microsaccades, and this association was equally present across all the SFs tested. These combined results support the proposal that microsaccades enhance visibility across a broad variety of SFs. More generally, our findings suggest that microsaccades modulate everyday perception not just in exceptional circumstances, but as a habitual rule.

Materials and methods

Subjects

Fifteen subjects (seven males, eight females) with normal or corrected-to-normal vision participated in the experiments. Thirteen subjects were naive and were paid $15/session. Experiments were carried out under the guidelines of the Barrow Neurological Institute's Institutional Review Board (protocol number 04BN039) and conformed with the World Medical Association Declaration of Helsinki. Written informed consent was obtained from each subject.

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 four sessions of ~1 h, each including 50 randomly interleaved 30-s trials. The first session was counted as a training session and not included in the analyses.

While fixating a small red spot (0.5° diameter) on the center of the screen, subjects were asked to continuously report whether an unchanging stimulus was faded/fading (button press) or intensified/intensifying (button release) (Martinez-Conde *et al.*, 2006; McCamy *et al.*, 2012). The stimulus did not change physically, but it appeared to fade or intensify as a function of the observer's fixation dynamics. Naïve subjects were not informed, before the experiment, that the only changes to the appearance of the stimulus were illusory.

The stimulus was a Gabor patch with the following fixed parameters: Gaussian standard deviations of $x = 1.5°$ and $y = 1°$; sine wave phase of 0. The Gabor was presented at an eccentricity of 6°, with one of five randomly selected SFs (0.375, 0.75, 1.5, 3, or 6 cpd), and sustaining a maximum contrast of 40% from peak-to-trough and the same average luminance (50%) as the background. The position of the Gabor varied randomly across trials at one of the eight points of the compass to control for possible contrast adaption effects across trials. The orientation of the Gabor also varied randomly between 0° and 360° in each trial, to control for orientation adaptation effects (Martinez-Conde *et al.*, 2006; McCamy *et al.*, 2012). To start the trial, subjects pressed a key and the stimulus appeared on the screen. Subjects were instructed to release the button as soon as they saw the stimulus. After 30 s, 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.

Eye movement analyses

Eye position was acquired noninvasively in both eyes at 500 Hz (EyeLink 1000, SR Research). Saccades were identified with a modified version of the algorithm developed by Engbert & Kliegl (Engbert & Kliegl, 2003; Laubrock *et al.*, 2005; Engbert, 2006; Engbert & Mergenthaler, 2006; Rolfs *et al.*, 2006) with $\lambda = 5$ (used to obtain the velocity threshold) and a minimum saccadic duration of 6 ms. Microsaccades were defined as saccades with magnitude < 1.5° in both eyes (Betta & Turatto, 2006; Martinez-Conde *et al.*, 2006, 2009; Troncoso *et al.*, 2008b; McCamy *et al.*, 2013a,b), as per the distribution of microsaccade magnitudes found in our dataset (Fig. 1A). To calculate microsaccade properties such as magnitude and peak velocity we averaged the values for the right and left eyes. Figure 1B shows the microsaccadic peak velocity-magnitude relationship (Fig. 1B).

Microsaccade correlations with reported transitions

Let X_M and X_R be the stochastic processes representing the onsets of microsaccade, and intensification report (R). For example, if $S_1, S_2, \ldots, S_k$ are the start times of all the microsaccades for a given subject, then X_M for that subject will be given by $X_M(t) = 1$ if $t = S_i$ for some $1 \leq i \leq k$ and $X_M(t) = 0$ otherwise; similarly for intensification reports.

We obtained correlations of microsaccades with reports of intensification for each subject, using $\xi_{MR}(t) = \sum_{n=-\infty}^{n=\infty} X_M(n+t)X_R(n)$ and then converting ξ_{MR} to a rate (similarly for transitions to fading) (McCamy *et al.*, 2012). For each subject, correlations were smoothed using a Savitzky-Golay filter of order 1 and a window size of 151 ms (Martinez-Conde *et al.*, 2006). Average correlations are the average of the smoothed correlations (Fig. 5).

