



Visual sensitivity for luminance and chromatic stimuli during the execution of smooth pursuit and saccadic eye movements



Doris I. Braun^a, Alexander C. Schütz^{a,b}, Karl R. Gegenfurtner^{b,*}

^a Abteilung Allgemeine Psychologie, Justus-Liebig-Universität Gießen, Gießen, Germany

^b Allgemeine und Biologische Psychologie, Philipps-Universität Marburg, Marburg, Germany

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ABSTRACT

Visual sensitivity is dynamically modulated by eye movements. During saccadic eye movements, sensitivity is reduced selectively for low-spatial frequency luminance stimuli and largely unaffected for high-spatial frequency luminance and chromatic stimuli (Nature 371 (1994), 511–513). During smooth pursuit eye movements, sensitivity for low-spatial frequency luminance stimuli is moderately reduced while sensitivity for chromatic and high-spatial frequency luminance stimuli is even increased (Nature Neuroscience, 11 (2008), 1211–1216). Since these effects are at least partly of different polarity, we investigated the combined effects of saccades and smooth pursuit on visual sensitivity. For the time course of chromatic sensitivity, we found that detection rates increased slightly around pursuit onset. During saccades to static and moving targets, detection rates dropped briefly before the saccade and reached a minimum at saccade onset. This reduction of chromatic sensitivity was present whenever a saccade was executed and it was not modified by subsequent pursuit. We also measured contrast sensitivity for flashed high- and low-spatial frequency luminance and chromatic stimuli during saccades and pursuit. During saccades, the reduction of contrast sensitivity was strongest for low-spatial frequency luminance stimuli (about 90%). However, a significant reduction was also present for chromatic stimuli (about 58%). Chromatic sensitivity was increased during smooth pursuit (about 12%). These results suggest that the modulation of visual sensitivity during saccades and smooth pursuit is more complex than previously assumed.

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1. Introduction

Voluntary eye movements such as saccades and smooth pursuit play a central role for the selection and accumulation of information in primate vision. Saccadic and pursuit eye movements determine, what, when and how we see things (for reviews see Gegenfurtner, 2016; Hayhoe & Ballard, 2005; Kowler, 2011; Schütz, Braun, & Gegenfurtner, 2011; Spering & Montagnini, 2011). In primates saccadic eye movements project rapidly images of selected objects on the foveal region of high visual acuity. While providing high-acuity information at the new fixation location, each saccade also comes at the cost of a high-speed displacement of the whole retinal image. However, even though we execute up to 4 saccades per second, our perception of the visual world appears clear and stable, undisturbed by any rapid retinal image shifts or motion blur. Why do we perceive so little of the retinal image displacements and how is perceptual stability achieved?

These questions have puzzled researchers for a long time and the knowledge about visual stability, perisaccadic modulation of visual perception and the underlying neuronal behavior in different brain structures has grown impressively (for review see Castet, 2010; Dodge, 1900; Krock & Moore, 2014; Matin, 1974; Morrone, 2014; Wurtz, 2008).

One factor contributing to visual stability is the reduction of visual sensitivity shortly before and during the execution of saccades (Volkman, 1986; Wurtz, 2008). At least two passive sources and one active source cause saccadic suppression. First, due to the fast retinal motion during saccades, sensitivity to chromatic contrasts and high-spatial frequency luminance contrasts is lost (Burr & Ross, 1982). This is a passive consequence of the fast retinal speeds during saccades and the lower sensitivity to high temporal frequencies. However, this effect does not abolish perception altogether. Motion perception is possible even at 800 deg/s as shown by Burr and Ross (1982) for very low spatial frequency stimuli. Also, during saccades the smeared intra-saccadic image can be perceived (Campbell & Wurtz, 1978; Castet & Masson, 2000; Ilg & Hoffmann, 1993; Matin, Clymer, & Matin, 1972) if the illumination

* Corresponding author.

E-mail address: gegenfurtner@uni-giessen.de (K.R. Gegenfurtner).

in a dark room is limited to the saccade duration (typically during 50–70 ms). Similarly, [Castet and Masson \(2000\)](#) showed that intra-saccadic motion perception was possible and not suppressed when the spatiotemporal characteristics of visual stimuli were optimized. The probability to detect motion and to discriminate motion direction of a low spatial frequency grating during saccades depended on the retinal image motion and it was best when gratings moved at a velocity that corresponded to the peak saccadic velocity. They concluded that visual factors determine largely the degree of intra-saccadic perception and that motion perception is functioning during saccades.

