Contrast sensitivity revealed by microsaccades

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Microsaccades are small rapid and involuntary eye movements that occur during fixation in an apparently stochastic manner. They are known to be inhibited in response to sensory transients, with a time course that depends on the stimulus parameters and attention. However, the temporal precision of their onsets and the degree to which they can be used to assess the response of the visual system to basic stimulus parameters is currently unknown. Here we studied microsaccade response properties as a function of the contrast and spatial frequency of visual onsets. Observers ($n = 18$) viewed and silently counted 2-min sequences of Gabor patches presented briefly (100 ms) at 1 Hz. Contrast and spatial frequency were randomized in different experiments. We found that the microsaccade response time, as measured by the latency of the first microsaccade relative to stimulus onset following its release from inhibition, was sensitive to the contrast and spatial frequency of the stimulus and could be used to extract a contrast response function without the observers' response. We also found that contrast detection thresholds, measured behaviorally for different spatial frequencies, were highly and positively correlated ($R = 0.87$) with the microsaccade response time measured at high contrast (>4 times the threshold). These results show that different measures of microsaccade inhibition, especially the microsaccade response time, can provide accurate and involuntary measures of low-level visual properties such as contrast response and sensitivity.

Introduction

During fixation of gaze, our eyes move constantly in a random-walk-like movement called drift, along with occasional rapid, small, and involuntary eye movements called microsaccades (Barlow, 1952; Steinman, Haddad, Skavenski, & Wyman, 1973). Microsaccades and saccades have similar properties and appear to share the same mechanisms that are involved in orienting attention in space and time (Martinez-Conde, Otero-Millan, & Macknik, 2013; Otero-Millan, Macknik, Langston, & Martinez-Conde, 2013; Rolfs, 2009). This suggests that microsaccades could reveal the involuntary deployment of attention and could be used to study attention and cognition (Engbert, 2006) as well as attention deficits (Fried et al., 2014). Since microsaccade onsets appear stochastically, with unclear temporal precision, they are typically described in terms of probability or rate modulation across time. This description is justified by a dynamical model that links fluctuations of neural activations in superior colliculus to microsaccade onset times (Engbert, Mergenthaler, Sinn, & Pikovsky, 2011), thus describing these onsets as stochastic observations of time-varying activations in the early or low-level visual system. The most important finding related to this time-varying process is the phenomenon of microsaccade inhibition, or the "freeze effect" for microsaccades (Hafed & Ignashchenkova, 2013; Rolfs, Kliegl, & Engbert, 2008). In response to sensory events, microsaccades are first inhibited and their probability or rate decreases (minimum around 200

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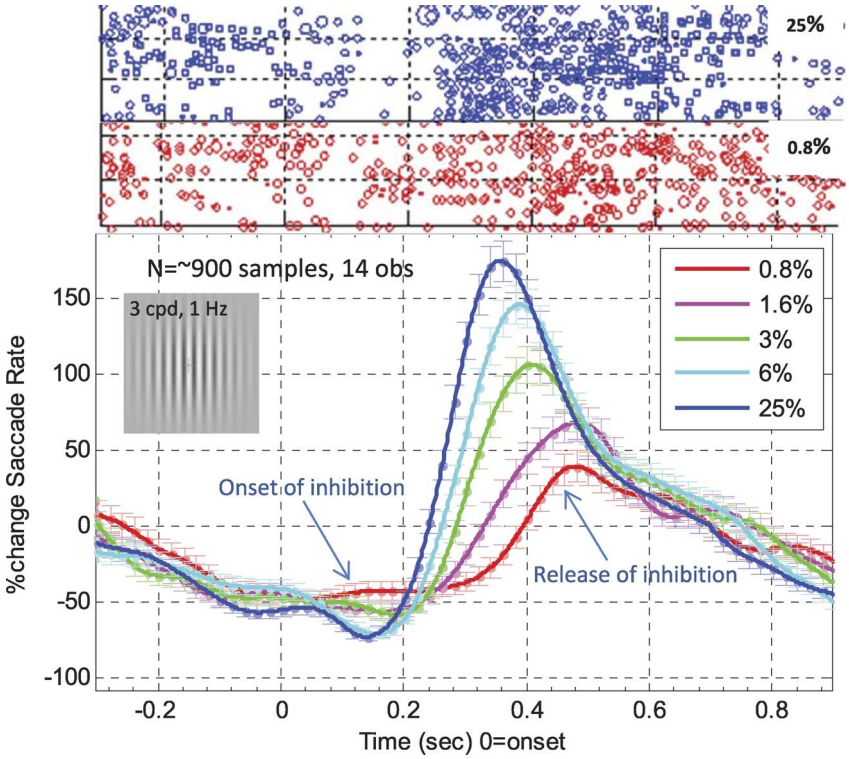

Figure 1. The effect of contrast on microsaccade rate modulation. The stimuli consisted of Gabor patches (3 c/°) with varied contrast, briefly flashed (100 ms) at 1 Hz in passive viewing (an example is shown in the lower panel). The upper panel shows two raster plots of microsaccade onsets for samples of 300 epochs for low- (0.8%, in red) and high-contrast (25%, in blue) patches. Each line in these plots represents one epoch and each dot one microsaccade, with the size proportional to the microsaccade size. The lower panel shows rate-modulation functions for different contrast levels, time-locked to the stimulus onset (time 0) and averaged across all epochs ($n \approx 900$) from all observers ($n = 14$), expressed as the percentage relative to the average rate in each epoch. Error bars denote one standard error of the mean across epochs, down-sampled for clarity. The rate-modulation functions for 25% and 0.8% correspond to the raster plots in the upper panel. Note the different maxima and latencies of the modulation functions for different contrast levels around ~400 ms, corresponding to the release from inhibition, and minima before 200 ms, corresponding to the onset of inhibition.