Microsaccade correlation baselines

For any given subset of experimental trials (e.g. trials with a SF of 3 cpd), we defined the microsaccade rate baseline as the rate

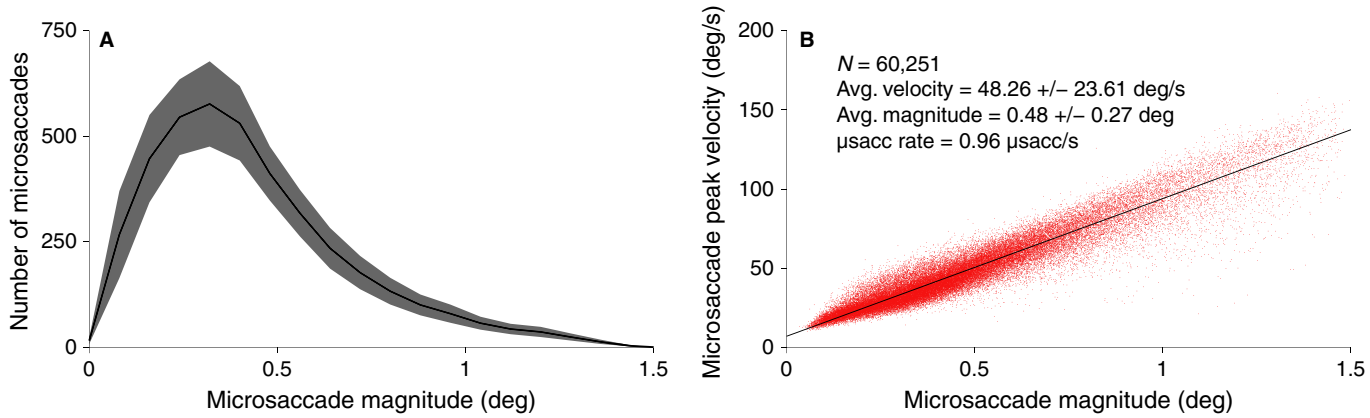

FIG. 1. Descriptive microsaccade statistics. (A) Microsaccadic magnitude distribution across subjects (n = 15). Shadows indicate the SEM across subjects. (B) Microsaccadic peak velocity–magnitude relationship for all subjects combined. Each red dot represents a microsaccade with peak velocity indicated on the y-axis and magnitude indicated on the x-axis. Inset: microsaccade parameters.

of microsaccades produced far from the changes in visibility that took place during that subset. Thus, we calculated these microsaccadic rates using data 700 ms away from all reported transitions (i.e. perceptual intensification or fading) in both directions of time. The microsaccades produced during this period are independent of the transitions, as they occurred outside of subjects' reaction times window in both directions of time (McCamy *et al.*, 2012, 2014).

Statistical methods

To analyze the effect of target SF on various variables (e.g. time faded per trial, microsaccade rates), we conducted separate single-factor repeated measures ANOVAS with the different SF levels as the within-subjects factor. We calculated Pearson and Spearman correlation coefficients to determine the correlation between microsaccade rates and perceptual switching rates across subjects. All other tests were two-tailed paired t-tests as indicated in the main text. Significance levels were set to $\alpha = 0.05$ throughout.

Results

Perceptual fading and intensification dynamics as a function of spatial frequency

Subjects fixated a small spot on the center of a computer screen and continuously reported, via button press/release, whether an unchanging visual target (a Gabor patch with a SF of 0.375, 0.75, 1.5, 3 or 6 cpd), presented at an eccentricity of 6°, was faded/fading or intensified/intensifying (Martinez-Conde *et al.*, 2006; McCamy *et al.*, 2012). Targets of all SFs faded for a significant amount of time, but fading dynamics differed across SF conditions (Fig. 2). The time faded per trial differed with SF ($F_{4,56} = 6.15$, $P < 0.001$, MSE = 20.70, $\eta_p^2 = 0.31$), tending to be shorter for the intermediate SFs (0.75, 1.5, and 3 cpd) (Fig. 2A). Fading onsets per minute also differed across targets of different SFs ($F_{4,56} = 8.51$, $P < 10^{-4}$, MSE = 9.972, $\eta_p^2 = 0.378$); the 0.375 cpd SF target produced the most numerous perceptual transitions and the 3 cpd SF the least (Fig. 2B). Moreover, the durations of fading and intensification periods varied with target SF; the 3 cpd SF target resulted in the longest intensification periods and the 0.375 cpd SF target produced the smallest difference between the length of fading and intensification periods (Fig. 3).

Microsaccade rates

As a coarse first approach, we measured the global microsaccade rates across SF conditions, and found no significant differences (Fig. 4; $F_{4,56} = 1.71$, $P = 0.16$, MSE = 0.008, $\eta_p^2 = 0.11$). This apparently null result is consistent with a prior study (Mostofi *et al.*, 2016), and provides a plausible explanation for previous failures to find a significant relationship between microsaccade production and visual perception as a function of SF. Next, we examined the timing of microsaccades with respect to perceptual fluctuations, by locking variations in microsaccade rates to perceptual transition reports. This finer analysis revealed that microsaccade rates dynamically changed within each trial, transiently increasing before perceptual transitions to intensification and transiently decreasing before perceptual transitions to fading, for all the SFs tested (Fig. 5) – even though their global values were comparable across SF conditions (Fig. 4).