The second passive source of suppression results from the clear image seen before and/or after saccades that temporally masks the smeared intra-saccadic images ([Campbell & Wurtz, 1978](#); see also [Castet, Jeanjean, & Masson, 2002](#)). To point out that the presence of clear images cause the lack of intra-saccadic perception [Campbell and Wurtz \(1978\)](#) used the term “saccadic omission”. The third source is an active process that reduces sensitivity selectively for low-spatial frequency luminance stimuli. As mentioned above, these stimuli would still be visible at high retinal speeds and thus have to be suppressed actively. [Volkmann, Riggs, White, and Moore \(1978\)](#) measured contrast sensitivity to four flashed sinusoidal gratings presented in a Ganzfeld during saccades. Compared to fixation, contrast sensitivity for low-spatial frequency gratings of 0.21/deg was significant reduced by more than 0.6 log units but not for gratings of 4.5 c/deg. In similar detection studies, the selectivity of contrast sensitivity reduction for achromatic stimuli of low spatial frequency was confirmed ([Burr, Holt, Johnstone, & Ross, 1982](#); [Burr, Morrone, & Ross, 1994](#); [Ross, Burr, & Morrone, 1996](#); [Ross, Morrone, Goldberg, & Burr, 2001](#)). [Burr et al. \(1994\)](#) measured contrast sensitivity for the detection of flashed horizontal sinusoidal gratings during saccades. The gratings varied in spatial frequency and were presented either in luminance or color (red-green). They found a selective suppression during saccades only for the detection of achromatic sinusoidal gratings of low-spatial frequencies; here contrast sensitivity was reduced by 0.5–1 log units, while for luminance gratings of high-spatial frequencies (>0.5 cpd) or chromatic gratings the sensitivity was similar or even enhanced compared to fixation.

When an interesting object moves, primates can stabilize it on the fovea by smooth pursuit eye movements. While pursuit results in optimal vision for the foveated moving target, the stationary background is swept across the retina into the opposite direction. For moving stimuli presented in the periphery, sensitivity is mainly determined by retinal temporal frequency, but slightly reduced by 6–12% depending on the retinal movement direction relative to the pursuit direction ([Schütz, Delipetkos, Braun, Kerzel, & Gegenfurtner, 2007](#)). Similarly, the perceived motion smear is asymmetrically modulated during pursuit ([Bedell & Lott, 1996](#)). An asymmetric modulation in the opposite direction was found for supra-threshold motion perception ([Terao, Murakami, & Nishida, 2015](#)). Compared to saccades, the modulation of visual sensitivity for flashed stimuli is very different during pursuit: The sensitivity for low-spatial frequency luminance stimuli is only slightly suppressed by 5%, but the sensitivity for isoluminant color and for luminance stimuli with spatial frequencies above 3 cpd is actually increased by 15% ([Schütz, Braun, & Gegenfurtner, 2009a, 2009b](#); [Schütz, Braun, Kerzel, & Gegenfurtner, 2008](#)). This sensitivity enhancement starts already 50 ms before pursuit onset and scales with pursuit velocity. It was speculated that these effects are caused by an increase in contrast gain along the parvocellular pathway because the magnocellular pathway cannot process stimuli defined by color or high-spatial frequency luminance variations ([Born & Bradley, 2005](#); [Maunsell, Nealey, & DePriest, 1990](#); [Merigan, Byrne, & Maunsell, 1991](#); [Movshon & Newsome, 1996](#)). Along these lines it has also been shown that smooth pursuit

increase the temporal resolution for color ([Terao, Watanabe, Yagi, & Nishida, 2010](#)). An increased response to colored stimuli during pursuit was also observed in visually evoked EEG potentials ([Chen, Valsecchi, & Gegenfurtner, 2017](#)).

Contrary to most paradigms in scientific studies, smooth pursuit and saccades rarely occur in isolation in the real world. Often, a sudden motion onset in the peripheral visual field leads to a saccade, followed by pursuit of the moving object ([Dorr, Martinetz, Gegenfurtner, & Barth, 2010](#)). Because of the limited range of acceleration and speed, the pursuit system depends on support from the saccadic system when a target suddenly starts to move or changes direction or speed or moves too fast. Also, more recent neurophysiological and anatomical studies revealed that both eye movement systems are controlled by overlapping cortical and subcortical regions and networks ([Krauzlis, 2004, 2005](#); [Orban de Xivry & Lefèvre, 2007](#)). For tracking, saccades and pursuit are combined and therefore visual sensitivity is modified differently during the initiation and execution of these two eye movements. The combination of initial saccades followed by pursuit in order to reach and to follow a moving target might therefore allow some insights into ongoing neural processes modulating the sensitivity of our visual system.

Our aim was to compare the temporal modulation of visual sensitivity during saccades, pursuit and a combination of both. We wanted to know, if color sensitivity is reduced by saccadic suppression during saccades, whether the dynamics of perisaccadic sensitivity are different when saccades are initiated to moving targets and whether and when color sensitivity would be improved by pursuit. We found a significant visual sensitivity reduction for color during saccades to static and moving targets but not for pursuit alone. For comparison we therefore measured contrast sensitivity for luminance stimuli of high- and low-spatial frequency and chromatic stimuli during fixation and at fixed points in time during both eye movements, i.e. 15 ms or 300 ms after saccade initiation and 300 ms after pursuit target onset. Our results show that saccadic suppression is not quite as selective as proposed by [Burr et al. \(1994\)](#) because contrast sensitivity for chromatic stimuli was reduced significantly during saccades.

