Are the visual transients from microsaccades helpful? Measuring the influences of small saccades on contrast sensitivity

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ABSTRACT

Like all saccades, microsaccades cause both spatial and temporal changes in the input to the retina. In space, recent studies have shown that these small shifts precisely relocate a narrow (smaller than the foveola) high-acuity retinal locus on the stimulus. However, it has long been questioned whether the temporal modulations resulting from microsaccades are also beneficial for vision. To address this question, we combined spectral analysis of the visual input to the retina with measurements of contrast sensitivity in humans. Estimation of how different types of eye movements redistribute the power of an otherwise stationary stimulus shows that small saccades contribute more temporal power than ocular drift in the low-frequency range, suggesting a specific role for these movements in the encoding of low spatial frequencies. However, an influence on contrast sensitivity was only found for saccades with amplitudes larger than 30′. Contrast thresholds remained highly similar in the presence and absence of smaller saccades. Furthermore, saccades of all amplitudes, including microsaccades, were strongly suppressed during exposure to the stimulus. These findings do not support an important function of the visual transients caused by microsaccades.

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1. Introduction

The visual functions of microsaccades have long been debated (Collewijn & Kowler, 2008; Rolfs, 2009). Several recent findings provide evidence that microsaccades, like saccades with larger amplitudes, serve important *spatial* functions. Studies with accurate localization of the line of sight have shown that, during examination of fine spatial detail, microsaccades precisely shift gaze among nearby objects of interest (Ko, Poletti, & Rucci, 2010). This strategy appears to take advantage of a small preferred retinal locus of fixation which enhances performance in high-acuity tasks (Poletti, Listorti, & Rucci, 2013). In addition, microsaccades also seem to be part of the normal oculomotor strategy by which humans maintain their gaze spatially close to a marker when requested to do so (Cornsweet, 1956; Engbert & Kliegl, 2004; Cherici et al., 2012), even though strict fixation can also be maintained by means of ocular drift alone (Steinman et al., 1973).

Besides these spatial effects, it has long been argued that microsaccades may also serve important *temporal* functions. According to a popular proposal—but subject to sharp disagreement (*e.g.*, Collewijn & Kowler, 2008)—the visual transients caused by microsaccades are necessary for preventing the progressive fading experienced when stimuli are artificially immobilized on the retina (Ditchburn, Fender, & Mayne, 1959; Martinez-Conde et al., 2006). Furthermore, contrast thresholds to stationary low-frequency gratings have been found to be lower in a relaxed fixation condition with small saccades than under strict fixation (Deubel & Elsner, 1986), suggesting that temporal modulations resulting from microsaccades may enhance sensitivity to low spatial frequencies.

Since recent studies have shown that the input luminance fluctuations resulting from ocular drift amplify high spatial frequencies (Rucci et al., 2007), a microsaccade enhancement of low spatial frequencies raises the interesting hypothesis that ocular drift and microsaccades may serve complementary functions in transforming spatial information into temporal modulations. Complementary roles for microsaccades and drift are supported by neurophysiological findings, which have suggested the existence of distinct neuronal populations that selectively respond to the input signals elicited by ocular drift and microsaccades (Riva Sanseverino et al., 1979; Kagan, Gur, & Snodderly, 2008). However, the effect opposite to that described by Deubel and Elsner (1986)—*i.e.,* an adverse consequence of microsaccades on visual sensitivity—has also been reported (Ditchburn, 1955; Beeler, 1967; Zuber & Stark, 1966; Hass & Horwitz, 2011; but see Krauskopf, Graf, & Gaarder, 1966) with a reduction in contrast sensitivity at the time of microsaccades

similar to the "saccadic suppression" of larger saccades (Volkmann et al., 1978; Ross et al., 2001).

Surprisingly, no previous study has examined the actual information content of the input transients caused by microsaccades, nor specifically isolated the influences of these transients on contrast sensitivity thresholds in human observers. To start filling this gap, here we coupled spectral analyses with measurements of human contrast sensitivity. We (a) examine how the abrupt changes in the retinal stimulus caused by microsaccades and small saccades transform the spatial frequency content of a static stimulus into a spatiotemporal frequency distribution on the retina; and (b) assess the impact of these transformations on visual sensitivity at low and high spatial frequencies.

2. Materials and methods

2.1. Subjects

Five subjects (all females, age range: 21–31 years) with normal vision participated in this study. All observers, with the exception of one of the authors (NM), were naïve about the purpose of the experiment and were compensated for their participation. All participants gave their informed consent following the procedures approved by the Boston University Charles River Campus Institutional Review Board. The work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus

Stimuli were displayed on a fast phosphor monitor (Iyamaya HM204DT) at a resolution of 800 × 600 pixels and vertical refresh rate of 200 Hz in a dimly illuminated room. The monitor was calibrated to linearize the relationship between the input gray level and the displayed luminance. Subjects looked at stimuli from a fixed distance of 126 cm from the monitor. A dental-imprint bite bar and a head-rest restricted head movements. Stimuli were observed monocularly with the right eye, while the left eye was patched.

A Generation 6 Dual Purkinje Image (DPI) eye-tracker (Fourward Technologies) was used to record eye movements. This system possesses a time delay of about 0.25 ms and an internal noise level of less than 20″ (Crane & Steele, 1985), yielding a resolution—measured by means of an artificial eye—of approximately 1′. Vertical and horizontal eye positions were sampled at 1 kHz and recorded for subsequent analysis.

2.3. Stimuli

Stimuli consisted of 2D Gabor patterns oriented at ±45° (Fig. 1A). Their contrast varied across trials following the Parametric Estimation by Sequential Testing (PEST) procedure (Taylor & Creelman, 1967), always starting from an initial contrast level at least one order of magnitude above threshold. The frequency of the Gabor grating was either 0.8 cycles/deg (low spatial frequency condition) or 10 cycles/deg (high spatial frequency condition). In both cases, the standard deviation of the Gabor was 2.25°. Stimuli were displayed over a uniform field with luminance of 21 cd/m². To minimize transients not resulting from eye movements, in each trial, the contrast of the stimulus first increased gradually from zero to the selected level over a period of 500 ms (ramp-up phase) and then remained at the constant value determined by the PEST procedure for another 500 ms (plateau phase), as shown in Fig. 1C.

