

Spatiotemporal profile of peri-saccadic contrast sensitivity

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Sensitivity to luminance contrast is reduced just before and during saccades (saccadic suppression), whereas sensitivity to color contrast is unimpaired peri-saccadically and enhanced post-saccadically. The exact spatiotemporal map of these perceptual effects is as yet unknown. Here, we measured detection thresholds for briefly flashed Gaussian blobs modulated in either luminance or chromatic contrast, displayed at a range of eccentricities. Sensitivity to luminance contrast was reduced peri-saccadically by a scaling factor, which was almost constant across retinal space. Saccadic suppression followed a similar time course across all tested eccentricities and was maximal shortly after the saccade onset. Sensitivity to chromatic contrast was enhanced post-saccadically at all tested locations. The enhancement was not specifically linked to the execution of saccades, as it was also observed following a displacement of retinal images comparable to that caused by a saccade. We conclude that luminance and chromatic contrast sensitivities are subject to distinct modulations at the time of saccades, resulting from independent neural processes.

Keywords: contrast sensitivity, eye movements, active vision, peri-saccadic sensitivity

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Introduction

With each saccade (rapid ballistic eye movement), the image of the visual scene sweeps across the retina at high speed; yet, this dramatic change of the visual input completely escapes our notice. In natural viewing conditions, many factors contribute to this temporary blindness, including retinal smear (stimuli displayed throughout the eye movement result in blurred retinal images) and masking by the high-contrast images acquired before and after the saccade (Matin, Clymer, & Matin, 1972). However, even in experimental conditions where these factors are controlled for (with stimuli flashed briefly in an otherwise empty visual field), peri-saccadic sensitivity is found to be strongly and selectively modulated.

The sensitivity to flashed stimuli modulated in luminance contrast and with low spatial frequency is reduced by 0.5–1 log unit, whereas high spatial frequencies and

stimuli modulated in chromatic contrast are detected with the same sensitivity peri-saccadically and during steady fixation (Burr, Holt, Johnstone, & Ross, 1982; Burr, Morrone, & Ross, 1994; Diamond, Ross, & Morrone, 2000; Uchikawa & Sato, 1995; Volkman, 1986). The suppression of low-frequency luminance-defined stimuli is contingent on the preparation and execution of a saccade; it is not observed when the displacement of retinal images is simulated (by sweeping the stimulus display at saccadic speeds) while the observer maintains steady fixation. This constitutes strong evidence that contrast sensitivity is actively suppressed during saccades, possibly via extraretinal “efference copy” or “corollary discharge” signals generated by the oculomotor system (Diamond et al., 2000).

Burr et al. (1994) and Diamond et al. (2000) proposed that saccadic suppression may occur as early as in the lateral geniculate nucleus (LGN), which encompasses three segregated populations of neurons: the parvocellular (P), koniocellular (K), and magnocellular (M) pathways

(Hendry & Reid, 2000; Merigan & Maunsell, 1993). A selective suppression of activity in the M pathway would account for the suppression of low spatial frequency luminance modulations (and of motion signals), preferentially processed by M neurons, while sparing the sensitivity to chromatic contrast and high-frequency modulations of luminance contrast, preferentially processed by the K and P pathways. Forward and backward masking experiments suggest that suppression is achieved by a gain reduction of the M neurons' response (Burr et al., 1994; Burr, Morgan, & Morrone, 1999), which Diamond et al. (2000) modeled as the result of the interaction between the retinal input and an extraretinal corollary discharge signal. This hypothesis—that saccadic suppression is achieved with a gain reduction of visual responses under the control of extraretinal signals—predicts suppression to be homogeneous across the retinal space, reducing contrast sensitivity by a constant divisive factor. The conclusions from two psychophysical studies, however, challenge this prediction. Mitrani, Mateeff, and Yakimoff (1970) and Osaka (1987) argued that the magnitude and time course of suppression is different for small luminance-modulated stimuli flashed in the proximity of the fovea, being stronger peri-saccadically (Osaka, 1987) and recovering more quickly after the saccade (Mitrani et al., 1970) than for peripheral flashes. However, because both studies measured detection performance (percent correct responses for stimuli set to be near threshold during steady fixation), their results would be equally compatible with a constant suppression factor across the retinal space, producing a larger and quicker drop of correct detection responses in the most sensitive retinal regions.

Our first experiment addressed these issues by measuring contrast sensitivity for small luminance-modulated stimuli, flashed at various times relative to saccade onset and at various spatial locations. We quantified suppression by comparing sensitivity at matching locations during steady fixation and peri-saccadically, and we characterized the time course of the sensitivity change across the range of stimulus locations. Results were analyzed after encoding stimulus locations in both their screen coordinates as well as in retinal coordinates, computed by taking into account the position of the eyes at the time of stimulus presentation. In this way, the comparison of the dynamics in both coordinate systems allowed to identify the frame of reference in which saccadic suppression occurs.

Peri-saccadic suppression is selective for luminance contrast, but the sensitivity to chromatic contrast varies around the time of saccades too. The variation has the opposite sign and different dynamics relative to saccadic suppression: An enhancement of color contrast sensitivity is observed post-saccadically, starting about 100–200 ms after the completion of the saccade. Interestingly, a similar pattern of suppression/enhancement is observed

in coincidence with another class of eye movements: smooth pursuit (Schütz, Braun, Kerzel, & Gegenfurtner, 2008), during which sensitivity to low-frequency luminance modulation is decreased and sensitivities to high-frequency modulations and to chromatic contrast are enhanced.

The co-occurrence of luminance contrast suppression and chromatic contrast enhancement is suggestive of a link between the two phenomena. The same extraretinal signal proposed to trigger the suppression of M responses may be responsible for the enhancement of the P pathway, as suggested for the case of smooth pursuit (Schütz et al., 2008). Another hypothesis proposes that suppression and enhancement both result from the effect of saccades on luminance signals. P cells probably carry both chromatic information and an achromatic signal; a saccade might destroy the notional equiluminance of the chromatic stimuli, thereby making the target more visible (Morgan, 1994).

To investigate the relationship between peri-saccadic suppression and post-saccadic enhancement, our second experiment measured sensitivity to stimuli similar to those in our first experiment but equiluminant to the background and modulated in chromatic contrast only. As in our first experiment, we varied stimulus position to ask whether the modulations of contrast sensitivity depend on stimulus position, both during a saccade and during a 300-ms post-saccadic epoch. In addition, we measured chromatic contrast sensitivity in a condition where saccadic retinal motion was simulated while observers maintained steady fixation. This approach allowed us to ask whether the post-saccadic enhancement is tied to the execution of a saccade, as peri-saccadic suppression is (Diamond et al., 2000), testing the hypothesis that both phenomena can be explained by an active extraretinal modulation of visual sensitivity at the time of eye movements.