2. Methods

2.1. Subjects

Thirteen students of Giessen University performed the experiments, with 9, 8 and 12 subjects in Experiments 1 to 3. Subject's age varied between 21 to 29 years (average age: 24.22 years). All subjects had normal vision and were naïve regarding the purpose of the experiments. They completed the testing in 20–30 sessions over a period of 3–4 months, typically with 3–4 different 15 min sessions on one day. Experiments were approved by the local ethics committee (LEK 2013–0018) and were in line with the declaration of Helsinki. Participants signed an informed consent form at the beginning of the experiment and were paid for participation.

2.2. Apparatus

Stimuli were presented on a Display++ LCD monitor (Cambridge Research Systems Ltd., Riverside, Kent, UK), driven at a 120-Hz refresh rate. At a viewing distance of 90 cm the active screen area subtended 42.5 deg horizontally and 24.45 deg vertically on the subject's retina. With the spatial resolution of 1.920 x 1.080 pixels this results in 45 pixels per degree. All three experiments were conducted in a dark room and the monitor had a background luminance of 103 cd/m². In addition, Experiments 2 and 3 were measured with activated ceiling lights and a white paper wall of 90 x

220 cm surrounding the monitor screen and covered its dark frame. Here the background luminance of the monitor was reduced to 46 cd/m² to match the luminance of the white paper context. Stimulus presentation was controlled by OpenGL (Experiment 1) or by the Psychtoolbox (Experiments 2 and 3) (Brainard, 1997; Pelli, 1997).

2.3. Eye movement recording and analysis

Eye position signals were recorded with the Eyelink 1000 Desktop Mount (Eyelink 1000, SR Research Ltd., Osgoode, Ontario, Canada) a video-based infrared eye tracker and sampled at 1000 Hz. For offline analysis, eye position signals were filtered and differentiated over time to obtain the eye velocity signals. A Butterworth filter with a cut-off frequency of 30 and 20 Hz on position and velocity respectively was used. Saccades were detected online, when two consecutive velocity samples exceeded 50 and 100 deg/s, respectively. For offline analysis, the Eyelink saccade detection algorithm was used. Smooth pursuit onset was determined as the intercept of the best fitting linear regression, taken from all regressions fitted to the eye velocity in running 80 ms windows, within a slope range of 10 to 200 deg/s² (Schütz, Braun, & Gegenfurtner, 2007).

2.4. Stimuli

A combination of bull's eye and cross-hair (Thaler, Schütz, Goodale & Gegenfurtner, 2013) with an outer circle diameter of 0.6 degree and an inner circle of 0.2 deg and was displayed in red as eye movement target. The target to measure contrast sensitivity at low-spatial frequencies was a horizontal line that spanned the whole monitor screen to prevent any image motion on the retina during both types of eye movements. It was modulated vertically by a Gaussian distribution with a standard deviation of 0.15°, such that most of its energy was below 1 cpd (Schütz et al., 2008). Its contrast was modulated either along the L-M axis of the DKL color space (Derrington, Krauskopf, & Lennie, 1984) to measure chromatic contrast sensitivity or along the L + M axis to measure luminance sensitivity. These line stimuli were flashed for one refresh cycle of the monitor (8 ms) either 2 deg above or below the eye movement target. To measure contrast sensitivity for high-spatial frequencies, we used a horizontal grating with a vertical spatial frequency of 10 cpd and a vertical extent of 1.2 deg. The grating was flashed either 0.6 deg above or below the eye movement target, such that the border of the grating touched the eye movement target. Since the path of saccades and pursuit movements were both horizontal and parallel to these stimuli, there was no difference in the retinal input in the different eye movement conditions.

2.5. Procedure

Subjects were seated in a dark room at a table in front of the monitor and the eye tracker. They viewed the stimuli on the monitor binocularly with their heads stabilized by an adjustable chin- and forehead-rest. Before each experiment, subjects received a short instruction about the task regarding the experiment and few demonstrations of the different trial types. Subjects were asked to initiate each trial by a button press and to follow with their eyes closely the eye movement target on a gray monitor screen. After each trial, they were asked to indicate the location of the flashed line (above or below the eye movement target) by pressing one of two keys. Feedback was provided by a beep. 150 trials were collected in each session lasting about 10–12 min. 3–4 sessions were completed during one hour of testing with breaks in between. For the first experiment, data of 7 to 14 sessions were

collected from each subject; for the second and third experiment, data of 3–4 sessions for the two conditions were collected.