2.4. Procedure

Data were collected in separate experimental sessions, each with approximate duration of 1 h. Every session started with
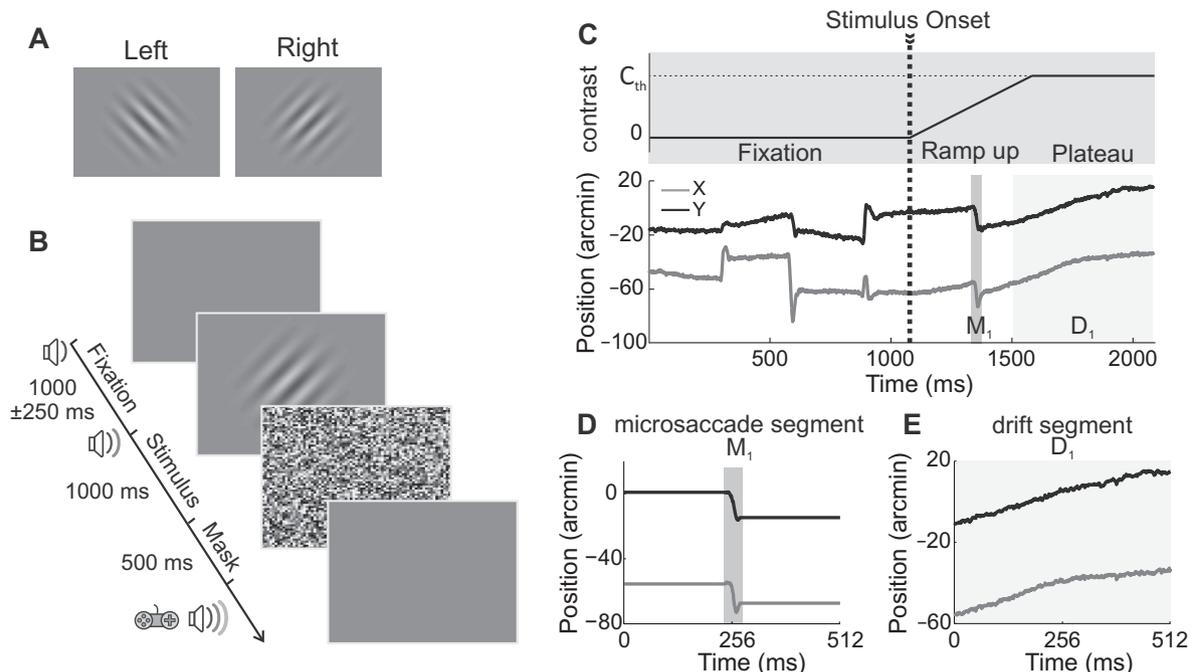

Fig. 1. Experimental design and methods. (A) Subjects reported whether a Gabor grating was tilted by 45° to the left or to the right. Stimuli were displayed at either 0.8 cycles/deg (low spatial frequency) or 10 cycles/deg (high spatial frequency). (B) Stimuli were presented for 1 s after a fixation period with random duration and were followed by a high-contrast mask. (C) Stimulus contrast increased gradually from zero to the desired level (C_{th}) in 500 ms (ramp-up phase) and then remained constant for another 500 ms (plateau phase). The dashed vertical line indicates the start of the stimulus presentation interval. An example of recorded eye movements in a trial is also shown (bottom traces) together with the selected periods used for the spectral analyses of the retinal input (shaded regions M_1 and D_1). (D–E) Examples of the microsaccade (D) and drift segments (E) used for the spectral analysis. Segments had duration of 512 ms and consisted of one isolated microsaccade/small saccade (D) or a period of continuous, uninterrupted drift (E). In D, pre- and post-saccadic drift modulations were eliminated from the trace to isolate the impact of the saccadic gaze shift.

preliminary operations which were necessary to: (a) position the subjects in the apparatus; (b) tune the eye-tracker to optimally measure eye movements; (c) perform a calibration procedure to convert the eye-tracker data into visual angles; and (d) start the data acquisition protocols. These preparatory operations lasted for a few minutes and allowed the subjects to adapt to the low level of light in the room. They were repeated before each block of trials within a session. Data were then recorded in blocks of 50 trials, with four blocks collected in each session. The duration of these blocks was chosen so that subjects were never constrained in the experimental setup for longer than 10 min consecutively. Brief breaks (5–10 min) separated consecutive blocks and allowed the subject to rest.

Conversion of the eye position measurements given by eye-tracker into degrees of visual angle was performed by means of a gaze-contingent calibration procedure identical to the one used in our previous experiments (Ko, Poletti, & Rucci, 2010; Poletti, Listorti, & Rucci, 2013) and, therefore, only briefly summarized here. It consisted of two steps. In the initial phase, the subject sequentially fixated on the nine points of a 3×3 grid evenly spaced within the working area of the display. For each fixation point, the mean output voltage from the eye-tracker was estimated and used to set up a preliminary transformation based on a bilinear interpolation. In the second phase, the subject fine-tuned this mapping. They fixated again on each of the points of the grid and corrected for possible conversion errors by adjusting the position of a red cross displayed in real time at the estimated center of gaze. This refinement phase was repeated every five trials for the central marker only, to correct for possible drifts in the signals and ensure accurate gaze localization throughout the experimental session.

In a forced-choice procedure, subjects were asked to report whether a low-contrast grating was tilted to the left or to the right by 45° (Fig. 1B). The orientation of the grating varied randomly across trials. Each trial started with the subject fixating at the center of the uniform field. The onset of the ramp-up phase occurred after a random delay (750–1250 ms) from the moment in which the line of sight was within the central 2° window of the display and was signaled by a tone. The entire period of stimulus presentation, given by the combination of the ramp-up and the plateau phase, was 1 s. The stimulus was then followed by a white noise high-contrast mask, which remained on the monitor for 500 ms. Subjects reported the orientation of the grating using a joypad after the appearance of the mask. Feedback about the correctness of the responses was given to the subject by means of two distinct tones.

To ensure normal oculomotor activity, subjects were only told that the grating would be most visible at the center of the display and left free to explore the stimulus. With the exception of the initial fixation threshold to start a trial, at no point during the course of the experiment they were required to maintain fixation. Only one spatial frequency, either high or low, was tested in each experimental session. Subjects practiced with a block of 10 trials at the beginning of each session to familiarize/remind themselves about the stimulus characteristics and the task.