ms after onset), then increases above baseline (maximum around 400 ms) before returning to baseline (see the example in Figure 1). This stereotypical time course of microsaccade rate (decrease–increase–baseline) is modulated by the properties of the stimulus as well as by attention and expectation (for a review, see Rolfs, 2009). It is observed for visual as well as for auditory events (Rolfs et al., 2008; Valsecchi & Turatto, 2009; Widmann, Engbert, & Schroger, 2014) and even for illusory (not physical) events (Bonneh et al., 2010; Laubrock, Engbert, & Kliegl, 2008). The modulation typically affects the latency of the inhibition onset and its depth, and the latency of the release from inhibition and its amplitude.

The pattern of microsaccade rate modulation as a function of stimulus parameters, attention, and some cognitive factors has been studied in recent years, although with limited quantitative results. For example, prolonged inhibition has been found for lower visual contrast (Rolfs et al., 2008), but the exact relation between microsaccade rate modulation and stimulus contrast, as well as other low-level properties of the stimulus such as spatial frequency, has not yet been studied. The effect of stimulus saliency presents an additional challenge to understanding the underlying mechanisms involved. Whereas saliency derived from the sensory intensity of the stimulus, such as contrast, has been found to shorten the inhibition period (Rolfs et al., 2008), saliency derived from perceptual deviance, such as an oddball tone or a visual image, has been found to prolong it (Bonneh et al., 2013; Valsecchi, Betta, & Turatto, 2007; Valsecchi & Turatto, 2009; Widmann et al., 2014). This discrepancy could be accounted for by the combined effect of the known dependency of sensory-response latency on contrast (Bell, Meredith, Van Opstal, & Munoz, 2006; Oram, 2010) and by the finding of a prolonged microsaccade inhibition for attended stimuli (Bonneh, Adini, Fried, & Arieli, 2011; Valsecchi et al., 2007).

In the current study we parametrically investigated the effect of the contrast and spatial frequency of fixated visual onsets on the temporal properties of

microsaccades, and their relation to contrast sensitivity. Our goal was to obtain involuntary measures that do not require any behavioral response or explicit perceptual decisions, and thus could be used in the future with noncommunicating individuals. The general methodology used was therefore based on passive viewing of a regular (every second) slide show of visual onsets having different properties mixed in random order. We developed a primary measure for the microsaccadic response function, based on the latency of the first microsaccade in an optimally chosen time window, averaged across epochs. We termed this measure "microsaccade response time" (msRT). In the first two experiments, we measured the effect of contrast and spatial frequency on 14 and 18 observers, respectively. In an additional experiment, we tested half of the sample ($n = 9$) on a behavioral measure of contrast sensitivity. We found that the contrast detection thresholds measured for different spatial frequencies were highly and positively correlated with the msRT at high contrast.

Methods

Subjects

Overall, 20 observers (ages 25–50) with normal or corrected-to-normal vision, including the first author, participated in the experiments: 14 in the contrast experiment, 18 in the spatial-frequency experiment, nine in the contrast detection experiment.

Apparatus

Stimuli were displayed on a 22-in. CRT monitor using an in-house-developed platform for psychophysical and eye-tracking experiments (PSY) developed by the first author (YSB), running on a Windows PC. The video format was true color (RGB), at a 100-Hz refresh rate, with 1024×768 pixel resolution occupying a $33.4° \times 25.4°$ area. Luminance values were gamma corrected. For presenting very low-contrast stimuli when testing detection threshold, luminance dithering (2×2 pixels) was applied. The sitting distance was 0.6 m, and all experiments were administered in dim light.

Eye movements were recorded monocularly, with an EyeLink 1000 infrared system (SR Research, Ontario, Canada), with a sampling rate of 500 Hz and a spatial resolution of less than 0.01°. Movements of the head were limited by a chin and forehead rest. Recording was from the right eye, though viewing was binocular. A standard nine-point calibration was performed before each session, though the absolute position of the eyes was never used and was not important in the study.

Stimuli and procedure

In three eye-tracking experiments, observers passively viewed a "slide show" of repeated visual onsets, while silently counting the displayed items and reporting the total number at the end of the run. In these experiments, Gabor patches were flashed for 100 ms, at a repetition rate of exactly 1 Hz. A static small (0.12° diameter) fixation point was constantly presented. Each run consisted of 100 presentations lasting for 100 s, and each observer was tested in multiple runs, as specified for each of the following experiments. In the *contrast experiment*, the Gabor patches had a spatial frequency of 3 c/° and an envelope of four cycles, with varied contrast of 0.8%–50% in factor-2 jumps presented in random order (see Figure 1, for example). Among the 14 participants, 10 were tested in five runs each and four were tested in 10–20 runs each. In the *spatial-frequency experiment*, the Gabor patches had a fixed contrast of 25% with varied spatial frequency from a predefined list of 0.2, 1, 2, 4, 6, and 8 c/°, with a fixed envelope of $\sigma = 2.7°$, presented in random order (see Figure 3, for example). Among the 18 participants, five were tested in five runs each, six in 10 runs each, and seven in ~20 runs each.