2.6. Psychophysical data analysis

We measured the temporal profile of chromatic detection rate in Experiment 1. To quantify pre-(α) and post-saccadic (β) levels of sensitivity as well as the time (μ), magnitude (δ) and temporal extent (σ) of saccadic suppression, we fitted the detection rate with the following model:

$$pc(t) = \begin{cases} \alpha - (\delta - 1 + \alpha)\varphi(t, \mu, \sigma), & t < \mu \\ \beta - (\delta - 1 + \beta)\varphi(t, \mu, \sigma), & t \geq \mu \end{cases} \quad (1)$$

$\varphi(t, \mu, \sigma)$ is a Gaussian probability distribution, normalized to a peak value of unity, μ corresponds to the time of peak saccadic suppression.

To measure contrast thresholds in Experiments 2 and 3, the contrast of the flashed line stimulus was adjusted by an adaptive staircase according to the subject's responses. Psychometric functions were analyzed using the psignifit toolbox for Matlab (Wichmann & Hill, 2001).

2.7. Threshold measurements for luminance and chromatic contrast thresholds

Before the actual experiments, we measured for each participant his/her individual contrast sensitivity functions during fixation to select the contrast levels at which a detection rate of approximately 75% and 85% correct responses was reached. To measure isoluminance settings individually, contrast thresholds were measured at five angles around each, the red-green or the luminance axis in the DKL-color space (Derrington et al., 1984; Krauskopf, Williams, & Heeley, 1982). In Fig. 1A the ten contrast thresholds are shown for one observer. In Fig. 1C the same thresholds are plotted in the contrast space of L- and M-cones. Due to the high sensitivity of the red-green color-opponent mechanism (Chaparro, Stromeyer, Huang, Kronauer, & Eskew, 1993; Gegenfurtner & Hawken, 1996), the thresholds typically fall on a line. The line, which we fitted with a linear regression, indicates the direction of constant luminance, i.e. the isoluminant axis. For all other observers the five chromatic thresholds fell along similar lines. For all experiments, the central stimulus with photometric isoluminance was chosen since this stimulus was clearly detected by a color-opponent mechanism. This method for determining isoluminance is more elaborate than heterochromatic flicker photometry, and it has the big advantage that it can be performed with exactly the stimuli also used in the experimental task, rather than the high temporal frequency and low-spatial frequency stimuli mandatory for flicker photometry.

2.8. Experiment 1: Temporal profile of color sensitivity during saccades and pursuit

In the first experiment we measured the temporal profile of detection rates for chromatic stimuli at the contrast of 75% and 85% detection rate during three different eye movement tasks as shown in Fig. 2. First a central fixation target appeared for 600–1150 ms. It was replaced by an eye movement target which randomly stepped to the left or right by different amounts and then randomly moved or not to elicit the three eye movements described below. The chromatic line was flashed at any time from 100 ms before to 500 ms after the eye movement target onset. Observers were asked to follow the eye movement target and to indicate by the location of the flashed line by button press. Data from 7 to 14 sessions were collected for each subject and averaged.

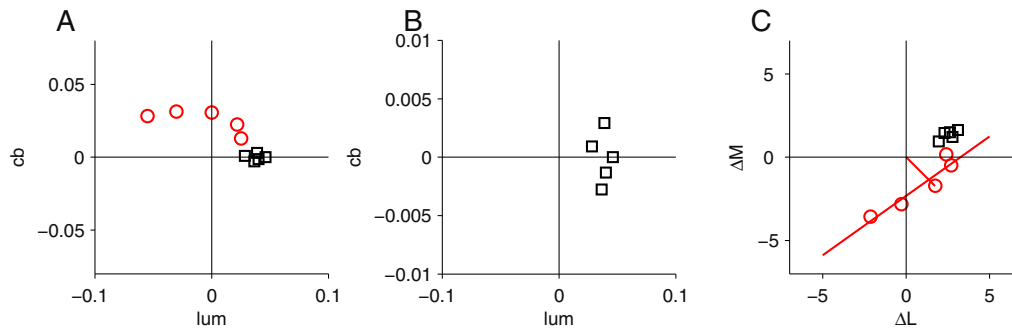


Fig. 1. Determination of isoluminance. (A) Detection thresholds for five stimuli at different angles around the main red-green (red circles) and luminance (black squares) axis in the DKL-color space (Derrington et al., 1984; Krauskopf et al., 1982). (B) Same thresholds as in A, with a smaller vertical axis scale. (C) Same thresholds as in A, plotted in cone contrast space. Thresholds for the stimuli around the red-green axis follow a line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