2.5. Data analysis

Contrast thresholds resulting in 75% performance were measured by fitting a cumulative log-normal psychometric function to the data collected during the adaptive PEST procedure (Hall, 1981). This operation was performed using a maximum likelihood procedure (Wichmann & Hill, 2001) based on the data collected in all the valid trials. These were the trials with optimal, uninterrupted tracking and in which the line of sight remained within 2.25° from the center of the display. This distance is equal to one standard deviation of the stimulus Gaussian envelope and ensured that the fovea was exposed to approximately uniform contrast during

the measurement. Subjects remained within this area even without an explicit requirement for strict fixation, and only 6% of the trials were discarded for exceeding this threshold. The contrast sensitivity values reported in Fig. 4 are the inverse of Michelson contrast thresholds.

Recorded eye movement traces were segmented into separate periods of drift and saccades based on the velocity of the trajectory. Periods of blinks were automatically detected by the DPI eye-tracker and removed from data analysis. Eye movements with minimal amplitude of 3′ and peak velocity higher than 3°/s were selected as saccades. Consecutive events closer than 15 ms were merged together into a single saccade, a method which automatically took care of possible post-saccadic overshoots (Deubel & Bridgeman, 1995). For each event, we defined the time of saccade onset and offset as the instants immediately before and after the event at which the eye speed became greater and lower than 2°/s, respectively. Saccade amplitude was given by the modulus of the vector connecting the eye positions at these two instants. Microsaccades were defined as saccades with amplitude smaller than 30′. Classification of eye movement data was performed automatically and then validated by visual inspection.

Saccade rates were estimated over consecutive non-overlapping time intervals after aligning all trials with the onset of stimulus presentation (time $t = 0$ in Fig. 5). To ensure selection of trials in which microsaccades (or small saccades) could exert an influence, only trials with contrast in the 60–90% performance range were included in the analysis of rates in Fig. 5.

2.6. Retinal input analysis

Spectral analyses were conducted to estimate how different types of eye movements convert spatial information into spatiotemporal luminance modulations on the retina. To achieve high-resolution estimations of spectral densities, we used a recently developed model (see Supplementary information in Kuang et al., 2012), which links the power spectrum of the retinal input, S, to the characteristics of eye movements and the spectral distribution of the external scene I:

$$S(\mathbf{k}, \omega) = I(\mathbf{k})Q(\mathbf{k}, \omega) \tag{1}$$

where $\mathbf{k}$ and ω represent spatial and temporal frequencies, respectively, and $Q(\mathbf{k}, \omega)$ is the Fourier Transform of the displacement probability of the stimulus on the retina $q(\mathbf{x}, t)$, i.e., the probability that the eye moved by $\mathbf{x}$ in an interval t.

The model in Eq. (1) relies on the assumptions that (1) the external stimulus possesses spatially homogenous statistics, and (2) the fixational motion of the retinal image is statistically independent from the external stimulus. The assumption of independence may not hold in restricted regions of the visual field, e.g., in the fovea, where stimulus-driven movements may yield statistical dependencies between retinal motion and the image. It is, however, a very plausible assumption when considered across the entire visual field, as the estimation of the power spectrum entails. For the specific experiments of this study, the assumption of independence seems to also hold within fovea, as we could not detect any dependence between gaze shifts and foveal stimulation. This model has provided excellent approximations of the power spectra of visual input signals measured during ocular drift in a previous study (Kuang et al., 2012).

Given an external stimulus with power I_0 at spatial frequency $\mathbf{k}_0$, Eq. (1) shows that the average spatiotemporal power made available by eye movements at temporal frequency ω, is proportional to $Q(\mathbf{k}_0, \omega)$. Therefore, to examine the individual consequences of ocular drift and microsaccades, we directly estimated the corresponding $Q(\mathbf{k}, \omega)$ in the frequency domain on the basis

of trace segments that only contained the considered type of eye movements. Under the model assumptions, this approach is equivalent to reconstructing the spatiotemporal input movie to the retina and then estimating its spectrum, but it enables much higher spatial resolution.

For ocular drift, we used uninterrupted non-overlapping drift segments of 512 ms recorded during presentation of the stimulus (Fig. 1C and E), an approach similar to that of our previous studies (Kuang et al., 2012; Aytekin, Victor, & Rucci, 2014). For microsaccades, we extracted each event from its original trace and placed it at the center of an artificial 512 ms trace in which the eye remained immobile before and after the saccade. In this way, we isolated the microsaccade input modulations from those of the pre-and post-saccadic drifts (Fig. 1D). This approach enabled quantitative comparison with the spectrum of the visual input present during ocular drift. Strictly speaking, saccades yield a non-stationary visual input to the retina. The result of this analysis is designed to capture the frequency characteristics of the input signal that drives the responses of standard linear (or linear–non-linear) models of ganglion cells in the initial period of fixation immediately following a saccade (Desbordes & Rucci, 2007; Rucci, 2008). For completeness, we also examined the spectrum of the retinal input resulting from sequences of eye movements that contained both drift and microsaccades (dashed line in Fig. 3F). In this case, $Q(\mathbf{k}, \omega)$ was estimated over trace segments that contained two drift periods separated by a microsaccade, again recorded during stimulus exposure.

Power spectra were estimated individually for each subject and then averaged across observers. To summarize our results in two dimensions (space and time), power spectra in Fig. 3 are presented after taking radial averages in the spatial frequency plane ($k = ||\mathbf{k}||$). We will use the term dynamic power to indicate the total power made available by eye movements at nonzero temporal frequencies. The data in Fig. 3F represent the estimated dynamic power after integration across all temporal frequencies that were not contaminated by DC leakage (all frequencies above 3.9 Hz).

3. Results

We recorded the eye movements of human observers in a forced-choice discrimination task in which subjects reported the orientation (±45°) of a Gabor grating displayed at either low (0.8 cycles/deg) or high (10 cycles/deg) spatial frequency, as illustrated in Fig. 1. The contrast of the stimulus varied across trials following an adaptive procedure to measure 75% contrast thresholds. To ensure natural oculomotor activity, strict fixation was not enforced in this experiment. Observers were only instructed to look around the central region of the display and told that the probability of correctly discriminating the stimulus would be higher here, but they could freely explore the stimulus using microsaccades as well as saccades with larger amplitudes.