Microsaccade rates were significantly higher than baseline for four of the five SFs tested (0.375, 0.75, 3 and 6 cpd; all P-values < 0.03, two tailed paired t-tests), but not for the 1.5 cpd SF (Fig. 6A; $P = 0.06$, two tailed paired t-test), in the [−700, −300] ms interval before transitions to intensification (heretofore the peak interval; this is within the reaction times of subjects doing an equivalent perceptual task with a Gabor that physically faded and intensified; McCamy *et al.*, 2012, 2014). Thus, transiently increased microsaccade production restored the visibility of faded targets for a variety of SFs. Microsaccade rate increases in the peak interval differed across the SFs tested ($F_{4,\ 56} = 2.82$, $P = 0.03$, MSE = 0.231, $\eta_p^2 = 0.168$); we found that (peak interval rate – baseline rate) decreased linearly with SF (Fig. 6B; $F_{1,14} = 5.22$, $P = 0.038$, MSE = 0.657, $\eta_p^2 = 0.272$), suggesting that microsaccades become less important to the reversal of fading as target SF increases. In addition, we found that microsaccade rates in the [−700, −300] ms interval before transitions to fading (heretofore the trough interval) were significantly lower than baseline rates for all SFs tested (all P-values < 10^{-4}, two tailed paired t-tests). This decrease below baseline in the trough interval was significantly different across the SFs tested ($F_{4,56} = 3.249$, $P = 0.018$, MSE = 0.062, $\eta_p^2 = 0.188$); we found a parametric decrease in (baseline rate – trough interval rate) with SF ($F_{1,14} = 4.738$, $P = 0.047$, MSE = 0.086, $\eta_p^2 = 0.253$). This result suggests that microsaccades become less important to the prevention of fading with increasing SF. Our combined data indicate that microsaccades modulate target visibility at a wide range of SFs,

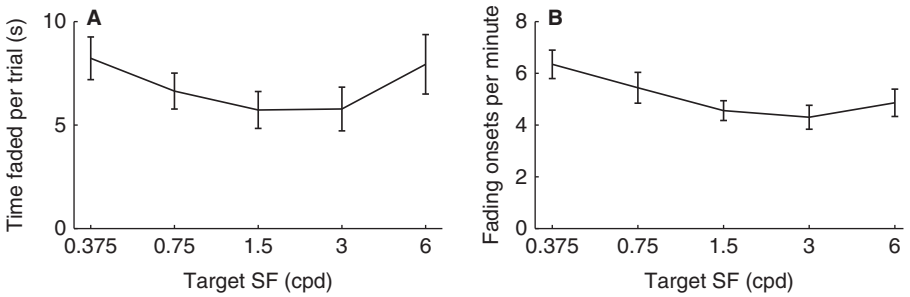

FIG. 2. Perceptual fading dynamics. (A) Average time that targets of different spatial frequencies (SFs) faded per trial. (B) Fading onset rate for each target SF. Error bars indicate the SEM across subjects (n = 15).