In an additional *contrast detection experiment*, the observers were tested on the psychophysical contrast detection threshold as a function of spatial frequency, also known as the contrast sensitivity function. The detection thresholds were measured in a subset of the observers ($n = 9$) for the same stimuli as in the spatial-frequency experiment, using a standard temporal two-alternative forced-choice staircase procedure (one up, three down) applied to target contrast, as previously done (e.g., Bonneh & Sagi, 1998) and described here. Each trial was initiated by the observer via a button press while fixating a small fixation circle (0.65° diameter). The fixation circle disappeared after 200 ms, followed by a blank interval of 500 ms, followed by two stimulus displays each presented for 100 ms, with 1000 ms between onsets. The two displays consisted of four white crosses, 3.3° in size, in four corners with 10° eccentricity. The Gabor target was presented in one of the displays, and the observers reported which display had the target by pressing one of two buttons. Auditory feedback was given for errors, and target contrast was adaptively updated via the staircase procedure. Luminance dithering (2×2 pixels) was applied for low-contrast targets. All frequency conditions were randomly interleaved with independent staircases. A staircase was terminated after eight reversals but not before all other interleaved staircases were terminated.

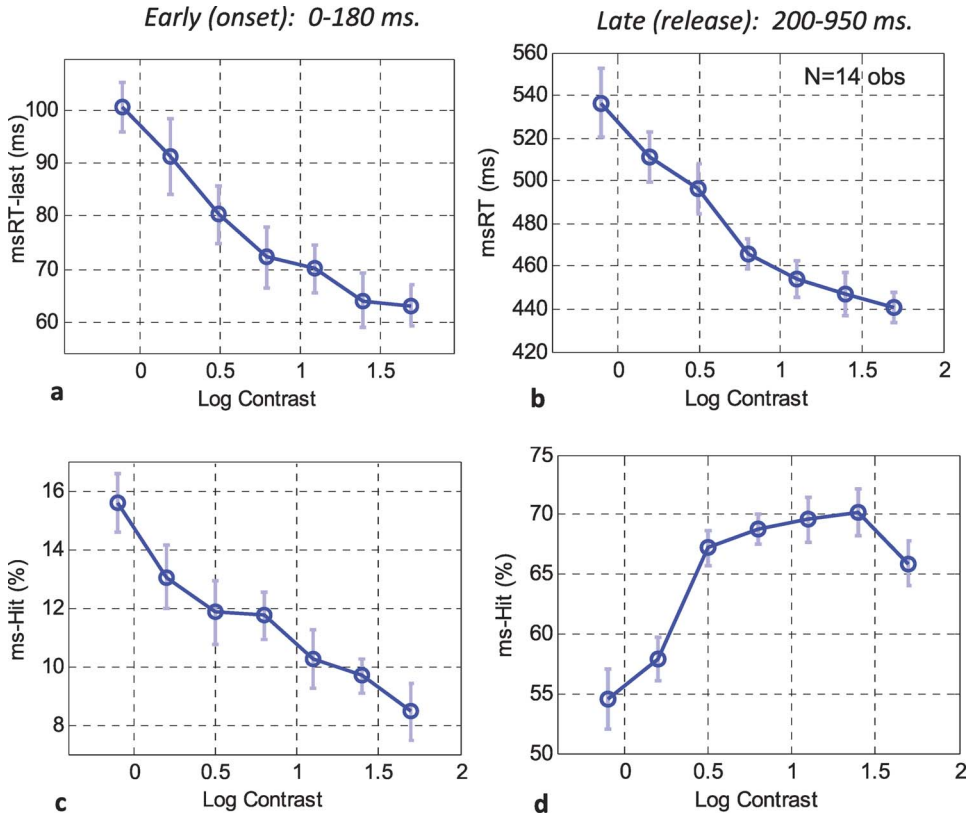

Figure 2. The effect of contrast on microsaccade inhibition and release times. Two measures are shown: microsaccade RT (the onset of the last/first microsaccade, upper panels; a–b, respectively) and the microsaccade hit rate (percentage of occurrence, lower panels; c–d), assessed in two time windows, early (0–180 ms, the onset of inhibition, left panels; a, c) and late (200–950 ms, release of inhibition, right panels; b, d). Values were first averaged and normalized within observers, then averaged across observers and readjusted by the grand average. Error bars denote one standard error across observers. Contrast is plotted in log units, ranging from 0.8% to 50%. As shown, the measures for both the onset of and release from inhibition decrease monotonically with contrast in the tested range (by ~50 ms for the onset in a, ~100 ms for the release in b). On the other hand, the percentage of epochs with microsaccades, as a function of contrast, decreases in the early time window (c) but increases and becomes saturated in the late time window shown in (d).

Threshold was determined as the geometric mean of the last six reversals. Participants were tested on three or four runs each (but two tested on only one run).

Data analysis

Microsaccade detection

Microsaccades were detected using the algorithm introduced by Engbert and Kliegl (2003), as in our previous study (Bonneh et al., 2010). Raw data were first smoothed with a window of 15 ms to optimize microsaccade extraction. This smoothing was found to be critical for lower quality or noisy recordings. The permitted velocity range was 8°/s–150°/s, and the permitted amplitude range was 0.08°–2°, with a minimum duration of 9 ms; eye movements outside these ranges were rejected. The rejection rate varied across recordings and was in the range of 1%–15%, with an average of 5.5%. For each run, a plot of microsaccade peak velocity versus microsaccade magnitude was manually examined to verify the linear relation known as the main sequence (Bahill, Clark, & Stark, 1975).

Epoch extraction

Epochs were extracted, time-locked to stimulus onset, with one epoch per stimulus presentation. Periods of missing data, such as during eyeblinks, were locally discarded from further analysis with an additional margin of 0.05 s, without discarding the whole epoch.