While the stimuli used in the two experiments presented here were similar (small and brief modulations of luminance or chromatic contrast), the methodological approach of each experiment was optimized to its specific aims. **Experiment 2** was designed to measure potentially small effects: the post-saccadic enhancement of chromatic contrast sensitivity, previously reported to be in the order of a factor of 2, and the absence of peri-saccadic suppression of chromatic contrast sensitivity (Burr et al., 1994; Diamond et al., 2000). To maximize the precision of the method, we adopted a 2AFC color identification task combined with an adaptive method to sample the psychometric curve (QUEST; Watson & Pelli, 1983) and we performed all analyses at the single-subject level. **Experiment 1** measured the large peri-saccadic suppression of sensitivity to luminance contrast and aimed at estimating its variations across a wide and densely sampled range of stimulus positions and timings. For this experiment, we favored efficiency over precision and used

a seen/not seen task with analyses performed on data pooled across subjects. Two previous studies (Burr et al., 1994; Diamond et al., 2000) measured saccadic suppression with both a forced choice identification task and a seen/not seen task and reported comparable estimates of the effects, demonstrating the validity of this approach for peri-saccadic stimuli.

Methods

Experiments were performed in part at the Philipps-Universität Marburg (Germany) and in part at the Neuroscience Institute of the CNR in Pisa (Italy). Experimental procedures, approved by the local ethics committees, were in line with the declaration of Helsinki. Care was taken to produce comparable experimental conditions with the different equipment of the two laboratories. A total of nine observers participated in the experiments (age range: 22–46, four naives and one subject familiar with the goals of the study for [Experiment 1](#) and two authors and two naives for [Experiment 2](#)), all with normal or corrected-to-normal vision.

Visual stimuli were produced by CRT devices, driven at 100-Hz refresh rate and covering at least the central 60 deg × 50 deg of the visual field. Subjects had their head stabilized with a chin rest and eye movements were monitored. Contrast sensitivity was measured for 2D Gaussian blobs (standard deviation: 1 deg in both spatial dimensions) flashed for one monitor frame on a uniform background. Either the stimulus was modulated in luminance ([Experiment 1](#)) or it was equiluminant to the background and modulated in chromaticity ([Experiment 2](#)). The contrast of the stimulus was varied from trial to trial to determine psychometric functions. For statistical analysis, we used the Psignifit Matlab package (Wichmann & Hill, 2001a, 2001b), which fits the data set with integral-of-Gaussian functions and provides estimates of the perceptual threshold and its standard error (based on 1999 Monte Carlo simulations). Sensitivity was defined as the inverse of the threshold.

In both [Experiments 1](#) and [2](#), we tested two main conditions. In the “saccade condition,” trials began with subjects gazing at a fixation spot (FP, a black spot of 0.4-deg diameter, located 7.5 deg left of the screen center). After a variable delay (randomly chosen between 700 and 1100 ms), the fixation target was extinguished; an identical target (the saccade target, ST) was presented 7.5 deg to the right of the screen center eliciting a 15-deg rightward saccade. In the “steady fixation condition,” no saccade target was presented and subjects maintained their gaze on a fixation point that remained visible throughout the duration of a trial. An additional condition (“simulated saccades”) was tested only in [Experiment 2](#) (see below).

Experiment 1: Sensitivity to luminance contrast

Apparatus. Stimuli were generated on a PC using C++ and OpenGL routines and displayed on a 1.6 m × 1.2 m screen (located at 1.14 m from the observer) by a CRT projector (Electrohome Marquee 8000, resolution: 1152 × 864 pixels). Eye movements were recorded with an infrared eye tracker (SR Research Eyelink II running at 500 Hz). Saccades were detected with a velocity criterion (200 deg/s). The start and end of a saccade were defined as the first and last samples with a velocity above 20 deg/s, respectively. Trials were discarded (i) if the start point or the end point of the saccade differed by more than 2 deg from the target position, (ii) if the saccade latency was negative or larger than 300 ms, and/or (iii) if the stimulus presentation occurred more than 100 ms before or 150 ms after saccade onset. Based on these criteria, about 15% of all trials were excluded from further analysis.

Stimuli. A 2D Gaussian blob (standard deviation: 1 deg in both spatial dimensions) was displayed against a gray background (CIE coordinates: $x = 0.324$; $y = 0.329$; luminance: 12 cd/m²) and it appeared along the horizontal meridian, at a random location between ±30 deg relative to the screen center (white symbols in [Figure 1A](#); stimuli were never presented at ±1.5 deg around the fixation and saccade targets). The visible screen (70 deg × 50 deg) was surrounded by very low ambient light (<0.1 cd/m²). The stimulus was brighter than the background, with incremental contrasts of 6, 12, 18, 24, and 46%, which varied from trial to trial according to the method of constant stimuli. Three additional contrast levels (4, 8, and 20%) were tested in the steady fixation condition. Subjects reported detection of the stimulus by pressing a key on the computer keyboard (seen/not seen task). This task has been successfully used in two previous saccadic suppression studies (Burr et al., 1994; Diamond et al., 2000) yielding similar sensitivity estimates as a 2AFC procedure.

Data analysis. For each subject, a minimum of 1400 and a maximum of 3500 trials were collected, with a grand total of 13,521 trials. Analyses were performed on data pooled across the five subjects: Trials were sorted according to the stimulus location and stimulus time relative to saccade onset, then divided into bins of at least 30 samples using a sliding spatiotemporal window (for some spatiotemporal bins, this pooling method resulted in an uneven distribution of data from the different subjects). In a separate analysis, we confirmed that this unevenness did not systematically affect the estimates of threshold values. The width of the window in space and time and the step size by which it moved was variable for different analyses (see figure legends). Behavioral data were analyzed after coding the spatial location of the stimuli in either screen coordinates or retinal coordinates; the