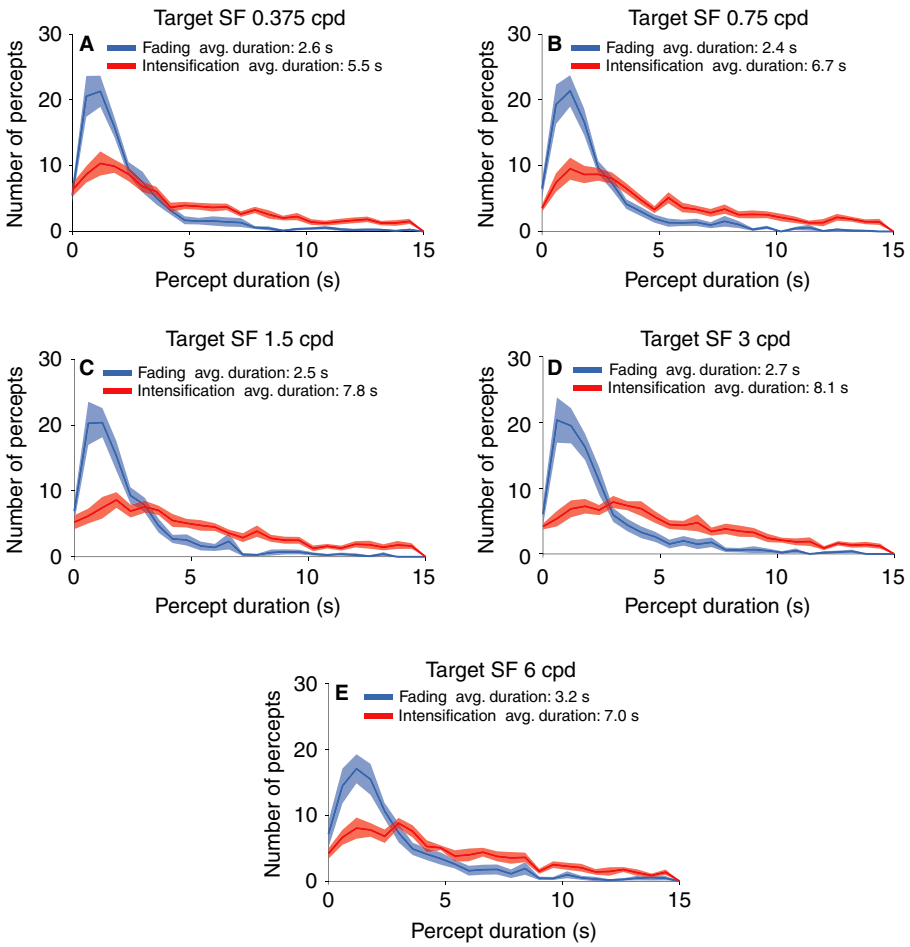

FIG. 3. Fading and intensification durations. (A–E) Distribution of the durations of intensification and fading periods for each target spatial frequency (SF). Red and blue shadows indicate the SEM across subjects (n = 15).

even if they appear to do so more effectively for lower than higher SF targets.

Microsaccade magnitudes

First, we analyzed the global average microsaccade magnitudes for the different SFs and found no significant differences across the SFs tested (Fig. 7; $F_{4,\ 56} = 2.180$, $P = 0.083$, MSE = 0.0004, $\eta_p^2 = 0.135$), an apparently null result ostensibly consistent with (Mostofi *et al.*, 2016; Spotorno *et al.*, 2016). Yet, when we analyzed microsaccade magnitudes in the peak interval (i.e. the [−700, −300] ms interval before transitions to intensification), we found that they were significantly larger than baseline microsaccade magnitudes for all the target SFs tested (Fig. 8A; all P-values < 0.04; two tailed paired t-test), in agreement with (Martinez-Conde *et al.*, 2006; McCamy *et al.*, 2012). Finally, to specifically address whether such increases in microsaccade magnitude during the peak interval differed across SFs, we submitted the variable (average peak magnitude – baseline magnitude) to an ANOVA. No statistical effect of SF was found, i.e. the average peak magnitude did not differ from baseline magnitude differently across SFs (Fig. 8B; $F_{4,\ 56} = 0.958$, $P = 0.4387$, MSE = 0.002, $\eta_p^2 = 0.064$). Thus, our results indicate

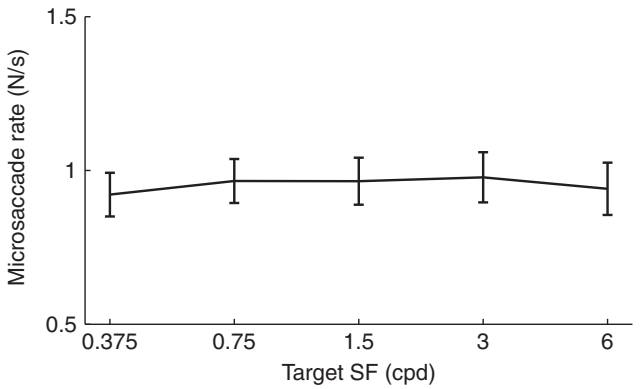

FIG. 4. Global microsaccade rates are equivalent across target spatial frequencies (SFs). Error bars indicate the SEM across subjects (n = 15).

that larger microsaccades reverse fading more efficaciously than small microsaccades, and that they do so equally well for all SFs.

In addition, we asked if individual subjects who differed in their microsaccade rates also might correspondingly differ in their rates of perceptual switching. Thus, we correlated the microsaccade rates and the fading and intensification onset rates of individual participants. The results were not significant, however: in the case of the intensification onset rates and global microsaccade rates of individual subjects, the Pearson correlation coefficient was r = 0.43 with a P-value of 0.13. The Spearman correlation coefficient was ρ = 0.27 with a P-value of 0.33. In the case of fading onset rates and microsaccade rates, the Pearson correlation coefficient was r = 0.45 with a P-value of 0.09. The Spearman correlation coefficient was: ρ = 0.37 with a P-value of 0.178.