Microsaccade rate analysis

The rate was calculated by convolving a raw rate estimate of 1 microsaccade per sample duration at the time of microsaccade onset with a Gaussian window having a sigma of 50 ms, as in our previous study

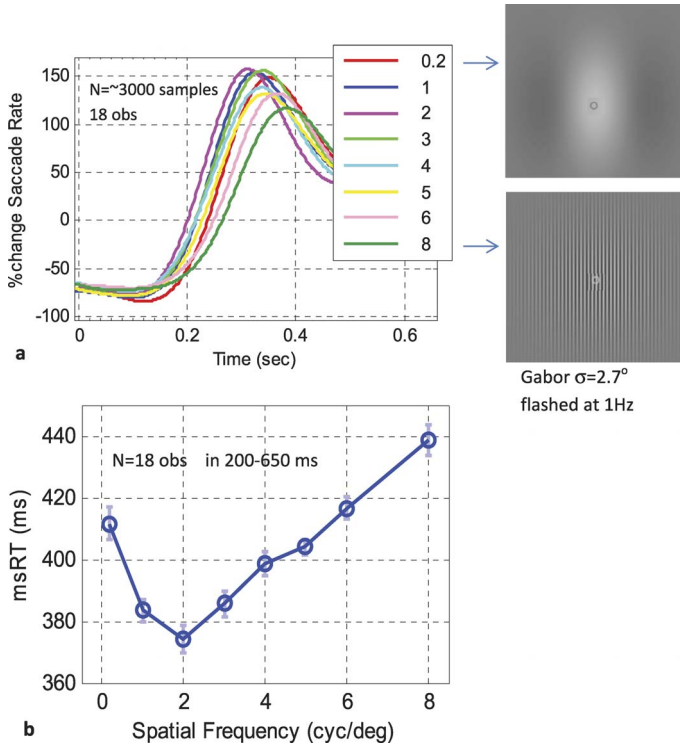

Figure 3. The effect of spatial frequency on microsaccade rate modulation and reaction time. Stimuli consisted of Gabor patches at high contrast (25%) with varied spatial frequency but fixed envelopes, briefly flashed at 1 Hz, in passive viewing. Examples of low- (0.2 c/°) and high-spatial-frequency (8 c/°) stimuli are shown in the upper panel. (a) Rate-modulation functions for different spatial frequencies, time-locked to the stimulus onset (time 0) and averaged across all epochs ($n \approx$ 3,000) from all observers ($n = 18$), are expressed as the percentage relative to the average rate in each epoch. Note the increase in latency (release from inhibition) and (to a lesser degree) the decrease in peak response with increasing spatial frequency for most frequencies (error bars are omitted for clarity). (b) Microsaccade RT, measured as the onset of the first microsaccade in a time window of 200–650 ms. Values were first averaged and normalized within observers, then averaged across observers and readjusted by the grand average. Error bars denote one standard error across observers. Note the gradual increase in msRT from 2 to 8 c/° and below 2 c/°.

(Bonneh et al., 2010). The rates were averaged across epochs to compute the event-related modulation of microsaccades. We considered an alternative method based on a causal window with better temporal precision (as applied by Widmann et al., 2014) but preferred our method for simplicity, given that the rate-modulation analysis did not determine our temporal results and was primarily used to motivate the main RT analysis. Because some samples were excluded from the analysis (see previous), there was a variable number of samples per data point (N specifies the average of this number across all data points). The group (all-observers) average and standard error of the micro-saccade rate were obtained by averaging all epochs from all observers, normalized by subtracting the mean per epoch. The rate was used only for obtaining preliminary observations (Figure 1).

Microsaccade reaction time

The msRT was computed per epoch as the latency of the first microsaccade after stimulus onset in different time windows. These windows were selected to separately explore early and late processes, as indicated by the rate-modulation functions, and were fine-tuned to minimize the average standard error in each experiment. Epochs with no microsaccades in the specified window were excluded from the average. To explore the onset of microsaccade inhibition (early window), we used the last microsaccade—whose response time we term here msRT-last—rather than the first. An additional measure of microsaccade hit rate was computed as the percentage of epochs that included at least one microsaccade in the specified time interval.

Statistical significance assessment

We used nonparametric permutation tests (Efron & Tibshirani, 1998) to test the dependence of the msRT on contrast and spatial frequency. These tests were performed across subjects. For each test, we randomly permuted (1,000 permutations) the labels of the observations (i.e., the contrast or spatial frequency of each epoch) and recalculated the msRT functions as already described. For contrast, we tested the significance of the correlation between msRT and log contrast. We computed this correlation after each permutation, and obtained the p value as a fraction of shuffles in which the original correlation was exceeded by the correlation of the permuted data (in absolute values). For spatial frequency, we used a similar test for the linear dependence between the frequency and msRT for data of 2 c/° and above. We similarly tested the significance of the difference between two specific points in the data by comparing these points to the difference in the permuted data.

Results

The results for the three experiments are summarized below: contrast, spatial frequency, and psychophysical detection threshold. The eye-tracking measures were then compared with the psychophysical thresholds.