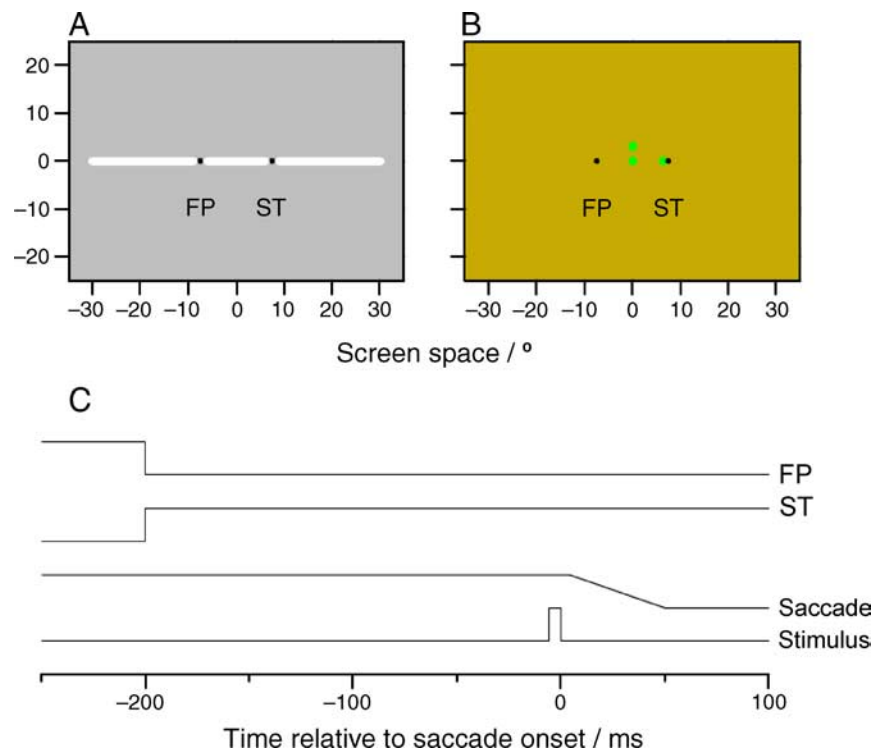


Figure 1. Spatial arrangement of the stimuli in (A) Experiments 1 and (B) 2, respectively, and (C) time course of presentations. Stimuli were 2D Gaussian blobs modulated in luminance contrast (Experiment 1) or they were modulated in chromatic contrast (along the red–green axis) and equiluminant to the yellow background (Experiment 2). Stimuli were presented for 1 monitor frame at variable delays from the onset of a 15-deg saccade. The white line in (A) represents the possible stimulus locations in Experiment 1, varied at random in the range ± 30 deg at gaze level, except in the ± 1.5 deg surrounding the fixation point (FP) and the saccadic target (ST). The green dots in (B) represent the tested locations in Experiment 2: at screen center and at two additional locations at or above gaze level.

latter were determined by subtracting the position of the eyes at the time of stimulus presentation from the position of the stimulus on the screen. In each spatiotemporal bin, detection rate (i.e., the proportion of trials where the stimulus was reported as “seen”) was plotted against stimulus contrast yielding psychometric curves. A representative sample curve is shown in Figure 2A. The contrast level yielding a detection probability of 0.5 was considered the perceptual threshold (T). Sensitivity (S) was defined as the inverse of threshold ($S = 1/T$). For fitting psychometric functions, we imposed a constraint on the slope parameter, such that the fitted curve could not grow from 0 to 1 in an interval smaller than the distance between two consecutive tested contrast values. In a small percentage of instances (3%), removing this constraint led to unrealistically small estimates of the standard error of the estimated thresholds while not significantly affecting the threshold values themselves. Error bars in Figures 3 and 4 report the larger standard error as estimated by the two fitting methods (unconstrained fit and fit with the slope constraint). Only data points for which both methods yielded an estimate of the SE are shown.

Experiment 2: Sensitivity to chromatic contrast

Apparatus. Experiment 2 employed a 35×27.5 cm CRT color monitor (Barco Calibrator, resolution: 464×645 pixels) viewed from 30-cm distance. Stimuli were generated using a specialized graphics board (Cambridge Research Systems VSG2/5) housed in a PC and controlled by customized Matlab (Mathworks) programs. Eye movements were monitored by an infrared limbus eye tracker (ASL 310). The PC sampled the raw data at 1000 Hz and stored the eye trace for offline quality checks: As in previous studies (e.g., Binda, Morrone, Ross, & Burr, 2010), the saccade onset was determined online by fitting the eye trace with a three-line-segment function. Here, the three segments correspond to the pre-saccadic, saccadic, and post-saccadic epochs; the point of intercept between the first and second segments then yields an estimate of the saccadic onset. This procedure is more complex than the standard velocity threshold. However, it is more appropriate for the ASL 310 eye tracker (which requires calibrations every few trials) given that a velocity threshold is more sensitive to changes of spatial