Discussion

Recent work on the contrast sensitivity thresholds of low and high SF targets found little or no link between (micro)saccade production and perception (Mostofi *et al.*, 2016; Spotorno *et al.*, 2016). These previous studies related overall (micro)saccade parameters (i.e. global rate) to overall measures of perception, however, so they might have missed a finer relationship between these two variables as a function of SF. To address this conceptual gap, here we time-locked transient changes in microsaccade rates and magnitudes to transient changes in the visibility of targets of various spatial frequencies.

Participants reported on the visibility of targets of various SFs (0.375, 0.75, 1.5, 3, and 6 cpd), while we measured their eye movements. As with previous research (Spillmann & Kurtenbach, 1992; Martinez-Conde *et al.*, 2006; Troncoso *et al.*, 2008a; McCamy *et al.*, 2012; Costela *et al.*, 2013), subjects reported that the

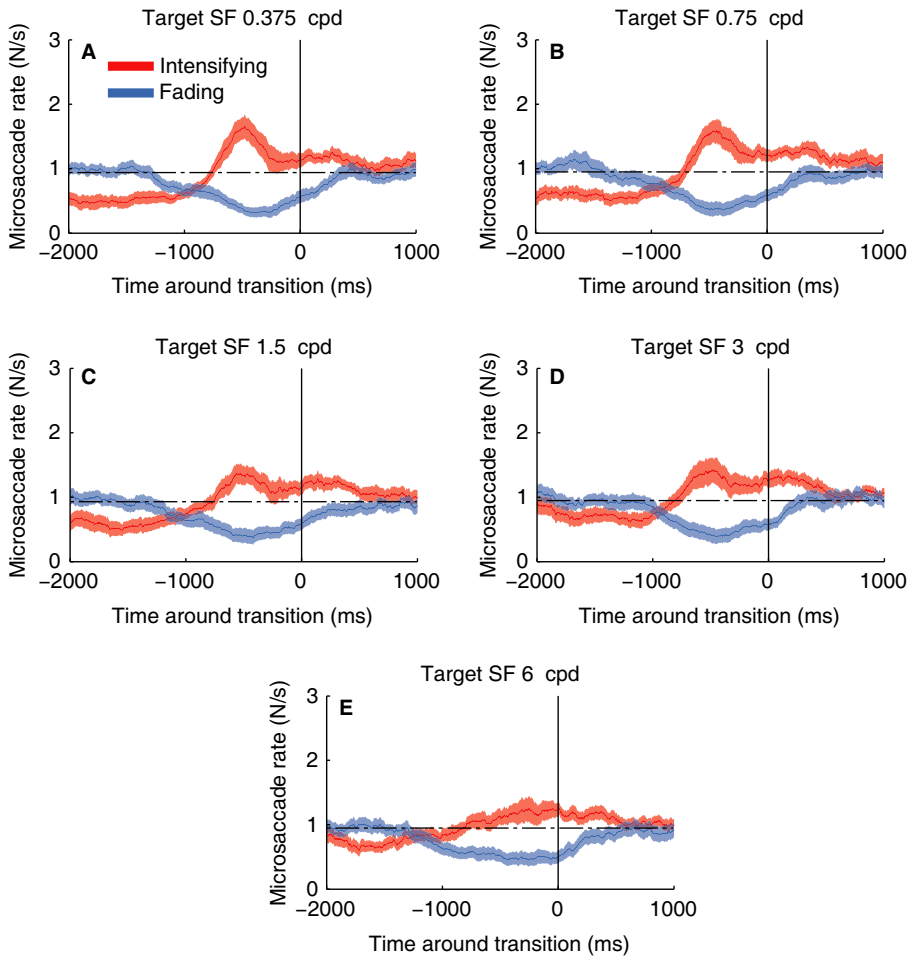

FIG. 5. Microsaccade rate correlations with reported transitions. (A–E) Average microsaccade rates [dashed horizontal line indicates average microsaccade rates for that target spatial frequencies (SF)] around reported transitions toward intensification vs. fading, for each target SF. The solid vertical line indicates the reported transitions (t = 0). Target SF is indicated at the top of each panel. Red and blue shadows indicate the SEM across subjects (n = 15).