Fig. 2 shows the characteristics of the recorded eye movements. Saccades were not frequent in these experiments, with an overall rate (the rate of saccades of all amplitudes including microsaccades) of only 0.65 saccades/s during the period of stimulus presentation. Thus, subjects were tested extensively in order to collect sufficiently large pools of data for the statistical analyses. We will examine saccade rates in detail later in this section (Fig. 5). Even though subjects were not forced to maintain fixation, they made relatively small saccades throughout the trial (Fig. 2A–C). The average saccade amplitude during the 500 ms period preceding the presentation of the stimulus was 41′ and was slightly larger, but not significantly different, than the average saccade amplitude occurring during the period of stimulus presentation
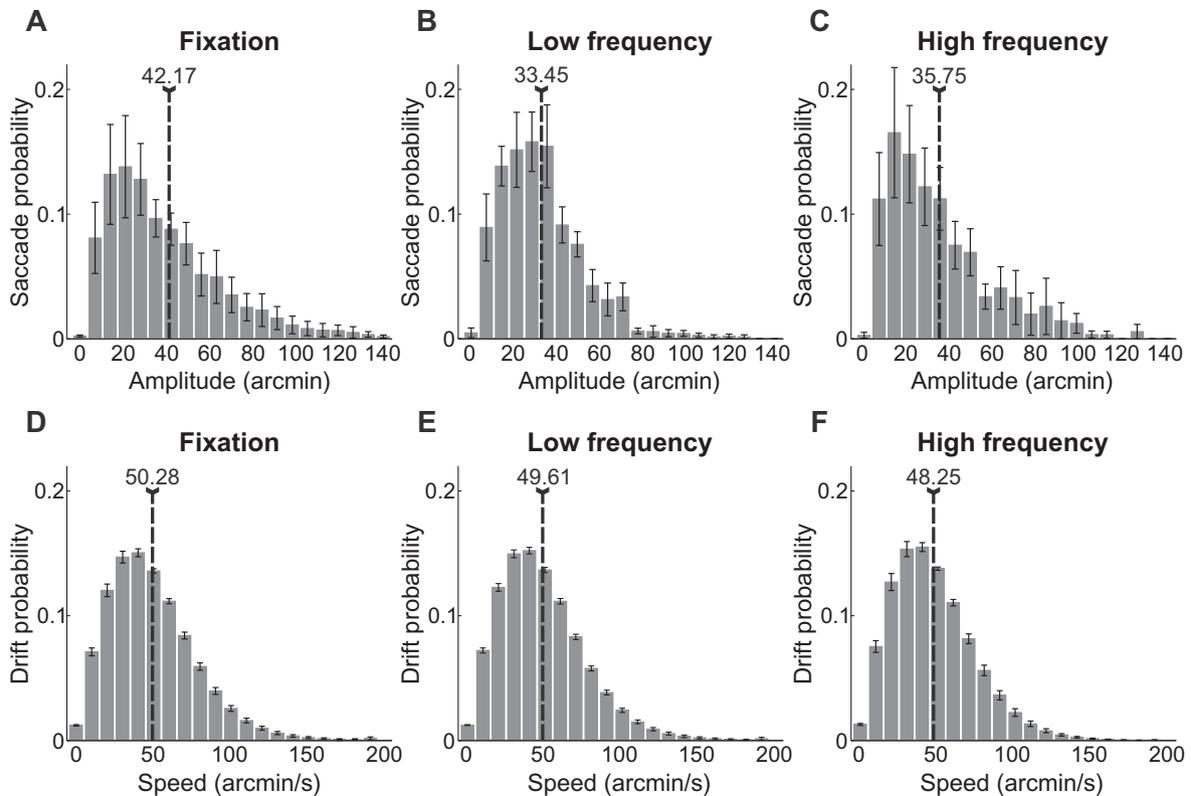

Fig. 2. Eye movements characteristics. (A–C) Distributions of saccade amplitudes during fixation (A) and during exposure to low (B) and high (C) spatial frequency stimuli. (D–F) Corresponding distributions for the instantaneous speed of ocular drift. Data represent averages across 5 observers. Dashed lines indicate mean values. Error bars represent SEM.

(35′; $p = 0.14$, paired two-tailed t-test). Similar saccadic amplitudes were measured during the exposure to low and high spatial frequency stimuli (Low frequency amplitude: 33′; high frequency: 36′; $p = 0.74$, paired two-tailed t-test). The mean value of the instantaneous drift speed was approximately 50′/s. The speed of ocular drift was virtually identical in the two conditions of high and low spatial frequencies and also remained similar in the various phases of the experiment (fixation vs. stimulus presentation; Fig. 2D–F).

To understand the potential consequences of the temporal transients introduced by eye movements, we first examined how these modulations reformatted external spatial information into a spatiotemporal input to the retina. In the absence of eye movements and other motor activity, a stationary scene would project to a static image on the retina. However, eye movements modulate input signals, shifting the power of a stationary stimulus from zero to non-zero temporal frequencies. This transformation is linear in space but not in time, as energy remains at the same spatial frequency of the external stimulus but migrates to new temporal frequencies. We studied this transformation following an approach similar to that of our previous studies (Kuang et al., 2012; Aytekin, Victor, & Rucci, 2014): different types of eye movements were selected and isolated from the recorded oculomotor traces and used to estimate how the resulting retinal motion redistributed energy at each individual spatial frequency (Fig. 1C–E).

Before analyzing the effects of microsaccades and small saccades, we first establish a comparison reference by examining the energy redistribution caused by ocular drift, the incessant intersaccadic motion of the eye. This redistribution can be regarded as a baseline, since ocular drift is always present when other types of eye movements do not occur. The data in Fig. 3A represent the temporal power made available by drift for a fixed-contrast grating at any given spatial frequency. Ocular drift redistributed the power of a static grating in a very specific way: at any nonzero temporal frequency, the power contained in the drift modulations

increased proportionally to the square of the spatial frequency over a broad frequency range (Fig. 3C). This spectral redistribution is very similar to that previously found when subjects freely observed images of natural scenes (Kuang et al., 2012). We have already emphasized in this previous study how such input reformatting counterbalances the spectral distribution of natural images, yielding temporal modulations with power equalized across a broad range of spatial frequencies on the retina. This effect eliminates predictable correlations in natural scenes and enhances luminance discontinuities.

The bottom row of Fig. 3 shows the results of a similar analysis applied to the retinal input changes caused by saccades of different amplitudes—and, for completeness, by sequences containing both drifts and microsaccades—during viewing of a grating at any given spatial frequency. The data in Fig. 3B represent the spatiotemporal power transiently made available on the retina by microsaccades (saccades smaller than 30′). These data show that microsaccades redistribute the power of the stimulus in a very different way than ocular a consequence of the faster displacements of the retinal image, the resulting power at nonzero temporal frequencies no longer increased with spatial frequency as in the case of ocular drift, but was more evenly distributed. Notably, microsaccade modulations contained more temporal power than drift modulations up to approximately 10 cycles/deg. This difference can be clearly appreciated by comparing the total dynamic power—i.e., the sum of all power at nonzero temporal frequency—given by ocular drift and microsaccades in Fig. 3F.