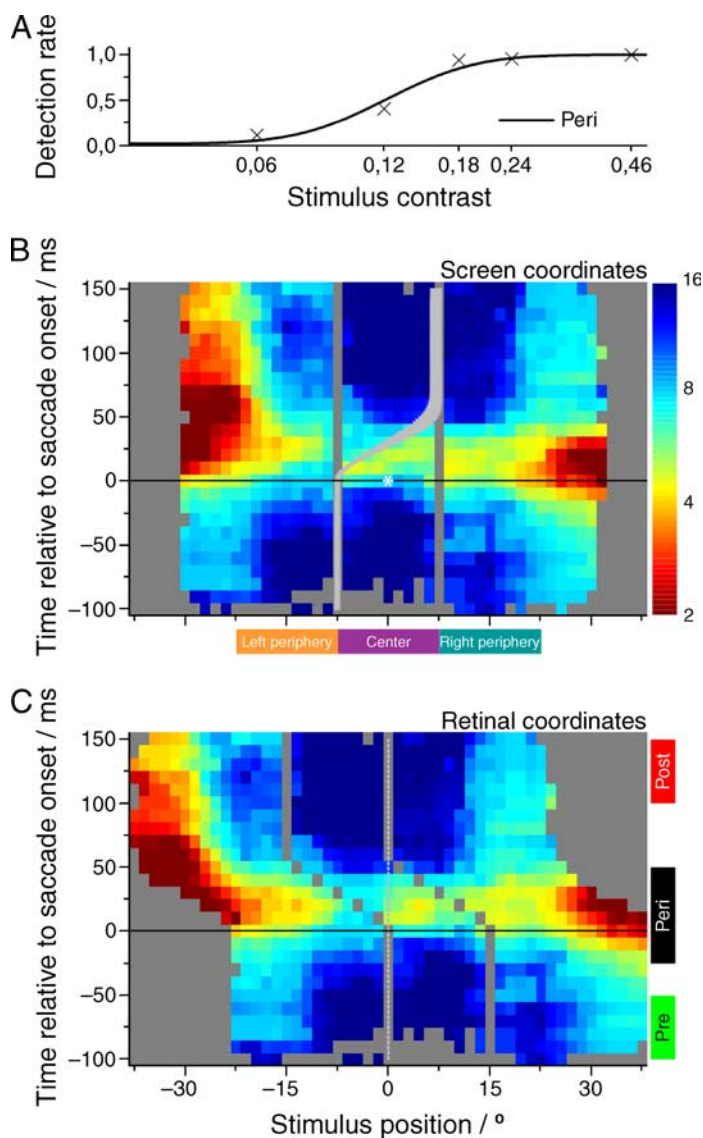


Figure 2. Luminance contrast sensitivity during fixation and saccades. (A) Sample psychometric curve for stimuli presented peri-saccadically at screen center (in the central 7.5-deg area). The threshold determined from this curve represents one data point in (B) (marked by white star). Threshold is defined as the contrast value allowing stimulus detection in 50% of trials (sensitivity = $1/\text{threshold}$); for example, the curve in (A) estimated a threshold of about 0.15 corresponding to a sensitivity of about 6.7. Sensitivity values as a function of the time of stimulus presentation relative to the saccade onset (y-axis) and stimulus location (x-axis), coded in (B) spatial or (C) retinal coordinates. Each sensitivity value (color-coded in the maps) was computed in a $20 \text{ ms} \times 7.5 \text{ deg}$ spatiotemporal window (including an average of 70 trials), which was shifted in steps of 10 ms and 1.5 deg. Colored boxes to the right of (C) show the pre-, peri-, and post-saccadic temporal windows used for data analysis shown in Figure 3. Colored boxes between (B) and (C) illustrate the left, center, and right spatial windows used for data analysis shown in Figure 4. The horizontal line at time = 0 ms marks the saccade onset.

gain. In a later offline analysis, the experimenter checked the quality of saccades and, when necessary, discarded the trial (this happened in about 5% of trials, due to a corrective saccade or unsteady fixation).

Stimuli. The 2D Gaussian blob (standard deviation: 1 deg in both spatial dimensions) was equiluminant to the yellow background (Commission Internationale de l'Eclairage (CIE) coordinates: $x = 0.48$, $y = 0.44$; luminance: 19.6 cd/m^2) and its chromatic contrast was modulated along the red–green axis. Note that the chromaticity of background was different from that in Experiment 1 (where the background was gray). The yellow background was chosen to maximize the chromatic contrast along the red–green axis attainable within the monitor gamut, while minimizing the stimulation of S cones. Equiluminance was established for each individual subject, by the minimum flicker technique (Boynton, 1979), adjusting the ratio of the red to green gun output to produce minimal flicker of the stimulus when modulated at 20 Hz. The color of the stimulus (red or green) was randomly chosen on each trial; at maximum contrast, the stimulus had CIE coordinates of $x = 0.62$, $y = 0.64$ for

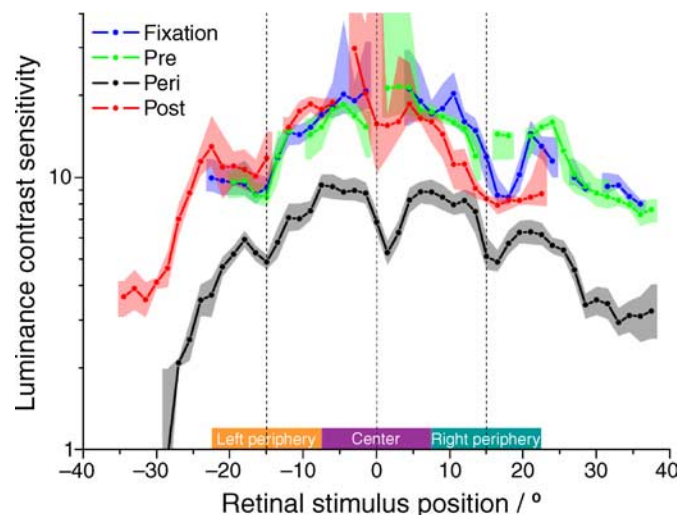


Figure 3. Sensitivity as a function of the stimulus retinal eccentricity. Colored lines represent contrast sensitivity as measured during saccades or during fixation. Each data point was computed in a 3-deg-wide spatial window, sliding across space in steps of 1.5 deg and including an average of 85 trials. The figure reports sensitivity values for steady fixation (where subjects maintained their gaze on a fixation spot located 7.5 deg left of screen center, blue line) and for three ranges of times relative to saccade onset (pre-saccadic (green): -100 to -50 ms, peri-saccadic (black): -25 to 50 ms, post-saccadic (red): 100 to 150 ms; see colored boxes in Figures 2 and 4). Standard errors of individual sensitivity values are shown as shaded areas. Missing data points are those for which the SE could not be reliably estimated (see Methods section). Colored boxes define the spatial windows used for data analysis shown in Figure 4. Light gray indicates eye position.

red and $x = 0.28$, $y = 0.59$ for green and produced a root-mean-squared (RMS) cone contrast of 0.31 relative to the background. RMS cone contrast was defined as: $\sqrt{[(\Delta L/L)^2 + (\Delta M/M)^2]/2}$, where L and M denote the excitation of L and M cones induced by the background and ΔL and ΔM denote the difference in cone excitation between the stimulus and the background. Cone excitation levels were computed using the CIE 1931 observer modified by Judd and Smith and Pokorny's copunctal points (following the procedure detailed in Appendix III of Kaiser & Boynton, 1996). Stimulus contrast was varied from trial to trial, using the adaptive QUEST procedure (Watson & Pelli, 1983). Subjects reported, in a 2-alternative forced-choice task, whether the stimulus was red or green. The stimulus was presented at the screen center (i.e., midway along the real or simulated saccade path); for two subjects, sensitivity at two additional stimulus positions was tested in separate sessions, one at gaze level 6.5 deg right of the screen center (i.e., aside the saccade target) and another at screen center 3 deg above gaze level (see green blobs in Figure 1B).