Contrast

The results for the contrast experiment are plotted in Figures 1 and 2. Figure 1 plots the microsaccade rate-modulation functions (the percentage relative to the grand-average baseline computed per epoch) for different target contrast levels, each averaged across all epochs ($n \approx 900$) from all observers ($n = 14$) together. The upper panel shows examples of the data that underlie the rate-modulation functions in terms of a raster plot with a dot for every microsaccade. All rate-modulation functions share the same shape: (1) early inhibition that starts prior to stimulus onset, possibly due to the temporal regularity (1 Hz), which allows for precise anticipation and does not depend on the stimulus; (2) stimulus-dependent inhibition that reaches the minimum (maximal rate inhibition) at 150–200 ms after onset; and (3) release from inhibition that strongly depends on contrast, in terms of both the latency of the release peak and its magnitude. Note that higher contrast results in faster onset and stronger rate inhibition, as well as faster release of inhibition and stronger magnitude of that release. This is manifested by the peaks of the rate-modulation functions, which were in the range of 300–500 ms after stimulus onset, depending on contrast. Note also that the magnitude of the peaks of these rate-modulation functions depends on the microsaccade probability as well as on the variability of microsaccade latency. We used this analysis to motivate and provide the basic insights, which we explore in the second analysis that follows. We therefore did not apply statistics to the rate-modulation functions, but the error bars indicate the strength of the measured effects.

The results of the second type of analysis are shown in Figure 2. Two measures were computed: the msRT (upper row) and the microsaccade hit rate (lower row), i.e., the percentage of epochs including one or more microsaccades in two time windows, early (0–180 ms, left panels) and late (200–950 ms, right panel; see Methods). Data were first averaged and normalized (de-meaned) for each observer ($n = 14$), then averaged across observers, with error bars reflecting one standard error of these means and thus the relative (across-contrasts) but not absolute RT variability. The baseline was then adjusted by the grand average across all contrast levels and observers. The time windows for the analysis were selected to capture the onset and release from inhibition observed in the microsaccade rate-modulation functions (Figure 1), with fine-tuning to minimize the average standard error across all contrast levels, for all observers together (see Methods). We note that optimizing these time windows per observer could further reduce variability.

The results (Figure 2a, b) show a monotonic decrease in msRT as a function of contrast expressed in log units, which is linear for increasing contrast levels up to about 1 log unit. This is true for both the early window (0–180 ms, Figure 2a, the last microsaccade latency averaged) and the late window (200–950 ms, Figure 2b), with effect sizes (the highest to lowest contrast difference) of ~50 ms and ~100 ms, respectively (~10 standard errors). Figure 2b and c shows that not all epochs had microsaccades that were included in the analysis. A very low percentage was found for the early window (Figure 2c), which decreased monotonically from 16% to 8% across the contrast range. In comparison, a much higher percentage (55%–70%) was found for the late window (Figure 2d), which increased with contrast but became saturated at a 70% level. A more linear function of the hit rate as a function of log contrast was found when the late window was narrowed to 250–600 ms to capture the peaks of the rate-modulation function (data not shown). When the early window was extended to 0–200 ms (instead of 180), the results were similar except that the latency (msRT-last) was less linear and more variable, presumably because 200 ms is a point of transition (see Figure 1). The statistical analysis (nonparametric permutation analysis, see Methods) revealed that all the linear correlations obtained (Figure 2a through c) were highly significant, $p < 0.001$.

Based on the pattern of microsaccade inhibition, as derived from the rate-modulation functions (Figure 1), we can interpret the results in Figure 2 as reflecting the properties of the onset of inhibition (0–180 ms, left plots) and its release (above 200 ms, right plot). Accordingly, the onset of microsaccade inhibition and its release were both faster with higher contrast. Moreover, inhibition was stronger with higher contrast (Figure 2c), and so was its release (Figure 2d), since the percentage of microsaccades following the release from inhibition was ~70% at high contrast and only ~55% at low contrast. We note that the onset of inhibition was computed as the msRT for the last microsaccade in the early window; however, very similar results were obtained when averaging the first microsaccade in this early window.

Spatial frequency

The results for the spatial-frequency experiment are plotted in Figure 3. Figure 3a plots the microsaccade rate-modulation functions (the percentage relative to the grand-average baseline per epoch) for different target frequencies, each averaged across all epochs ($n \approx$ 3,000) from all observers ($n = 18$) together. All rate-modulation functions show a pattern similar to that observed in the contrast experiment (Figure 1), with different frequencies showing different latencies. This was most evident for the inhibition-release stage, 300–

400 ms after stimulus onset, but reduced early microsaccade inhibition for the high frequencies is also visible (Figure 3a). Figure 3b shows the msRT in the window of 200–650 ms following stimulus onset, as a function of spatial frequency. Data were first averaged and normalized (de-meaned) for each observer ($n = 18$), then averaged across observers, with error bars reflecting one standard error of these means and thus the relative (across-frequencies) but not absolute RT variability. The baseline was then adjusted by the grand average across all frequencies and observers. The time window for the analysis was selected as the time range of the inhibition release, and fine-tuned to minimize the average standard error across all frequencies, for all observers together (see Methods). We note that optimizing the time window per observer could further reduce variability. The msRT was fastest (~370 ms) for 2 c/° and increased linearly (from ~370 ms to ~440 ms) with increasing frequency as well as decreasing frequency (410 ms for 0.2 c/°). The percentage of epochs with one or more microsaccades that could therefore participate in the analysis (graph not shown) was 60%–65% for all frequencies except 8 c/°, which exhibited ~55%. The statistical analysis (nonparametric permutation analysis, see Methods) revealed that the linear correlation between the msRT and spatial frequency observed for 2 c/° and above was highly significant ($p < 0.001$). Moreover, there was a significant msRT difference even between the spatial frequencies of 1 and 2 c/° ($p < 0.02$). We also investigated the early inhibition-onset period (0–180 ms), as we did for the contrast (graphs not shown). The hit rates were very low (3%–6%) and increased monotonically with spatial frequency (less inhibition for high frequency), whereas the msRT values did not display a clear pattern probably due to the small percentage of epochs involved.