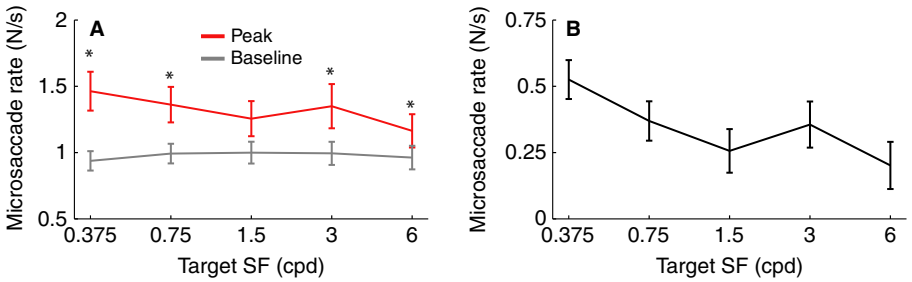

FIG. 6. Microsaccade rates in the peak interval compared to baseline rates. (A) The top line is the average microsaccade rate in the peak interval across spatial frequencies (SFs). The bottom line is the baseline rate across SFs. *Denotes a statistically significant difference between the peak interval and the baseline rate. (B) Difference between the two lines in (A). There was a significant linear decrease across SFs. Error bars indicate the SEM across subjects (n = 15).

perceptual state of the targets appeared to oscillate between the faded/fading state and the visible/intensifying state.

Microsaccade rates increased before transitions to visibility and decreased before transitions to fading for all SFs, in agreement with previous studies conducted with a single SF (Martinez-Conde *et al.*, 2006; Troncoso *et al.*, 2008a,b; McCamy *et al.*, 2012; Costela *et al.*, 2013). The lowest SFs showed the strongest correlations between microsaccade rate increases and intensification reports, and the highest SF (6 cpd) the weakest correlations. Yet, microsaccade production was significantly associated with increased target visibility for all the SFs tested. These data also indicate that targets fade or become harder to see less often in the presence of microsaccades.

Microsaccade magnitudes increased in the peak interval (reaction time interval preceding transitions to increased visibility) compared to baseline magnitudes, and did so in equivalent fashion across all SFs tested. Thus, bigger microsaccades resulted in larger perceptual gains than small microsaccades, for a wide range of SFs.

Our study goes beyond previous research that did not time-lock microsaccade occurrence to perceptual transitions on target visibility (Mostofi *et al.*, 2016; Spotorno *et al.*, 2016). Prior work measured grating discrimination (Spotorno *et al.*, 2016) or contrast sensitivity (Mostofi *et al.*, 2016) variations as a function of SF, and compared such metrics to global microsaccade rates (or occurrence) and global microsaccade magnitudes. These types of coarse analyses make it hard to appreciate the true effects of microsaccades on target visibility: indeed, we also found a lack of connection between microsaccade production and target SF in our dataset, when we looked at the global microsaccade rates only. Yet, once we time-locked transient changes in microsaccade rates to perceptual transitions, we found a significant relationship between microsaccade production and target visibility: increased microsaccade rates preceded visibility enhancements, and decreased microsaccade rates preceded visibility decrements. The present work also improves on previous studies in that 5 SFs were tested (whereas the prior reports limited themselves to 2 or 3 SFs), and subjects merely required to rest their heads on a chin-rest under binocular viewing conditions (Mostofi *et al.* 2016 used a bite bar and monocular viewing conditions). The more natural viewing conditions, larger range of SFs tested, and the finer and more appropriate analyses in the present study allow for more accurate conclusions as to the interaction between microsaccades, target SF, and perception.

Finally, our results do not support Mostofi *et al.* (2016)'s conclusion that neural transients created by microsaccades are unhelpful to vision. First, we note that Mostofi *et al.* (2016) formed their conclusion from the spectral analysis of the input to the retina and a measure of contrast sensitivity, rather than on the biophysical or

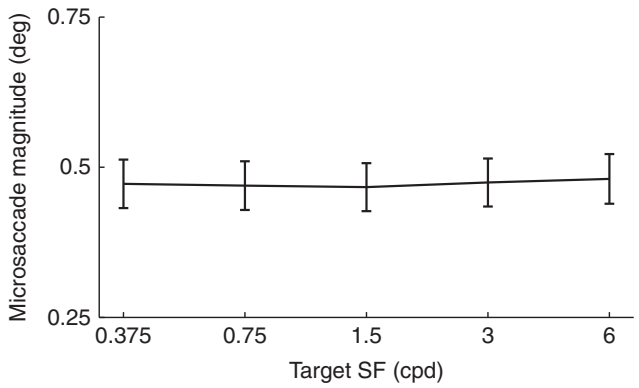

FIG. 7. Global microsaccade magnitudes are equivalent across target spatial frequencies (SFs). Error bars indicate the SEM across subjects (n = 15).