Simulated saccades condition. In addition to the “saccades” and “steady fixation conditions,” we tested a condition where the displacement of retinal images produced by saccadic eye movements was simulated by viewing the monitor screen through a small (4×3 cm) mirror caused to rotate at saccadic speeds by a galvanometric engine controlled by the VSG. The mirror was placed 27 cm in front of the monitor. Subjects were seated laterally to the monitor, with their right eye about 3 cm from the mirror; a patch covered the left eye. Through the mirror, subjects had a clear monocular view of the central area of the display (20×20 deg). They maintained fixation on the fixation point (FP) throughout an experimental session. The rotation of the mirror produced a 15-deg leftward shift of the displayed image, therefore reproducing the displacement of retinal images caused by a 15-deg rightward saccade and bringing the saccadic target (ST) to the former retinal position of FP. The duration and velocity of the mirror rotation were monitored throughout the experiment. The typical duration for a 15-deg displacement was 45 ms (about the same as the duration of eye movements observed in the real saccades condition). During the experiment, we also monitored the subjects' eye movements (with a second eye tracker, model: HVS SP150) to control fixation.

Data analysis. One thousand to two thousands trials were collected for each subject and condition (two subjects were tested with one stimulus position only; the other two with 3 stimulus positions), yielding a grand total of 12,132 trials. Data were analyzed at the single-subject level. Trials from each of the four tested subjects were ranked according to the delay of the stimulus presentation from the onset of the real/simulated saccade and grouped in contiguous bins of variable width (each bin included at least data from 30 trials). For each bin, the proportion of

correct responses was plotted as a function of the stimulus contrast. Performance varied from chance level (probability of correct response = 0.5) at low contrast to perfect behavior at high contrast. The contrast level allowing for a probability of correct responses of 0.75 was taken as threshold.

Results

We measured sensitivity to luminance and chromatic contrast with small 2D Gaussian blobs flashed for one monitor frame around the time of a 15-deg saccade (Figure 1). The choice of the stimulus represented a compromise between keeping the stimulus small enough to probe the spatial pattern of sensitivity, on the one hand, and to ensure a rich content of spatial frequencies that are peri-saccadically suppressed, on the other hand (Burr et al., 1982, 1994; Diamond et al., 2000; Uchikawa & Sato, 1995; Volkman, 1986).

In Experiment 1, we tested the saccade-related spatio-temporal profile of sensitivity to luminance contrast with stimuli presented at gaze level. Figure 2A shows a sample psychometric function for stimuli flashed in the central region of the screen. Thresholds were defined as the contrast for which the stimulus was reported as “seen” in 50% of trials.

Figures 2B and 2C shows the spatiotemporal map of contrast sensitivity (the inverse of threshold), with stimulus location encoded either in screen coordinates (panel B) or in retinal coordinates (panel C). For all positions, contrast sensitivity was strongly reduced from about 25 ms before saccade onset and throughout its duration, implying saccadic suppression. The peri-saccadic contrast sensitivity was not homogenous across the visual field, being higher in the more central regions compared to eccentric parts of the visual field.

In order to test whether the peri-saccadic topography of contrast sensitivity can be explained by a multiplicative modulation (gain control) of contrast sensitivity during fixation, we analyzed contrast sensitivity in three temporal windows as a function of the retinal location of the stimulus (Figure 3). The black curve shows data for the detection of stimuli presented peri-saccadically, i.e., from 25 ms before to 50 ms after saccade onset. Detection data for stimuli presented pre-saccadically (between 100 and 50 ms before saccade onset) are shown in green, whereas detection data for stimuli shown post-saccadically (between 100 and 150 after saccade onset) are shown in red. Control data representing sensitivity for luminance contrast stimuli during steady fixation are shown in blue. The peri-saccadic curve lies below the others, indicating suppression. The shape of all curves is similar, implying that suppression is well described as a sensitivity reduction by a scaling factor that is constant across retinal space.

Sensitivity during steady fixation (blue curve) clearly shows two local minima at 15-deg eccentricity, roughly corresponding to the locations of the blind spot. The same drops of sensitivity are observed for peri- and post-saccadic stimuli (black and red curves, respectively), whereas the local minimum in the +15 deg region (the pre-saccadic retinal location of the saccade target, right-most dashed line) is not evident for pre-saccadic presentations (green curve).

A small reduction of sensitivity in the blind spot regions was expected (in these regions, vision is monocular, predicting a reduction of sensitivity by a factor of about $\sqrt{2}$) and our success in detecting it indicates that the present seen/not seen technique is adequate for measuring contrast sensitivity, both peri-saccadically and in steady fixation conditions.

We note two additional features of the results in Figure 3. The curves tend to show a decline of sensitivity in the foveal region, which is consistent with the relatively low spatial frequencies of our stimuli; sensitivity tends to be lower in the far left retinal periphery than in the far right periphery during and after the saccade, possibly reflecting a different level of retinal adaptation before and after the saccade. During fixation and before the saccade, locations with eccentricity < -27.5 deg lay outside the screen area and they are therefore dark adapted (after the saccade, the same happens to locations with eccentricity > 27.5 deg). Thus, the saccade brings about a change in

mean luminance for all positions with eccentricity larger than 27.5 deg. In particular, for retinal positions left of -27.5 deg, the saccade causes an abrupt increase of mean luminance, which can explain the observed decrement of contrast sensitivity.

Figure 4B compares the time course of suppression for stimuli presented in the central region of the retina (eccentricity < 7.5 deg) and for stimuli in the left or right periphery (average eccentricity: ± 15 deg). The sensitivity in the left and right peripheries is not matched pre- and post-saccadically; it tends to be lower in the left retinal periphery than in the right periphery before the saccade, while the opposite trend is observed after the saccade. Because only positions with eccentricity < 22.5 deg were considered for this analysis, differences of adaptation level (discussed above) cannot directly account for this result; possible contributing factors include a general attentive enhancement at the screen center or residual inhomogeneities of the display luminance at these outer positions.

Peri-saccadically, the three time courses run parallel and the maximum sensitivity reduction (0.4–0.5 log unit) is observed right after the saccade onset for all positions. On the contrary, if stimuli positions are coded in screen coordinates (Figure 4A) rather than in retinal eccentricity, peak suppression occurs at different times for stimuli presented at the right, central, and left regions of the screen (respectively, at about 5, 15, and 30 ms after the saccade onset).