Microsaccade RT versus psychophysical detection thresholds

The results for the psychophysical contrast detection threshold as a function of spatial frequency (contrast sensitivity function, see Methods) are shown in Figure 4a. Half of the observers of the spatial-frequency experiment ($n = 9$) were tested, and the thresholds, expressed in log units, were averaged across observers. In Figure 4b, we compare the psychophysical thresholds (in log units) with msRT by expressing both in Z values (de-meaned and divided by standard deviation per observer, then averaged across observers). As shown, the two plots are indistinguishable except at 1 c/°. Note that the measure obtained for the whole group ($n = 18$; Figure 3b) was more similar to the detection threshold in terms of the relative value of the 1-c/° point. Similar to the contrast experiment, the msRT was proportional to log contrast threshold and not to the contrast itself. A more detailed comparison is provided in Figure 4c, showing a scatter plot of these Z values with one point per observer and frequency. This plot shows a very high correlation (three outliers of 63 points excluded), with $r^2 = 0.75$—i.e., 75% of the variance on the psychophysical threshold is captured by the msRT. The absolute values of msRT were also correlated with the detection thresholds (log units), as shown in Figure 4d. A significant correlation of $r^2 = 0.55$ (one outlier excluded) was found when the average across all frequencies per observer was used. This correlation implies that faster msRT corresponds to a better detection threshold, although it is not very high, indicating that there are additional sources of variability, perhaps in both of these measures. Note that the comparison of Z values disregards (via normalization) the msRT modulation gain, which could be related, for example, to the contrast gain obtained via inhibitory gain control. These effects can be studied in the future.

Discussion

When observers fixate while a transient stimulus is presented, the spontaneous and involuntary microsaccades are temporarily inhibited, a phenomenon known as microsaccade inhibition. Here we developed novel measures for this inhibition under conditions of passive viewing, which we term microsaccade response time (msRT), in specific temporal windows. These measures are not based on the rate-modulation analysis as done in previous studies (e.g., Rolfs et al., 2008). They demonstrate that microsaccade onset times, despite their stochastic nature, can be used to extract precise measures for the response of the visual system to low-level stimulus parameters such as contrast and spatial frequency. In the first experiment, we manipulated the contrast of visual stimuli and identified two important properties of the inhibition that are affected by contrast: the onset and release latencies relative to stimulus onset, as evident in the rate-modulation functions (Figure 1). Importantly, we found that both decreased as a function of contrast, with a linear relation to log contrast (Figure 2). In the second experiment, we mapped the response of the visual system to different spatial frequencies, presented at high contrast. We found that the msRT was highly correlated with the detection threshold measured psychophysically for different spatial frequencies (Figure 3). Next, we will discuss alternative measures for microsaccade inhibition, compare msRT to different behavioral measures for contrast sensitivity, discuss the