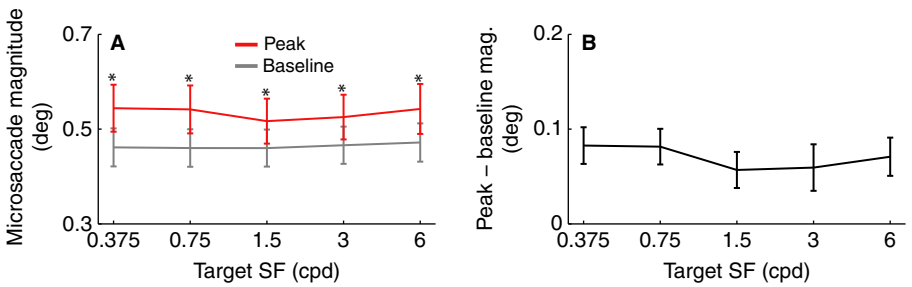

FIG. 8. Microsaccade magnitude dynamics do not change as a function of target spatial frequencies (SF). (A) Peak interval magnitude and baseline magnitude across target SFs. *Denotes a statistically significant difference between peak interval and baseline magnitudes. (B) Peak interval magnitude – baseline magnitude across target SFs. Error bars indicate the SEM across subjects (n = 15).

neurophysiological responses to microsaccades, which they did not measure. Even more critically, Mostofi *et al.* did not analyze transient variations in microsaccade rates throughout their experimental trials, or the temporal relationship of microsaccade production to transient variations in target perception. To properly assess the effects of the transients created by microsaccades on either perception or neural activity, one must time-lock microsaccade occurrence to a neural or a behavioral response in an ongoing fashion (i.e. as in the present study). Thus, Mostofi *et al.* neither had direct access to the neural transients from microsaccades, nor could they assess their effects on perception, because their experimental design did not allow such analyses. Whereas our present study did not have direct access to microsaccade-triggered neural transients either, it did analyze transient variations in microsaccade rates in connection to transient changes in perception. These analyses revealed that the prevalence of microsaccades transiently rose before periods of increased visibility, and transiently dropped before periods of diminished visibility for all SFs tested. In combination with our previous recordings of microsaccade-triggered neural transients in the primate visual system (Martinez-Conde *et al.*, 2000, 2002; Troncoso *et al.*, 2015), the present results support the proposal that transients from microsaccades are beneficial to perception (Livingstone *et al.*, 1996; Macknik & Livingstone, 1998; Martinez-Conde *et al.*, 2002, 2004). More generally, our findings suggest that microsaccades do not modulate perception in exceptional circumstances applying only to narrow stimuli sets or viewing conditions, but as a habitual rule.

Conflict of interest

The authors declare no conflict of interest.

Acknowledgments

We thank Daniel Cortes-Rastrollo, Manuel Ledo, and Rosario Malpica for technical and administrative assistance. This study was supported by a challenge grant from Research to Prevent Blindness Inc. to the Department of Ophthalmology at SUNY Downstate, the Empire Innovation Program (Awards to SLM and SMC), the Barrow Neurological Foundation (Awards to SLM and SMC) and the National Science Foundation (Award 113786 to SMC).

References

Betta, E. & Turatto, M. (2006) Are you ready? I can tell by looking at your microsaccades. *Neuroreport*, **17**, 1001.

Costela, F.M., McCamy, M.B., Macknik, S.L., Otero-Millan, J. & Martinez-Conde, S. (2013) Microsaccades restore the visibility of minute foveal targets. *PeerJ*, **1**, e119.

Ditchburn, R.W. & Ginsborg, B.L. (1952) Vision with a stabilized retinal image. *Nature*, **170**, 36–37.

Engbert, R. (2006) Microsaccades: a microcosm for research on oculomotor control, attention, and visual perception. *Prog. Brain Res.*, **154**, 177–192.

Engbert, R. & Kliegl, R. (2003) Microsaccades uncover the orientation of covert attention. *Vision Res.*, **43**, 1035–1045.

Engbert, R. & Mergenthaler, K. (2006) Microsaccades are triggered by low retinal image slip. *Proc. Natl. Acad. Sci. USA*, **103**, 7192–7197.

Laubrock, J., Engbert, R. & Kliegl, R. (2005) Microsaccade dynamics during covert attention. *Vision Res.*, **45**, 721–730.