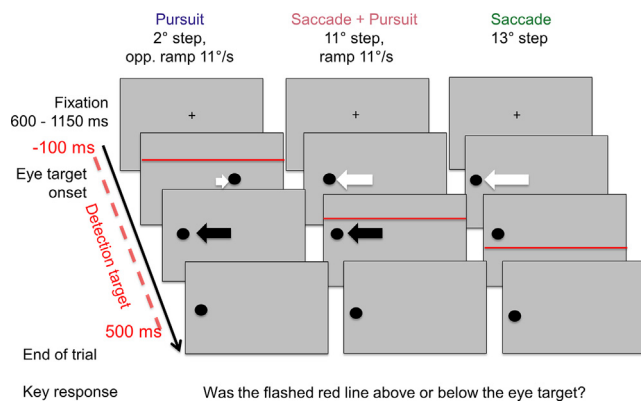


Fig. 2. Experimental paradigms and target sequences of Experiment 1. Chromatic Detection rate for chromatic targets was measured over time during pursuit, saccades combined with pursuit and saccades. Each trial began with fixation of a central fixation target. White arrows indicate steps of the eye movement target; dark arrows indicate ramps. A red horizontal line was flashed for 8 ms any time from 100 ms before to 500 ms after eye movement target onset. The observer's task was to follow the eye target and to indicate by button press whether the line flash was above or below the eye target. (A) Pursuit was elicited by a small horizontal step followed by a ramp in the opposite direction. (B) Saccades followed by pursuit were elicited by a large horizontal step of 11 deg, followed by a ramp in the same direction. (C) Saccades were elicited by a horizontal step of 13 degrees.

2.8.1. Pursuit to step-ramps

After a small step of 2 deg to the left or right of the central fixation point, the eye movement target moved for 500 ms horizontally at 11 deg/s in the opposite direction. We excluded 2008 of 5009 trials, in which pursuit onset could not be detected reliably (227), pursuit gain was lower than 0.7 (350) or a saccade or a blink occurred in a time window of ± 100 ms around the stimulus presentation (1712).

2.8.2. Saccades followed by pursuit to large steps and ramps in the same direction

The central fixation point was replaced by an eye movement target that appeared 11 deg to the left or right and then moved horizontally at 11 deg/s in the same direction. We excluded trials if a saccade could not be detected, if the saccade amplitude was smaller than 5° or if pursuit gain was lower than 0.7 (1563 of 5640 trials).

2.8.3. Saccades to stationary targets

The central fixation point was replaced by a stationary eye movement target appearing 13 deg to the left or right of the screen center. We excluded trials if a saccade could not be

detected or if the saccade amplitude was smaller than 5° (329 of 5316 trials).

2.9. Experiment 2: Contrast sensitivity for luminance and color during and after saccades

Contrast sensitivity was measured for low- and high-spatial frequency luminance and low-spatial frequency chromatic line targets during saccades to targets appearing randomly 10 deg to the left or right of the central fixation spot. For comparison, the line stimulus was flashed at fixed points in time: during central fixation, or about 15 ms and 300 ms after saccade onset. Data of 3–5 sessions were collected for each subject. We excluded trials, if a saccade or a blink occurred in a time window of ± 100 ms around the stimulus presentation in the fixation or the post-saccadic condition (505 of 12,368 trials) or if a saccade was not detected or its amplitude smaller than 7.5° in both saccade conditions (186 trials).

2.10. Experiment 3: Contrast sensitivity for luminance and color during steady-state pursuit

Contrast sensitivity was measured as in Exp. 2 for the detection of low-spatial frequency luminance and low-spatial frequency color line targets during steady-state pursuit, i.e. 300 ms after pursuit target onset in response to horizontal step-ramps of 11 deg/s and during fixation. Contrast sensitivity for the detection of high-spatial frequency luminance targets was measured in separate sessions. Data of 3–5 sessions were collected for each subject. We excluded trials, if a saccade or a blink occurred in a time window of ± 100 ms around the stimulus presentation (1209 of 16,456 trials) or if the pursuit gain in this time interval was lower than 0.7 or higher 1.3 (533 trials).

3. Results

3.1. Experiment 1: Temporal profile of color sensitivity during saccades and pursuit

In the first experiment we measured detection rates for briefly flashed horizontal red lines at different times relative to target motion onset to compare the dynamic effects of pursuit and saccadic eye movements over time. Fig. 3 shows the averaged horizontal eye position for the three eye movement conditions: pure pursuit in response to a step-ramp with a small backward step, saccades combined with pursuit in response to a step-ramp with a large step of 11 degrees and saccades in response to a large step of 13 degrees. All subjects were able to track the moving target by pure pursuit, by saccades or by a combination