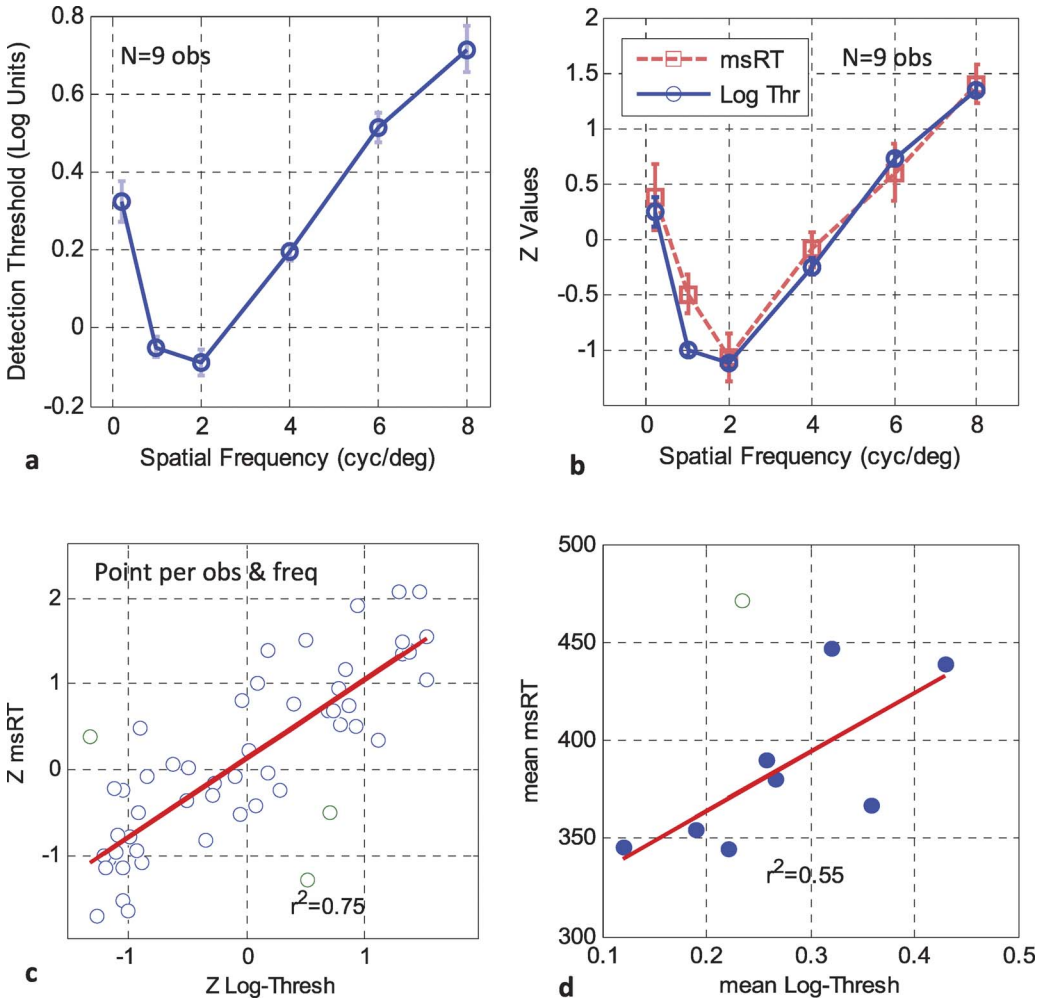

Figure 4. Microsaccade RT compared with the psychophysical contrast detection threshold in the spatial-frequency experiment. The detection threshold was measured in a standard two-alternative forced-choice staircase paradigm for a subset of the observers ($n = 9$). Values were first averaged and normalized within observers, then averaged across observers and readjusted by the grand average. Error bars denote one standard error across observers. (a) Contrast detection threshold expressed in log units. (b) The msRT for the same observers (from the experiment in Figure 3) expressed in *Z* values, superimposed on a *Z*-value plot of the threshold data from (a). Note the almost perfect match between the psychophysical threshold and the msRT measured for high-contrast stimuli in passive viewing. (c) A correlation plot of the individual observers' Z-value data from (b), comparing detection threshold and msRT. Each point represents one observer at one spatial frequency. Note the high correlation ($r^2 = 0.75$, $R = 0.87$, three outlier points omitted), which reflects relative measures within observers. (d) Correlation plot of the average contrast detection threshold and msRT. Data were averaged across frequencies, with each point representing one observer. A significant correlation ($r^2 = 0.55$, one outlier) was observed, showing that observers with higher overall contrast sensitivity also had faster msRT.

underlying physiological mechanisms, and finish by discussing the link to attention and awareness.

Alternative measures for microsaccade inhibition

Previous studies have assessed the properties of microsaccade inhibition as measures for sensory, attentional, and cognitive effects. These measures were typically based on differences between the rate-modulation functions under different experimental conditions, and specifically on the release-from-inhibition part (e.g., Rolfs et al., 2008; Widmann et al., 2014). We show this type of analysis in Figure 1. In the current study we developed measures based on the exact latency of specific microsaccades in specific temporal windows. In quantifying the onset of inhibition in the contrast experiment (Figure 2a), we computed the average latency of the last microsaccade in an early time window of 0–180 ms in each epoch. The percentage of epochs that had a microsaccade in this window and thus were included in the analysis was very low, 8%–16% for the full contrast range (Figure 2c).

Nevertheless, their onset times were highly informative and produced a consistent contrast dependency, with high contrast showing faster response, presumably representing earlier onset of inhibition. These "rare but precious" microsaccades that convey information in the temporal domain are reminiscent of the "rare but precious" microsaccades that convey information in the spatial domain (Hafed & Ignashchenkova, 2013; Pastukhov & Braun, 2010), where the directions of the rare microsaccades that do occur during inhibition have been found to be highly correlated with stimulus location.

We also explored alternative measures of the inhibitory process, such as different parameters of the rate-modulation function, including the latency and magnitude of the peak around 400 ms (Figure 1). These measures were sufficient to capture the contrast effect on the late inhibition release but were less sensitive to the inhibition onset. The primary difference between the methods is that the msRT ignores epochs without microsaccades, whereas the rate-modulation functions take them into account.

Another aspect of the msRT method is the choice of the temporal window. Our analyses of different data sets (including those that are not part of this study) revealed that the simple idea of selecting the time of the first microsaccade after stimulus onset does not produce reliable results, because it mixes microsaccades that precede inhibition with microsaccades after its release as well as with late microsaccades not related to the stimulus. We therefore divided the time range into two time windows—early and late—and fine-tuned the temporal windows to minimize the standard error across observers, averaged across all contrast or spatial-frequency conditions.

Microsaccade RT versus behavioral measures of contrast sensitivity

We compared our msRT measures for high-contrast Gabor patches, using different spatial frequencies, to the corresponding detection thresholds in the same observers. Importantly, we found a high correlation when the detection thresholds were expressed in log units, except for one minor discrepancy at 1 c/° (Figure 3). The behavioral measures we obtained for contrast sensitivity are compatible with previous studies on Gabor patches (Peli, Arend, Young, & Goldstein, 1993) but differ from full-field gratings, which typically exhibit the best sensitivity around 4–6 c/° (not 2 c/°). Several past studies have investigated the effect of spatial frequency and contrast on manual RT—i.e., the voluntary reaction time of observers to transient flashes of grating patches (Breitmeyer, 1975; Harwerth & Levi, 1978; Lupp, Hauske, & Wolf, 1976; Musselwhite & Jeffreys, 1985). All studies found that the RT decreases with contrast and increases with spatial frequency. In all these studies, the RT changed by 50–100 ms in the spatial-frequency range of 1 to 10 c/°, which is similar to or higher than our range (~60 ms). The absolute manual RT values were faster than those of msRT, typically 250–350 ms as compared with 360–440 ms found for msRT. Lupp et al. (1976) found that a greater distance from threshold produces shorter RTs without major changes in the shape of the curves, which is consistent with our finding of a correlation between msRT and the detection threshold (Figure 4c). One point of deviation is the lack of manual RT slowdown for the lowest frequencies (below 2 c/°). None of the studies, however, revealed such a slowdown, although none reached 0.2 c/°, and they measured RT for full-field gratings, which involve lateral inhibition much more than our small patches.