Similar results were also obtained for saccades with larger amplitudes than classical microsaccades (saccades in the 0.5–1° range) and are summarized in Fig. 3F. These modulations contained even more dynamic power than those resulting from microsaccades but possessed a similar spectral distribution. Thus, drift and microsaccades yield luminance modulations with highly different spatial frequency content. These results support complementary roles for these two types of eye movements in reformatting a static
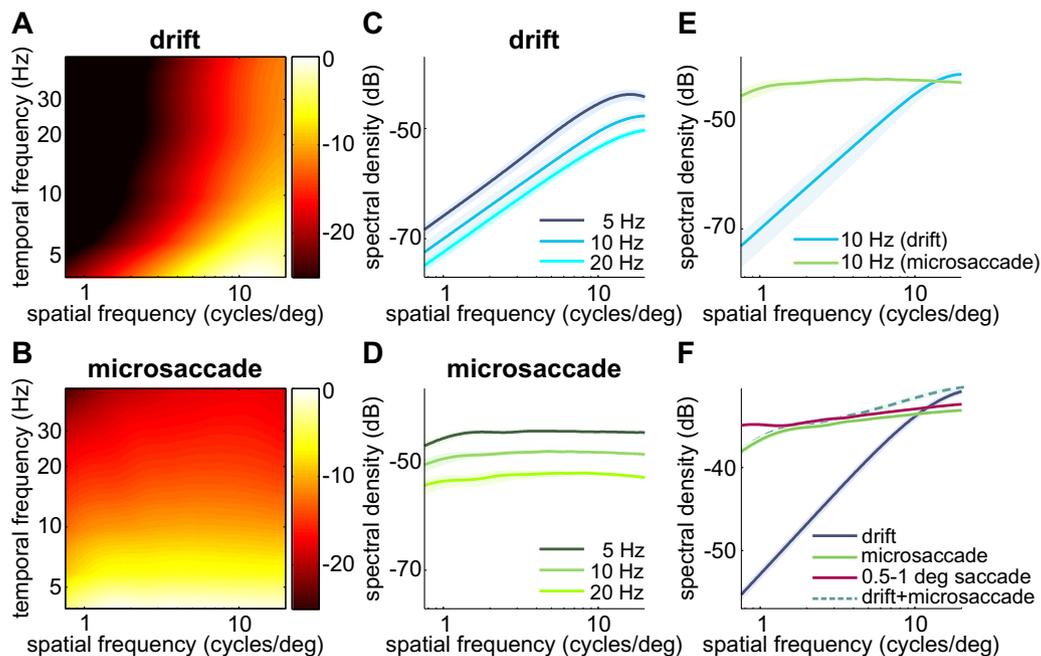

Fig. 3. Frequency content of the retinal input resulting from different types of eye movements. (A, B) Spatiotemporal spectra of the luminance modulations given by drifts (A) and microsaccades (B). (C, D) Spatial distributions at selected temporal frequencies. (E) Comparison between the power resulting from microsaccades and drift at one representative temporal frequency (10 Hz). (E) Comparison among the total temporal power resulting from different types of eye movements: drift, microsaccades, small saccades (saccades larger than 0.5° and smaller than 1°), and sequences that included both drift and microsaccades. At low spatial frequencies, microsaccades and small saccades contribute more temporal power than ocular drift. Shaded areas in C–F represent one SD.

stimulus into a suitable spatiotemporal input signal. Whereas drift enhances high spatial frequency vision, microsaccades and small saccades may enhance sensitivity to low spatial frequencies.

To test the theoretical predictions emerging from the spectral analysis of Fig. 3, we examined whether microsaccades and small saccades affect contrast sensitivity. We measured contrast thresholds at two spatial frequencies (0.8 and 10 cycles/deg) and compared the thresholds obtained in trials with different types of eye movements. The two spatial frequencies were selected within the ranges at which saccade and drift transients are predicted to have different effects on sensitivity. To isolate the possible effects of eye movements and attenuate the impact of the transients given by the stimulus presentation itself, the contrast of the stimulus increased gradually over a period of 500 ms (ramp-up phase) and then remained constant for an additional 500 ms (plateau phase).

Fig. 4A compares the mean contrast sensitivity measured in the trials in which the eye only moved by means of ocular drift—that is, the trials in which neither saccades nor microsaccades occurred during stimulus exposure—to that measured in the trials in which one or more microsaccades were present. Data represent the average contrast sensitivity (the inverse of Michelson contrast thresholds) across all observers. As mentioned above, this comparison required collection of large numbers of trials, as observers performed few microsaccades during stimulus presentation, an effect relevant on its own and analyzed later. In fact, despite our extensive data collection, for one subject we could not estimate contrast sensitivity in the high frequency condition because of the lack of microsaccade trials: only 3 trials out of 686 contained microsaccades during stimulus exposure. Hence, only data from 4 observers are included in this comparison in Fig. 4A.

Contrast sensitivity was little affected by the occurrence of microsaccades. In the high spatial frequency condition, we measured a small change in sensitivity well within the range of normal variability ($p = 0.54$, paired two-tailed t-test). Two subjects slightly improved their sensitivity in the presence of microsaccades, whereas the other two subjects did slightly worse. In the low spatial frequency condition, sensitivity values were almost identical in the trials with and without microsaccades ($p = 0.63$, paired two-tailed t-test). One observer exhibited a small improvement in the microsaccade trials, two others became slightly less sensitive with microsaccades, and the remaining two subjects gave virtually identical thresholds with and without microsaccades. Thus, our data did not support the hypothesis that microsaccade transients influence contrast sensitivity neither at low nor at high spatial frequencies.