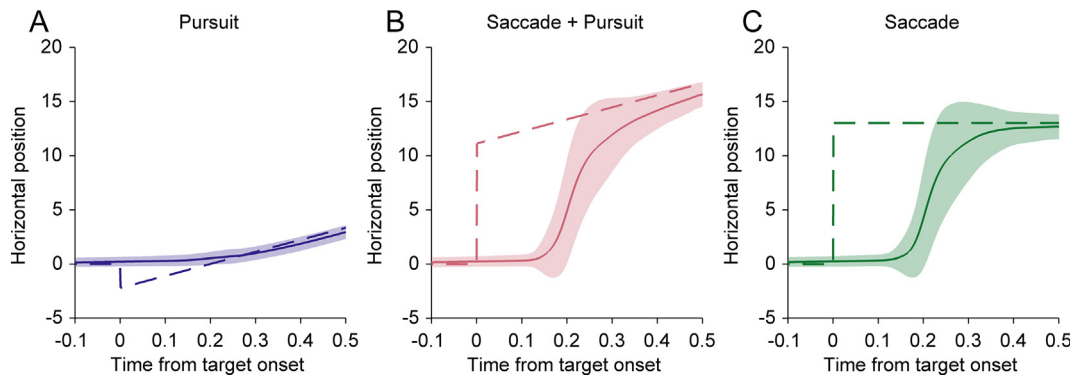


Fig. 3. Experiment 1, motion of eye movement target and resulting eye movement traces. The dashed line indicates the target position for the three eye movements over time, the solid line indicates the average eye position across all observers and the shaded region indicates 95% confidence intervals.

of saccades and pursuit. Since we used a larger step size for static than for moving targets, the amplitudes of saccades were quite similar in both conditions (moving targets: 11.7 ± 0.6 deg; static targets: 11.8 ± 0.8 deg). Pursuit gain was high for pure pursuit

responses (1.00 ± 0.04) and when pursuit was initiated after the initial saccades (0.98 ± 0.06).

In Fig. 4A&B we plotted for a single observer detection rates for the chromatic line flashed at different points in time with respect