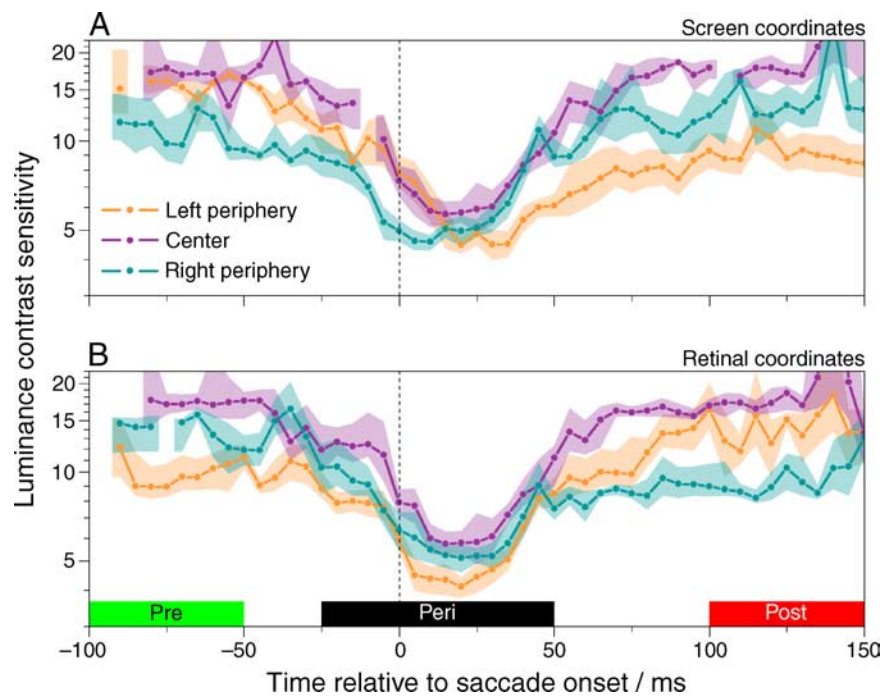


Figure 4. Time course of peri-saccadic suppression for three ranges of stimulus positions. The position ranges were: left periphery (orange line): -22.5 to -7.5 deg; center (magenta line): -7.5 to 7.5 deg; right periphery (green line): 7.5 to 22.5 deg, defined with respect to the screen center (screen coordinates, A) or in retinal coordinates (B). Each point was computed in a temporal window 10 ms wide, sliding across time in steps of 5 ms and including an average of 72 trials. Standard errors of individual sensitivity values are shown as shaded areas. Colored boxes illustrate the temporal windows used for data analysis shown in Figure 3.

Thus, the peri-saccadic suppression of sensitivity to luminance contrast appears to be homogeneous across retinal space (and inhomogeneous in external space).

Next, we asked whether a peri-saccadic change of sensitivity to chromatic contrast can be observed. As we did for luminance contrast sensitivity, we investigated its dependency on retinal eccentricity. **Experiment 2** measured sensitivity to stimuli similar in all respects to those employed in **Experiment 1**, except that they were equiluminant to the (yellow) background and modulated in chromatic contrast along the red–green axis. Sensitivity was measured with a 2AFC color discrimination task, given that the small expected size of the effects required a more sensitive technique than the yes/no task used in **Experiment 1**. Four subjects were tested with the stimulus presented at gaze level (as in **Experiment 1**), at a location midway between the fixation spot and the saccade target ($[x, y] = [0 \text{ deg}, 0 \text{ deg}]$, see inset in **Figure 5B**). Following the same logic of **Experiment 1**, we asked whether any

peri-saccadic sensitivity modulation depends on the stimulus eccentricity. To this end, two of the four subjects were tested at a different, more peripheral location ($[x, y] = [6.5 \text{ deg}, 0 \text{ deg}]$, i.e., next to the saccade target, see inset in **Figure 5A**). Finally, because the saccade causes both these stimulus locations to become foveal at different times during the movement of the eyes, the same two subjects were also tested with the stimulus presented above the line of sight ($[x, y] = [0 \text{ deg}, 3 \text{ deg}]$, inset of **Figure 5C**), which remains in a parafoveal region at all times.

Figure 5 (black symbols) reports the results from one subject tested with all three stimulus locations (see insets), plotting sensitivity as a function of the delay of stimulus presentation from the onset of a saccade. Sensitivity to chromatic contrast was not suppressed in the peri-saccadic interval, but it rather increased during the saccade for stimuli presented at gaze level (**Figures 5A** and **5B**) and it remained approximately constant for stimuli presented above the line of sight (**Figure 5C**; for this stimulus position,

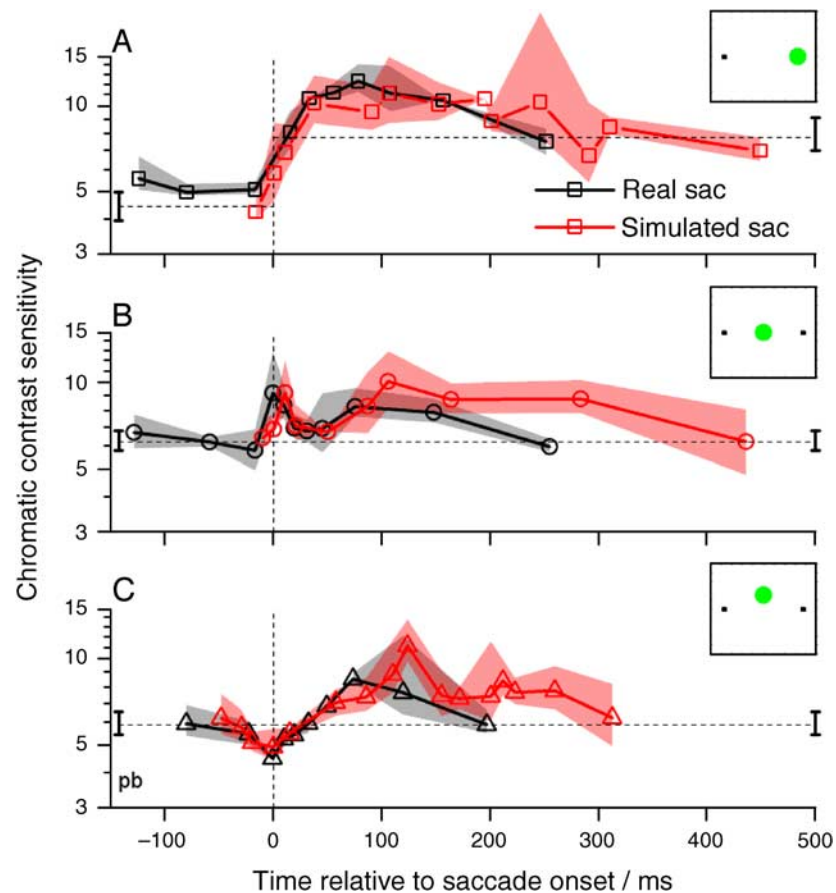


Figure 5. Sensitivity to chromatic contrast. Data from one subject (PB, an author) in **Experiment 2**. Sensitivity to chromatic contrast for three stimulus locations (A–C; see insets), measured while subjects maintained steady fixation at the fixation point (dotted lines for $t < 0$) or at the saccade target (dotted lines for $t > 0$ ms) and at various times from a saccade (black symbols) or from a simulated saccade (red), i.e., a displacement of the whole visual display simulating the retinal motion caused by a saccadic eye movement. Data points in each curve report sensitivity measures computed in contiguous bins of variable width, each including at least 30 trials. Standard errors of individual sensitivity values are shown as shaded areas. Sensitivity is the reciprocal of the root-mean-squared (RMS) cone contrast of the L and M cones at threshold ($\sqrt{[(\Delta L/L)^2 + (\Delta M/M)^2]}/2$; see **Methods** section for more details).