Fig. 4B reports the results of a similar analysis for small saccades with amplitude in the 0.5–1° range. Unlike microsaccades, these movements exerted a marked influence on contrast sensitivity at low spatial frequency, which sharply improved in the trials with one or more saccades. On average across the five observers, the contrast sensitivity value measured in the trials which contained at least a small saccade increased by 39% relative to the measurement obtained in the drift-only trials. This sensitivity enhancement was visible in all observers, with a minimum individual increment of approximately 10%, and was highly significant ($p = 0.03$, paired two-tailed t-test). As predicted, it was specific for low spatial frequency stimuli: no perceptual benefit was observed during presentation of a high-frequency grating, a condition in which contrast sensitivity changed very little in the presence/absence of small saccades ($p = 0.88$, paired two-tailed t-test). This improvement was not caused from a possible spatial role of saccades in relocating the center of gaze toward regions of higher contrast. In the low-frequency condition, only 53% of the saccades moved the line of sight toward the center of the stimulus ($p = 0.51$; t-test). This percentage was actually higher with high frequency gratings (59% of saccades; $p = 0.11$), the condition in which we measured no perceptual improvement in the saccade trials.

To summarize, the predicted enhancement in low-frequency sensitivity was only observed in the presence of saccades with amplitude larger than 0.5°. Contrary to prediction, contrast thresholds at low spatial frequencies were virtually identical in the presence/absence of microsaccades. Furthermore, in agreement with the predictions of the spectral analysis, no significant change was found in contrast sensitivity at high spatial frequencies neither for microsaccades nor for larger saccades.

We have already remarked that the saccade rate was low during exposure to the stimulus. In fact, this rate was not constant throughout the course of the trial, but decreased to very low values during the period of stimulus presentation. This effect was particularly pronounced during the later stimulus interval, the plateau phase of constant contrast, presumably the most important period for executing the task. It occurred for saccades of all sizes, both microsaccades and small saccades, during presentation of both low and high spatial frequency stimuli. Across all subjects and stimulus conditions, the overall rate for saccades of any size (including microsaccades) was approximately of only one saccade/microsaccade every 3.5 s during the plateau phase, *i.e.*, one saccade every 7 trials.

The right column in Fig. 5, summarizes the temporal evolution of the rates of microsaccades and small saccades during
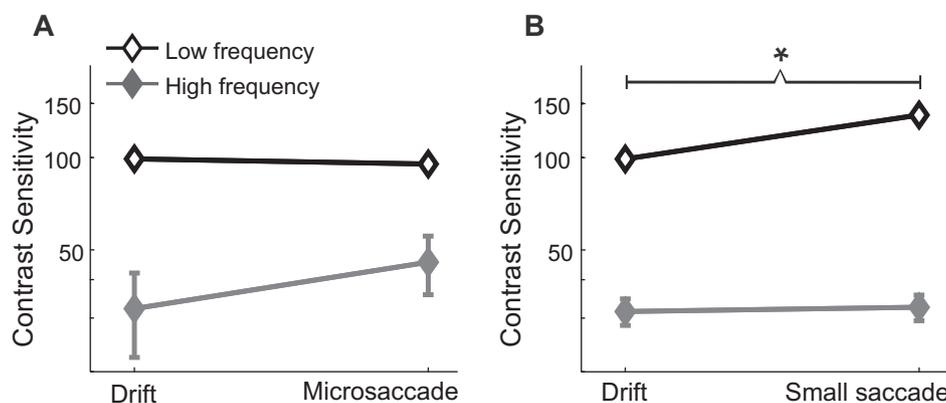
Fig. 4. Contrast sensitivity with different types of eye movements. (A) Comparison between the average sensitivities measured in the drift-only trials (Drift) and in the trials in which one or more microsaccades occurred during stimulus exposure (Microsaccade). Results are shown for both low (0.8 cycles/deg) and high (10 cycles/deg) spatial frequency stimuli. (B) Same as in A, but for small saccades with amplitudes in the 0.5–1° range. Data points represent averages across all observers ($N = 5$), except in the high-frequency condition of A ($N = 4$; one observer not included because microsaccades were too rare). Errorbars represent SEM. Asterisk marks statistical significance ($p < 0.05$; two-tailed paired t-test).

observation of high spatial frequency gratings. The average microsaccade rate decreased from 0.79 microsaccades/s before stimulus onset to 0.36 microsaccades/s during the entire period of exposure to the stimulus ($p = 0.03$; paired one-tailed t-test) and to 0.11 microsaccades/s during the plateau phase of constant stimulus contrast ($p = 0.02$; paired one-tailed t-test; Fig. 5B). All subjects exhibited this suppression, which ranged individually from 42% to 63% (average across subjects: 54%) and reached an average value of 86% during the plateau phase. A similar suppression also occurred for small saccades ($p = 0.03$; paired one-tailed t-test), with a reduction in rate of 66% (89% during the plateau phase; Fig. 5D).

A suppression of saccades during viewing of high-frequency gratings may be expected from our spectral analysis, as in this frequency range the input modulations caused by saccades and ocular drift contain approximately equal power. However, a very similar suppression was also observed with low-frequency stimuli (left column in Fig. 5), the condition in which transients from small saccades were actually helpful. In this condition, microsaccade rates decreased from 0.58 microsaccades/s before stimulus onset to 0.35 during the period of stimulus presentation and to 0.17 microsaccades/s during the plateau period, a change which barely fell short of significance ($p = 0.06$, paired one-tailed t-test). Again, all subjects exhibited this suppression, which ranged from 12% to 70% (average across observers: 40%) in the entire period of stimulus presentation and from 32% to 100% (average: 71%) during the plateau phase. One subject never performed a microsaccade in the plateau phase out of 721 trials. Similarly, the rate of small saccades decreased from 0.55 to 0.32 saccades/s during the entire period of stimulus presentation ($p < 0.01$, paired one-tailed t-test) and to 0.2 saccades/s during the plateau phase ($p = 0.01$, paired one-tailed t-test), yielding an average suppression in the two intervals of 42% and 63%, respectively. No significant differences were found between the rates measured in the presence of high and low spatial frequency stimuli neither for microsaccades nor small saccades.

In sum, subjects actively suppressed saccades during the presentation of the stimulus. This suppression occurred for both microsaccades and small saccades during viewing of both low and high spatial frequency gratings. Thus, even though the transients from small saccades are beneficial for contrast sensitivity at low spatial frequencies, humans tend to minimize these movements during careful examination of spatially homogeneous gratings.

4. Discussion

Are microsaccade transients helpful? We addressed this question by following an integrated theoretical and experimental approach, which consisted of two components: a spectral analysis of the input to the retina and measurements of contrast sensitivity. Spectral analyses of retinal input signals have shown that microsaccades and small saccades yield more temporal power at low spatial frequencies than ocular drift, suggesting a possible contribution of these movements to low-frequency vision. Measurements of contrast sensitivity confirmed these predictions for small saccades, but not for microsaccades, and revealed a strong suppression of both movements during exposure to the stimulus. These results do not support an important role for microsaccade transients in visual perception.