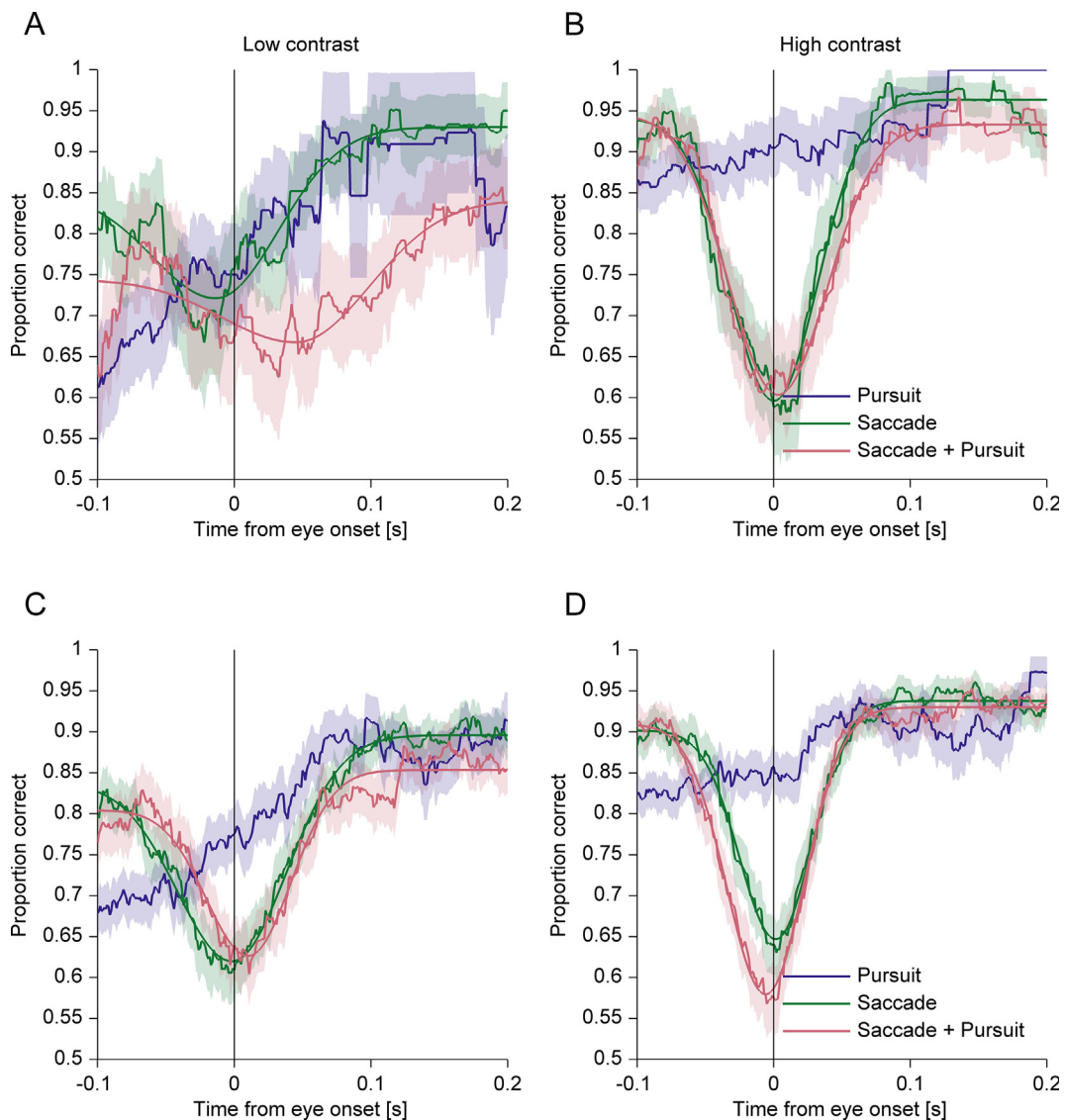


Fig. 4. Experiment 1, time course of detection rate for pursuit and saccades to static and moving targets. (A & B) Observer S2. (C & D) Average data across nine observers. (A & C) Low contrast. (B & D) High contrast. (A–D) Continuous lines represent the mean detection rate; shaded areas represent the standard error of the mean detection rate. The smooth curves represent Gaussian fits to the average detection rates according to Eq. (1).

to eye movement onset. Depending on the type of eye movement and the contrast level of the line, the temporal profiles of detection rates are quite different. Whenever saccades were executed, detection rates dropped by about 10% for lines presented at the lower (75%) color contrast and by 30% for lines presented at the higher (85%) color contrast. After saccade onset, detection rates improved again over the next 100 to 150 ms in both contrast conditions. During smooth pursuit, the profiles of detection rates looked quite different. In this particular subject, the detection rate for the low contrast condition was quite low 100 ms before pursuit onset and increased steadily over time.

In Fig. 4C&D the average detection rates across all subjects show characteristic modulations of chromatic sensitivity depending on the type of eye movement. 100 ms before any eye movement, detection rates ranged between 70–85% correct for the low contrast and around 84–94% correct for the high contrast. For both saccade tasks, the average detection rates started to drop continuously 70–50 ms before saccade onset and reached the lowest detection rate around saccade onset.

To quantify the time course of suppression in more detail, we fitted a Gaussian suppression model to the data of the two saccade conditions (Eq. (1), Fig. 5, Table 1). The amplitude of chromatic suppression was highly significant for both types of saccades and both contrast levels (all $t_s > 6.48$, all $p_s < 0.001$) and there was no influence of saccade type or contrast level (all $F_s < 1.97$, all $p_s > 0.198$). The time of peak suppression was close to saccade onset and differed from saccade onset only in the condition with saccade and pursuit at high contrast ($t(8) = -3.23$, $p = 0.012$). Here, suppression reached its maximum 12 ms before saccade onset (Fig. 5B). The width of suppression was significantly larger than zero for both types of saccades and both contrast levels (all $t_s > 7.09$, all $p_s < 0.001$) and there was no influence of saccade type or contrast level (all $F_s < 3.14$, all $p_s > 0.114$). Consistent with our

manipulation, the pre-saccadic level of detection rate was lower for the low than for the high contrast ($F(1,8) = 20.74$, $p = 0.002$). In the same way, the post-saccadic level was also significantly lower for the low than for the high contrast ($F(1,8) = 16.44$, $p = 0.004$). The difference between post- and pre-saccadic detection rate was significantly different from zero only in the saccade and pursuit condition at high contrast ($t(8) = 2.57$, $p = 0.033$). This could be a signature of post-saccadic enhancement (Burr et al., 1994; Knöll, Binda, Morrone, & Bremner, 2011) or an enhancement of color sensitivity by pursuit (Schütz et al., 2008).

As expected, detection rates during pursuit were different from saccades; until 50 ms before pursuit onset detection rates were lower compared to saccades but increased rapidly with pursuit onset (see Fig. 4). During a time period of about 100 ms after pursuit onset color sensitivity was better compared to saccades. When we fitted the same model to the pursuit data, the level of detection rates was higher after than before pursuit (low contrast: 0.21 ± 0.19 , $t(8) = 3.23$, $p = 0.012$; high contrast: 0.08 ± 0.08 , $t(8) = 3.09$, $p = 0.015$). This is consistent with previous findings for rising detection performance during onset of smooth pursuit (Schütz et al., 2008). In principle these findings could be interpreted as a suppression before pursuit onset, for instance caused by the requirements of pursuit preparation. However, in that case we would expect similar temporal modulations for different types of stimuli. Previous studies showed that detection performance for luminance stimuli does not show these modulations (Schütz et al., 2007), arguing against a general suppression due to pursuit preparation. Therefore the increase in detection performance for color stimuli is most likely due to an improvement of sensitivity before pursuit onset.