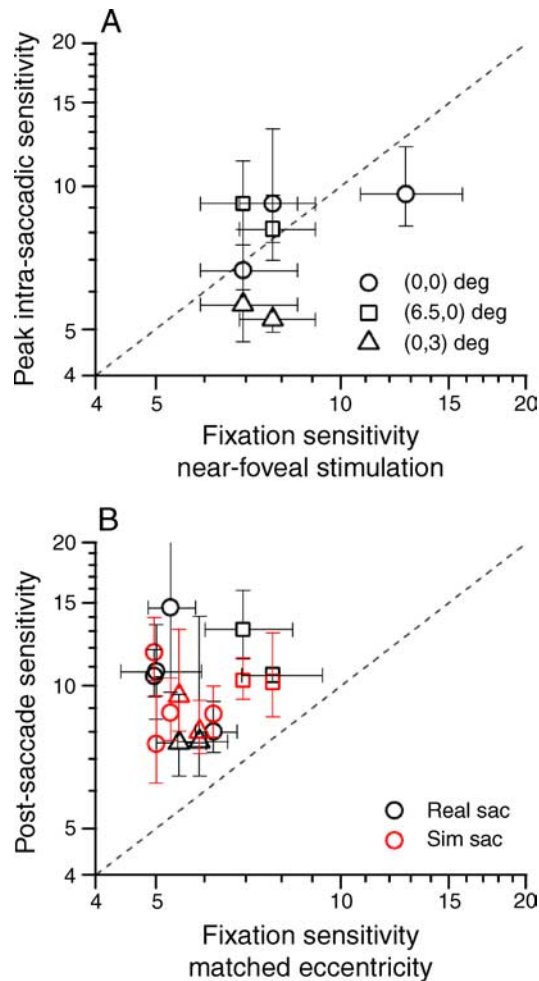


Figure 6. Chromatic contrast sensitivity during real and simulated saccades. (A) Peak chromatic contrast sensitivity observed for stimuli presented during a saccade plotted against the sensitivity for stimuli at 1-deg eccentricity, during steady fixation. The eccentricity of 1 deg was chosen to be close to the fovea, while producing small overlap between the stimulus and the fixation spot (always visible, like in all other experiments). (B) Peak sensitivity to chromatic contrast observed after a saccade or a simulated saccade against sensitivity at matching retinal eccentricities. Peak sensitivity was defined as the maximum sensitivity value in a time course like the ones in Figure 5, measured for each subject and condition; the average/standard deviation (across subjects and stimulus positions) of the delays from saccade onset where the peak sensitivity was observed were 153 ms/40 ms for the saccade condition and 149 ms/44 ms for the simulated saccade condition. Black symbols: real saccades. Red symbols: simulated saccades. Different symbol shapes refer to different stimulus locations. Data from four subjects were collected with the stimulus at position (0, 0) deg; two of the subjects were tested with the additional (6.5, 0) and (0, 3) deg positions. Error bars report standard errors of individual sensitivity values.

there is a tendency toward a peri-saccadic reduction of sensitivity; a bootstrap t -test with 2000 resamplings revealed that it is not statistically significant: $p > 0.1$ for both subjects tested with this stimulus position). During the saccade, the fovea sweeps over stimuli presented at gaze level and this reduction of stimulus eccentricity could explain the gradual (Figure 5A) or transient (Figure 5B) peri-saccadic sensitivity increase. To verify this hypothesis, we plot the peak sensitivity observed during the saccade against sensitivity at 1-deg eccentricity, for all tested subjects and positions (Figure 6A). All points lie close to the identity line, implying a good match between peri-saccadic and fixation sensitivity at comparable retinal locations.

After the saccade, chromatic sensitivity was higher than that observed during fixation. This post-saccadic enhancement of chromatic contrast sensitivity peaked around 100 ms after saccade onset. Figure 6B (black symbols) plots peak post-saccadic sensitivity against sensitivity at matched retinal locations observed during normal fixation. For all tested locations, chromatic contrast sensitivity was enhanced by about 0.3 log units relative to normal fixation.

To test whether this post-saccadic enhancement of sensitivity to chromatic contrast is tied to the active execution of a saccade or rather emerges as a by-product of the changes of retinal stimulation caused by an eye movement, we tested an additional condition: simulated saccades. Here, we asked subjects to maintain their gaze on a fixation point, while we displaced the whole visual display so to mimic saccadic retinal motion (see Methods section). Like we did for real saccades, we measured chromatic sensitivity at various times from the onset of the simulated saccade. The results are reported by red symbols in Figures 5 and 6. It is clear from inspection of these figures that real and simulated saccades caused a comparable enhancement of sensitivity to chromatic contrast, with very similar dynamics (compare black and red curves in Figure 5). A two-tailed paired t -test confirmed that peak sensitivity values observed after real and simulated saccades (black and red symbols in Figure 6B, respectively) were not statistically different with $p > 0.3$.

Discussion

We studied visual sensitivity for small stimuli, briefly flashed around the time of a saccade, and we characterized the spatiotemporal topography of sensitivity modulations.

Luminance contrast sensitivity for peri-saccadic stimuli was clearly multiplicatively reduced as compared to sensitivity for stimuli presented before or after saccades, or during fixation. This result is in line with previous reports (Burr et al., 1982, 1994; Diamond et al., 2000; Uchikawa & Sato, 1995; Volkmann, 1986).