Our spectral analysis extends and complements previous work in two important ways. First, it shows that previous findings on how ocular drift transforms the input to the retina (Kuang et al., 2012) are robust and continue to hold under very different viewing conditions. We have recently shown that during free viewing of natural scenes, incessant intersaccadic drifts shift the power of a static scene into the temporal frequency range at which retinal neurons respond best. This transformation treats spatial frequency harmonics unevenly, enhancing high frequencies in a way that counterbalances (whitens) the spectral density of natural images. As a consequence, the input signals impinging onto retinal receptors contain equalized spatial power within the temporal range of peak sensitivity of ganglion cells. This spectral equalization is an important computational step, traditionally attributed to neural processing (Srinivasan, Laughlin, & Dubs, 1982; Van Hateren, 1992). It discards predictable correlations in natural images and, together with the characteristics of retinal ganglion cells, enhances luminance discontinuities. Unlike our previous study on free examination of natural images, here subjects fixated on
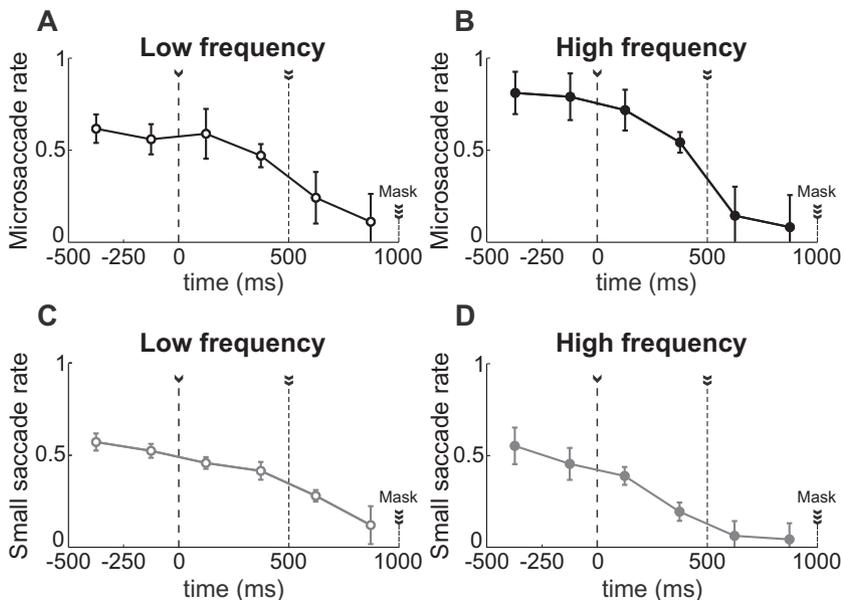

Fig. 5. Frequency of microsaccades and small saccades during the various phases of the experiment. Data points represent average rates across subjects estimated over non-overlapping 250 ms intervals after aligning trials with stimulus onset ($t = 0$). Results are shown for both microsaccades (A, B) and small saccades (C, D) during presentation of both low (A, C) and high spatial frequency stimuli (B, D). Errorbars represent SEM.

low-contrast gratings. Yet the spatiotemporal input transformations were highly similar: in both cases, the fraction of stimulus power that moved to nonzero temporal frequencies increased proportionally to the square of the spatial frequency. Thus, the spectral redistribution operated by ocular drift maintains its general characteristics independent of the specific stimulus and viewing conditions.

Second, the results of the spectral analysis of Fig. 3 complement previous findings on ocular drift by showing the consequences of saccades with small amplitudes. The abrupt displacements of the retinal image caused by microsaccades and small saccades possess more uniform spectral distributions than slow drift modulations. As a consequence, these movements give more temporal power than ocular drift in a spatial frequency range that extends up to approximately 10 cycles/deg. This power redistribution represents the average frequency content of the visual input transiently delivered by a saccade, the signal that—because of the temporal integration of retinal ganglion cells—presumably drives neural responses immediately after a saccade.

Simulations of the responses of ganglion cells during normal eye movements have already shown distinct regimes of neural activity at fixation onset and during late fixation (Desbordes & Rucci, 2007). Wide ensembles of coactive neurons emerge immediately after a saccade and progressively disappear during the course of fixation as responses become uncorrelated. The data in Fig. 3 show that these two regimes are caused by the different frequency contents of the input signals effectively driving neurons during early and late fixation. They suggest that different types of responses exhibited by cortical cells during microsaccades and drift (Kagan, Gur, & Snodderly, 2008) may originate from sensitivity to different spatial frequency ranges.

The spectral distributions of Fig. 3 raise the interesting proposal that transients from microsaccades and ocular drift may serve complementary roles in visual perception. However, our experimental results supported this proposal only partially. The expected improvement in contrast sensitivity was only found for saccades larger than 30′. As predicted, contrast thresholds were lower in the trials with small saccades during viewing of low, but not high, spatial frequency gratings. In contrast, no noticeable effect on sensitivity was observed in the presence of saccades with amplitude smaller than 30′, neither at low, nor at high spatial frequencies. Lack of an effect was expected at high spatial frequency, as microsaccades and drift may be equally beneficial in this range by yielding comparable temporal power. But the negative result at low spatial frequency conflicts with the predictions of the spectral analysis and does not support an important role for microsaccade transients in visual perception.

Furthermore a substantial reduction in the number of all saccades, including microsaccades, occurred during exposure to the stimulus, a robust effect present for all subjects in all tested conditions. This decrement in rate extended throughout the entire period of stimulus presentation and was most pronounced during the plateau phase of maximum contrast, presumably the most valuable interval of exposure. This phenomenon cannot be caused by the subject having already completed the task, as rates were estimated at contrast levels close to threshold, and in many trials the observer did not see the stimulus. It was a prolonged and sustained suppression that differed from the transient inhibition of microsaccades reported in response to stimulus changes (Engbert & Kliegl, 2003; Hafed & Ignashchenkova, 2013) and was suggestive of a progressively increasing focus of attention at the current fixation (Goffart, Hafed, & Krauzlis, 2012). It is important to notice that such reduction was not observed in previous experiments with stimuli that, unlike the gratings of this study, were not spatially homogenous (Rucci et al., 2007; Poletti, Listorti, & Rucci, 2013). In fact, the number of microsaccades actually increased during the course

of the trial in a previous experiment that required comparison of two approaching nearby regions (Ko, Poletti, & Rucci, 2010). Thus, microsaccade suppression only seems to occur when precise positioning of the preferred retinal locus of fixation is not necessary.