Livingstone, M.S., Freeman, D.C. & Hubel, D.H. (1996) Visual responses in V1 of freely viewing monkeys. *Cold Spring Harb. Symp. Quant. Biol.*, **61**, 27–37.

Macknik, S.L. & Livingstone, M.S. (1998) Neuronal correlates of visibility and invisibility in the primate visual system. *Nat. Neurosci.*, **1**, 144.

Martinez-Conde, S., Macknik, S.L. & Hubel, D.H. (2000) Microsaccadic eye movements and firing of single cells in the striate cortex of macaque monkeys. *Nat. Neurosci.*, **3**, 251–258.

Martinez-Conde, S., Macknik, S.L. & Hubel, D.H. (2002) The function of bursts of spikes during visual fixation in the awake primate lateral geniculate nucleus and primary visual cortex. *Proc. Natl. Acad. Sci. USA*, **99**, 13920–13925.

Martinez-Conde, S., Macknik, S.L. & Hubel, D.H. (2004) The role of fixational eye movements in visual perception. *Nat. Rev. Neurosci.*, **5**, 229–240.

Martinez-Conde, S., Macknik, S.L., Troncoso, X.G. & Dyar, T.A. (2006) Microsaccades counteract visual fading during fixation. *Neuron*, **49**, 297–305.

Martinez-Conde, S., Macknik, S.L., Troncoso, X.G. & Hubel, D.H. (2009) Microsaccades: a neurophysiological analysis. *Trends Neurosci.*, **32**, 463–475.

Martinez-Conde, S., Otero-Millan, J. & Macknik, S.L. (2013) The impact of microsaccades on vision: towards a unified theory of saccadic function. *Nat. Rev. Neurosci.*, **14**, 83–96.

McCamy, M.B., Otero-Millan, J., Macknik, S.L., Yang, Y., Troncoso, X.G., Baer, S.M., Crook, S.M. & Martinez-Conde, S. (2012) Microsaccadic efficacy and contribution to foveal and peripheral vision. *J. Neurosci.*, **32**, 9194–9204.

McCamy, M.B., Collins, N., Otero-Millan, J., Al-Kalbani, M., Macknik, S.L., Coakley, D., Troncoso, X.G., Boyle, G. *et al.* (2013a) Simultaneous recordings of ocular microtremor and microsaccades with a piezoelectric sensor and a video-oculography system. *PeerJ*, **1**, e14.

McCamy, M.B., Najafian Jazi, A., Otero-Millan, J., Macknik, S.L. & Martinez-Conde, S. (2013b) The effects of fixation target size and luminance on microsaccades and square-wave jerks. *PeerJ*, **1**, e9.

McCamy, M.B., Macknik, S.L. & Martinez-Conde, S. (2014) Different fixational eye movements mediate the prevention and the reversal of visual fading. *J. Physiol.*, **592**(pt 19), 4381–4394.

Mostofi, N., Boi, M. & Rucci, M. (2016) Are the visual transients from microsaccades helpful? Measuring the influences of small saccades on contrast sensitivity. *Vision Res.*, **118**, 60–69.

Riggs, L.A. & Ratliff, F. (1952) The effects of counteracting the normal movements of the eye. *J. Opt. Soc. Am.*, **42**, 872–873.

Rolfs, M., Laubrock, J. & Kliegl, R. (2006) Shortening and prolongation of saccade latencies following microsaccades. *Exp. Brain Res.*, **169**, 369–376.

Spillmann, L. & Kurtenbach, A. (1992) Dynamic noise backgrounds facilitate target fading. *Vision Res.*, **32**, 1941–1946.

Spotorno, S., Masson, G.S. & Montagnini, A. (2016) Fixational saccades during grating detection and discrimination. *Vision Res.*, **118**, 105–118.

Troncoso, X.G., Macknik, S.L. & Martinez-Conde, S. (2008a) Microsaccades counteract perceptual filling-in. *J. Vis.*, **8**, 1–9.

Troncoso, X.G., Macknik, S.L., Otero-Millan, J. & Martinez-Conde, S. (2008b) Microsaccades drive illusory motion in the Enigma illusion. *Proc. Natl. Acad. Sci. USA*, **105**, 16033–16038.

Troncoso, X.G., McCamy, M.B., Jazi, A.N., Cui, J., Otero-Millan, J., Macknik, S.L., Costela, F.M. & Martinez-Conde, S. (2015) V1 neurons respond differently to object motion and to self-generated motion due to eye movements. *Nat. Commun.*, **6**, 8114.

Yarbus, A.L. (1957) The perception of an image fixed with respect to the retina. *Biophysics*, **2**, 683–690.