The topography of the contrast sensitivity function (Figure 3) was similar for stimuli presented peri-, pre-, and post-saccadically or during steady fixation. In all conditions, sensitivity decreased with eccentricity except for local minima of sensitivity observed at about the fovea and at around ± 15 deg. The foveal decline of sensitivity is consistent with the relatively low spatial frequencies of our stimuli. The other two local minima occur at regions roughly corresponding to the blind spots; the drop of sensitivity in the +15 deg region, corresponding to the pre-saccadic retinal location of the saccade target, was less evident for stimuli presented in a pre-saccadic epoch; this relative pre-saccadic enhancement in the region of the saccade target may be related to the allocation of visual attention (Deubel & Schneider, 1996).

In a second set of experiments, we measured peri-saccadic chromatic contrast sensitivity for few crucial positions (see insets in Figure 5). In agreement with previous results (Burr et al., 1994; Diamond et al., 2000), we found sensitivity to be enhanced after the completion of the eye movement, with a peak effect of about 0.3 log unit occurring some 100 ms after saccade offset, uniform across the range of tested positions (which spanned some 15 deg of visual angle, at or above gaze level). Extending previous investigations, we observed the same enhancement of chromatic contrast sensitivity following simulated saccades, which suggests that the post-saccadic enhancement may be a by-product of the spurious retinal motion due to the movement of the eyes. Importantly, this finding dissociates the post-saccadic enhancement of chromatic sensitivity from saccadic suppression of luminance sensitivity, since the latter cannot be reproduced with a saccadic-like motion of the visual display (as demonstrated by Diamond et al., 2000).

Visual perception integrates relevant features (e.g., motion or form) across saccadic eye movements in a non-retinotopic coordinate system (Melcher, 2005; Melcher & Morrone, 2003), suggesting the possibility that saccade-related visual phenomena occur in coordinates attached to the external space. Here, we found that, when considering a screen-centered coordinate system, strongest peri-saccadic suppression of luminance contrast sensitivity occurred for different stimulus regions at different points in time relative to saccade onset. In contrast, the time courses of peri-saccadic suppression were aligned for different stimulus positions defined in retinal coordinates, with the maximum reduction of sensitivity (by a factor of about 0.5 log unit) occurring for stimuli presented immediately after the saccade onset. When plotting sensitivity as a function of the retinal coordinates of the stimuli, we found that peri-saccadic sensitivity was scaled by an approximately constant factor relative to sensitivity during steady fixation. Based on this finding, we conclude that peri-saccadic suppression can be best described as occurring in a retinotopic frame of reference, reducing sensitivity by a divisive factor that is constant across the retinal space.

A spatially homogeneous peri-saccadic reduction of contrast sensitivity specific to luminance signals is consistent with the hypothesis that saccades selectively suppress neural responses in the M pathway, via dynamic gain control mechanisms (Burr et al., 1994; Diamond et al., 2000; Ross, Burr, & Morrone, 1996). The selective impairment of the M pathway can also account for the specificity of saccadic suppression to low-frequency luminance modulations, which constitute the preferential stimulus for this system. A dynamic reduction of gain is consistent with the present and previous (Burr et al., 1999, 1994) results: It is divisive, implying a reduction of neural responses proportional to the response amplitude, hence predicting the observed reduction of sensitivity by a constant scaling (divisive) factor across the retina. The dynamic gain adjustment may be triggered by extraretinal signals: a copy or corollary of the oculomotor command interfering with visual inputs before the detection stage (Diamond et al., 2000). Concurrent evidence in support of a peri-saccadic gain reduction was recently obtained based on an equivalent noise analysis approach (Watson & Krekelberg, 2011). Physiological evidence supports the existence of a corollary discharge signal, relayed from the superior colliculus to the frontal eye fields through a specialized thalamic nucleus (Wurtz, 2008).

While psychophysical data are consistent with the hypothesis of a differential impact of saccades on the M and the P systems, little work has been dedicated to investigating the effect of saccades on the third geniculocortical pathway, the K system. Although the physiological properties of this system appear to be extremely heterogeneous, K cells are believed to be the primary target of color-opponent S-cone signals (Hendry & Reid, 2000) and S-cone isolating stimuli (i.e., stimuli modulated in chromatic contrast along the blue–yellow axis) have been employed in psychophysical studies to estimate the contribution of the K pathway to visual sensitivity (e.g., Sumner, Adamjee, & Mollon, 2002). Testing peri-saccadic sensitivity to this class of stimuli would provide information on the effect of saccades on activity in the K pathway; to our knowledge, no study has undertaken this investigation. The present experiments cannot address this issue, because the stimuli we employed (luminance modulations or modulation in chromatic contrast along the red–green axis with minimal stimulation of the S cones) were not designed to selectively stimulate the K pathway.

Neurophysiological investigations have revealed clear correlates of peri-saccadic suppression. Both electrophysiological measures in monkeys (Bremmer, Kubischik, Hoffmann, & Krekelberg, 2009; Ibbotson, Crowder, Cloherty, Price, & Mustari, 2008) and fMRI experiments in humans (Kleiser, Seitz, & Krekelberg, 2004) revealed peri-saccadic suppression of visual responses in relatively high-level visual areas, notably the motion-sensitive area MT. As for earlier visual structures, fMRI studies in

humans indicate suppression of visual responses in retinotopically defined V1 and in LGN (Sylvester, Haynes, & Rees, 2005; Vallines & Greenlee, 2006) and TMS results suggest a pre-cortical origin of peri-saccadic suppression (Thilo, Santoro, Walsh, & Blakemore, 2004). However, electrophysiological recordings in monkeys indicate that M, P, and K cells in LGN behave similarly during saccades; LGN and V1 responses are not or weakly suppressed peri-saccadically and they are, in fact, enhanced after the saccade (Leopold & Logothetis, 1998; Reppas, Usrey, & Reid, 2002). In an attempt to reconcile these findings, Wurtz (2008) has recently proposed that suppression occurs at subcortical stages other than the LGN. The superior colliculus (SC) is a likely candidate given its involvement in the preparation of saccadic eye movements and the plausible prevalence of inputs from the M pathway to this structure. Recent results (Berman & Wurtz, 2011) support this line of reasoning, showing that saccadic suppression of visual responses in SC is accompanied by similar suppression in neurons of the inferior pulvinar compartment of the thalamus that are connected to the cortical area MT.

It can be concluded from our current data that saccades produce a selective suppression of sensitivity to luminance contrast, constant across a wide range of retinal eccentricities and compatible with an extraretinal origin. Saccades also cause an enhancement of sensitivity to chromatic contrast, but this should be considered separately from peri-saccadic suppression, since it is not specifically linked to the active execution of a saccade and may emerge as a by-product of the rapid whole-field retinal motion resulting from the movement of the eyes.

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