Although our results may appear surprising, they are consistent with multiple previous findings. First, similar facilitatory effects of small saccades in the detection of low-frequency stationary gratings have been previously reported in the literature (Deubel & Elsner, 1986). These authors found higher sensitivity at 0.5 cycles/deg when subjects were asked to look at the center of the display rather than maintain strict fixation on a marker. This difference could have originated from the more frequent saccades/microsaccades in the relaxed fixation condition. However, it is known that (a) humans make fewer saccades during relaxed fixation compared to when they are requested to maintain precise fixation on a marker, and (b) saccades also tend to be larger in this condition (Cherici et al., 2012). Thus, an alternative possibility is that this low-frequency enhancement followed from changes in the amplitude of saccades rather than their frequencies. Indeed, Deubel and Elsner (1986) report that the average amplitude of the saccades immediately preceding perceptual decisions was larger than 1°, an observation consistent with our finding that only relatively large saccades affect contrast sensitivity.

Second, the spectral analysis of Fig. 3 only considers the average characteristics of retinal stimulation. However, it is well known that saccades are normally accompanied by temporary impairments in visual functions, which include a compression of space (Ross, Morrone, & Burr, 1997) and a reduction in sensitivity known as "saccadic suppression" (Volkmann et al., 1978; Ross et al., 2001). Several recent studies have emphasized that microsaccades bear no differences with larger saccades with respect to the underlying neural substrate (Hafed, Goffart, & Krauzlis, 2009), their impact on neural responses (Kagan, Gur, & Snodderly, 2008), and also their associated perceptual consequences (Lavergne et al., 2010; Hass & Horwitz, 2011; Hafed, 2013). Notably, both a compression of space (Hafed, 2013) and an increment in perceptual thresholds for luminance, but not chromatic, gratings (Hass & Horwitz, 2011) have been reported for microsaccades, effects similar to those observed for larger saccades (Burr, Morrone, & Ross, 1994; Diamond, Ross, & Morrone, 2000; Knöll et al., 2011). These considerations suggest that our contrast sensitivity measurements may depend on the balance between the positive influence of saccadic transients and the negative consequences of saccadic suppression. In this view, only the larger changes in the retinal stimulus caused by small saccades may overcome these perceptual impairments resulting in a net beneficial effect. Contrasting influence may balance out in the case of microsaccades.

Third, our results are in agreement with previous measurements of contrast sensitivity. Classical experiments on retinal stabilization—a laboratory condition in which the physiological motion of the retinal image is eliminated—have found a global reduction in contrast sensitivity during prolonged exposure to the stimulus (Koenderink, 1972; Kelly, 1979; Tulunay-Keesey, 1982). This effect is caused by a progressive fading of the image over periods much longer than the brief stimulus exposure used in our experiments. Indeed, previous experiments with brief stimulus presentations did not find any influence of retinal stabilization on contrast sensitivity at low spatial frequencies (Tulunay-Keesey & Jones, 1976; Rucci et al., 2007). That is, the microsaccades present when the retinal image was not stabilized had little consequences on contrast sensitivity. In contrast, different thresholds with and without retinal stabilization were found at high spatial frequencies, the range in which drift is expected to enhance vision (Rucci et al., 2007).

Fourth, our finding that only saccades larger than 30′ affect contrast sensitivity is in agreement with the results of studies

investigating whether microsaccades prevent image fading. According to a controversial proposal, microsaccade transients are essential for preventing the perceptual fading experienced under retinal stabilization (Ditchburn, Fender, & Mayne, 1959; but see Kowler & Steinman, 1980). The fading prevention hypothesis usually treats all the image equally without specifying whether some frequency bands should benefit from microsaccades more than others. However, studies on image fading commonly use low-frequency stimuli, and the global reduction in contrast sensitivity measured under prolonged retinal stabilization is more pronounced at low spatial frequencies. It has been recently observed that visibility of a 0.2 cycles/deg is enhanced by saccades larger than 30′, but that smaller saccades only have a very modest effect (McCamy et al., 2012). These previous results are in agreement with the findings of Fig. 4. They show that microsaccades (as defined in our study and in classical ones—see below) have little or no consequences in enhancing visibility. Furthermore, the spectral analysis of Fig. 3 also makes clear that the notion that fixational eye movements operate a general "refreshing" of neural activity is a simplistic assumption. Different types of eye movements yield highly different redistributions of the spectral density of the stimulus.

Related to this previous point, it is important to clarify our use of the term "microsaccade". In this study, as in our previous articles, microsaccades are saccades with amplitude smaller than 30′. This approach relies on the classical definition of microsaccades as movements that do not shift gaze away from the current point of fixation (e.g., Bridgeman & Palca, 1980). Since the average diameter of the rod-free region within the fovea is slightly larger than 1° (Curcio et al., 1990), saccades with amplitude of 30′ give an overlap between pre- and post-saccadic images larger than 50%. Classical studies used similar or even smaller amplitude thresholds. However, recent studies have inflated this threshold to include much larger movements, up to 1.5° or even 2°. This redefinition of a microsaccade is unjustified and changes the nature of previous debates (Collewijn & Kowler, 2008). It is unjustified because the overwhelming majority of saccades occurring during sustained fixation are smaller than half degree. For example, in a recent study in which the eye movements of a relatively large population of observers were recorded at high resolution, the 90th percentile of the average saccade distribution was only 31′ (Cherici et al., 2012). It changes the nature of classical debates, as the original questions were pertinent to movements that did not move the high acuity foveola to a different region of the scene. This study provides a further reason why it is important to pay attention to the amplitude: the smaller the saccade, the lower is the temporal power delivered to the retina. Only saccades larger than 30′ improved contrast sensitivity in our experiments.

In sum, the results of this study provide a negative answer to the specific question of whether microsaccade transients are helpful for vision. This negative result, however, should not be taken to imply that microsaccades are not useful in general. Studies with precise localization of the line of sight have already shown that humans use microsaccades to optimally position a narrow preferred retinal locus of fixation when needed (Ko, Poletti, & Rucci, 2010; Poletti, Listorti, & Rucci, 2013). Furthermore, it has been recently observed that motion sensitivity is enhanced immediately following a microsaccade, as demonstrated by an improved ocular following response to full field motion starting after the movement (Chen & Hafed, 2013). Thus, microsaccades have beneficial consequences for vision, even if these benefits do not come from their transients.

Acknowledgments

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