Microsaccade RT and its underlying physiological mechanisms

In trying to link our measures of msRT to physiological latencies, we can distinguish between the early component of microsaccade inhibition onset (Figure 2a) and its release (Figure 2b). These two measures differ in both the latency itself (60 ms vs. 460 ms for the highest contrast) and the effect of contrast on the change in latency: a 40-ms change in the onset of inhibition versus a 100-ms change in the latency of its release for the whole contrast range. This implies that the early latency effect is smaller (half) in magnitude, thus providing an interesting clue to the source of this latency: Contrast-induced changes in neural-response latency in behaving monkeys have been reported as larger in higher visual areas (STS) as compared with lower visual areas (V1; Oram, 2010). The magnitude of these reported changes roughly matches the current results: ~30 ms for a factor-10 change of contrast in V1 (compare with Figure 2a) and ~100 ms for a similar contrast change in STS (compare with Figure 2b). Other physiological studies of the V1 response to contrast in cats and monkeys (Albrecht, Geisler, Frazor, & Crane, 2002; Meirovithz et al., 2010) have reported a pattern similar to our microsaccade rate modulation (Figure 1), with increased magnitude and a shift of peak latency with contrast. More quantitatively, results with high-speed imaging (Meirovithz et al., 2010) and simple cell recording (Reich, Mechler, & Victor, 2001) in monkey V1 have reported comparable results (latency range of ~50–100 ms for a factor-10 contrast range), suggesting that the dependence of the onset of microsaccade inhibition on contrast could be related to V1 response latencies.

There is accumulating evidence for the role of the superior colliculus (SC) in generating microsaccades (Hafed, Goffart, & Krauzlis, 2009; Marino et al., 2012). There is also evidence for the effect of contrast on the timing and magnitude of the visual responses in the SC (Li & Basso, 2008; Marino et al., 2012). Unfortunately, it is not possible to directly compare these studies because of the difference in stimuli (peripheral luminance or square-wave grating patches vs. our fixated Gabor patches). Nevertheless, there are some notable similarities: shorter latency with increased contrast, a saturation effect (around 40% contrast for Li & Basso, 2008), and a latency range of 50–100 ms for a factor-10 change in contrast or luminance. Note that all of the SC response latencies were much shorter than the msRT for the release from inhibition (~450 ms, Figure 2b) but appear consistent with the temporal range of the onset of inhibition (50–100 ms, Figure 2a).

The model suggested by Engbert (2012) provides a good framework for interpreting the current results, assuming an integrative effect of low-level visual properties that affect feed-forward collicular responses and top-down cortical signals. Although the response latencies of the SC could account for the onset of microsaccade inhibition, they are less likely to account for the much longer latency of the release from inhibition, which we found to be highly correlated with contrast sensitivity for different spatial frequencies. This contrast sensitivity function is typically attributed to responses in the visual cortex (e.g., Meng et al., 2013), and could thus be mediated by the known connections between V1 and the SC.

Microsaccade RT and attention, perceptual saliency, and awareness

Current evidence indicates that the properties of microsaccades and microsaccade inhibition are determined by integrating low-level sensory responses and attention (e.g., Engbert, 2012). Although the current results are arguably determined by the low-level visual responses, they could be affected by attention. Visual attention is strongly linked with microsaccades, as indicated by the biased microsaccade direction under spatial cuing (Pastukhov & Braun, 2010; Pastukhov, Vonau, Stonkute, & Braun, 2012) and by the recent striking finding that microsaccades are associated with spontaneous spatial shifts in covert attention that have measurable consequences (Yuval-Greenberg, Merriam, & Heeger, 2014). Furthermore, the link between microsaccade inhibition and attention has been recently demonstrated by the finding that people with an attention deficit fail to suppress microsaccades around the anticipated stimuli, but normalize their oculomotor behavior with medication (Fried et al., 2014).

More relevant to the current results is evidence linking the duration of microsaccade inhibition and the allocation of attention in time (Pastukhov et al., 2012; Valsecchi, Dimigen, Kliegl, Sommer, & Turatto, 2009); this is also discussed in the Introduction. In these studies, prolonged inhibition was attributed to the engagement of attention, as reflected, for example, by the finding of associated P300 responses (Valsecchi et al., 2009). This poses a potential paradox: Whereas visual saliency is known to attract attention, and high-contrast stimuli are more salient than are low-contrast stimuli, they induce shorter rather than longer microsaccade inhibition. One answer is that the effect of contrast on microsaccade inhibition is determined primarily by low-level visual processes and physiological latencies, and not by high-level cognitive factors such as attentional engagement. Another answer is that the effect of attention on microsaccade inhibition is related not to the level at which certain stimuli attract attention but rather to the time of attention engagement, which corresponds in some way to the processing time. Low-contrast stimuli pose a higher processing demand due to increased uncertainty and noise, which need to be resolved, while attention is engaged and microsaccades are inhibited.

Whether explicit or conscious engagement of attention is critical for producing the effect of contrast or spatial frequency on msRT is currently unclear. In preliminary experiments with passive viewing without counting, and with cognitive load (silently subtracting 7), we found that explicitly attending the target is not critical for the msRT measure for contrast. Further investigation is required to study the effect of awareness, attention, and attentional load on the contrast response function measured via microsaccade inhibition.

Microsaccade RT as an implicit measure of low-level visual properties

The current results suggest that the msRT could be used to measure low-level visual properties implicitly, without the observer's response and perhaps even without attentional engagement. This may be useful in testing noncommunicating individuals such as nonverbal people with autism, people in a coma, or babies.

Keywords: microsaccades, oculomotor mechanics, contrast sensitivity, eye movements

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