In sum, we found clear suppression of detection performance in both conditions with saccades and an improvement of detection performance after eye movement onset in both conditions with

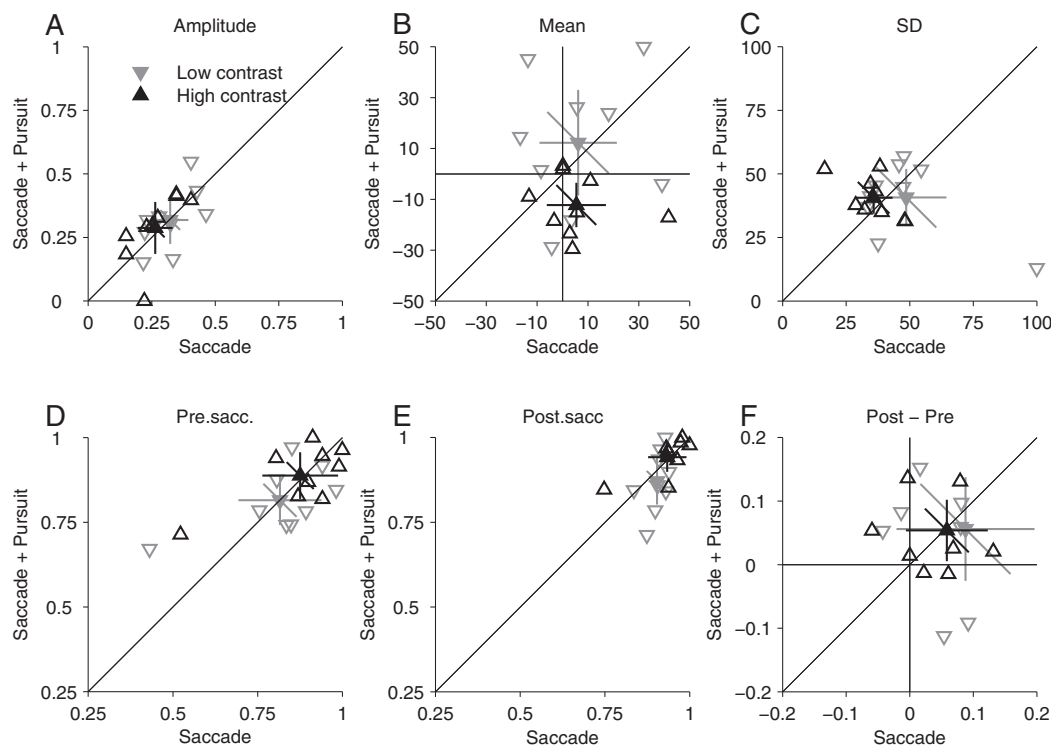


Fig. 5. Experiment 1, parameters of the Gaussian fits from Eq. (1) for saccades to static and moving targets. (A) Amplitude of saccadic suppression, δ . (B) Time of peak saccadic suppression, μ . (C) Standard deviation of saccadic suppression, σ . (D) Pre-saccadic detection rate, α . (E) Post-saccadic detection rate, β . (F) Difference between post- and pre-saccadic detection rate, $\beta - \alpha$. (A–F) Black and gray represent data for the high and low contrast conditions, respectively. Open symbols indicate individual observers, filled symbols the mean across observers. Error bars indicate 95% confidence intervals.

Table 1Averages \pm standard deviations of the Gaussian fits from Eq. (1).

	Low contrast		High contrast	
	Saccade	Saccade + Pursuit	Saccade	Saccade + Pursuit
Amplitude, δ	0.32 ± 0.09	0.32 ± 0.12	0.26 ± 0.09	0.29 ± 0.13
Time, μ	6.13 ± 19.80	12.27 ± 27.00	5.43 ± 15.14	-12.24 ± 11.36
Standard deviation, σ	48.62 ± 20.56	40.74 ± 14.61	35.81 ± 9.72	40.65 ± 8.24
Pre-sacc., α	0.82 ± 0.16	0.82 ± 0.10	0.88 ± 0.15	0.89 ± 0.09
Post-sacc., β	0.90 ± 0.03	0.87 ± 0.09	0.93 ± 0.07	0.94 ± 0.06
Post-Pre, $\beta-\alpha$	0.09 ± 0.14	0.06 ± 0.11	0.06 ± 0.08	0.05 ± 0.06

pursuit. However, during saccades, we did not find any differences between saccades to static or moving targets. Therefore, whatever sensitivity improvement there is during pursuit eye movements, it is suspended while an initial saccade is executed to a moving target. Overall, the time courses of color sensitivity showed quite strong differences regarding strength and timing of color suppression during saccades between individuals and between the two contrast levels used in this experiment.

3.2. Experiment 2: Contrast sensitivity for luminance and color during and after saccades

The results described above showed not only clear differences between subjects, but also between the two contrast levels. To study visual sensitivity during saccades in more detail, we measured and compared contrast thresholds during fixation as well as 15 ms and 300 ms after saccade onset for three different types

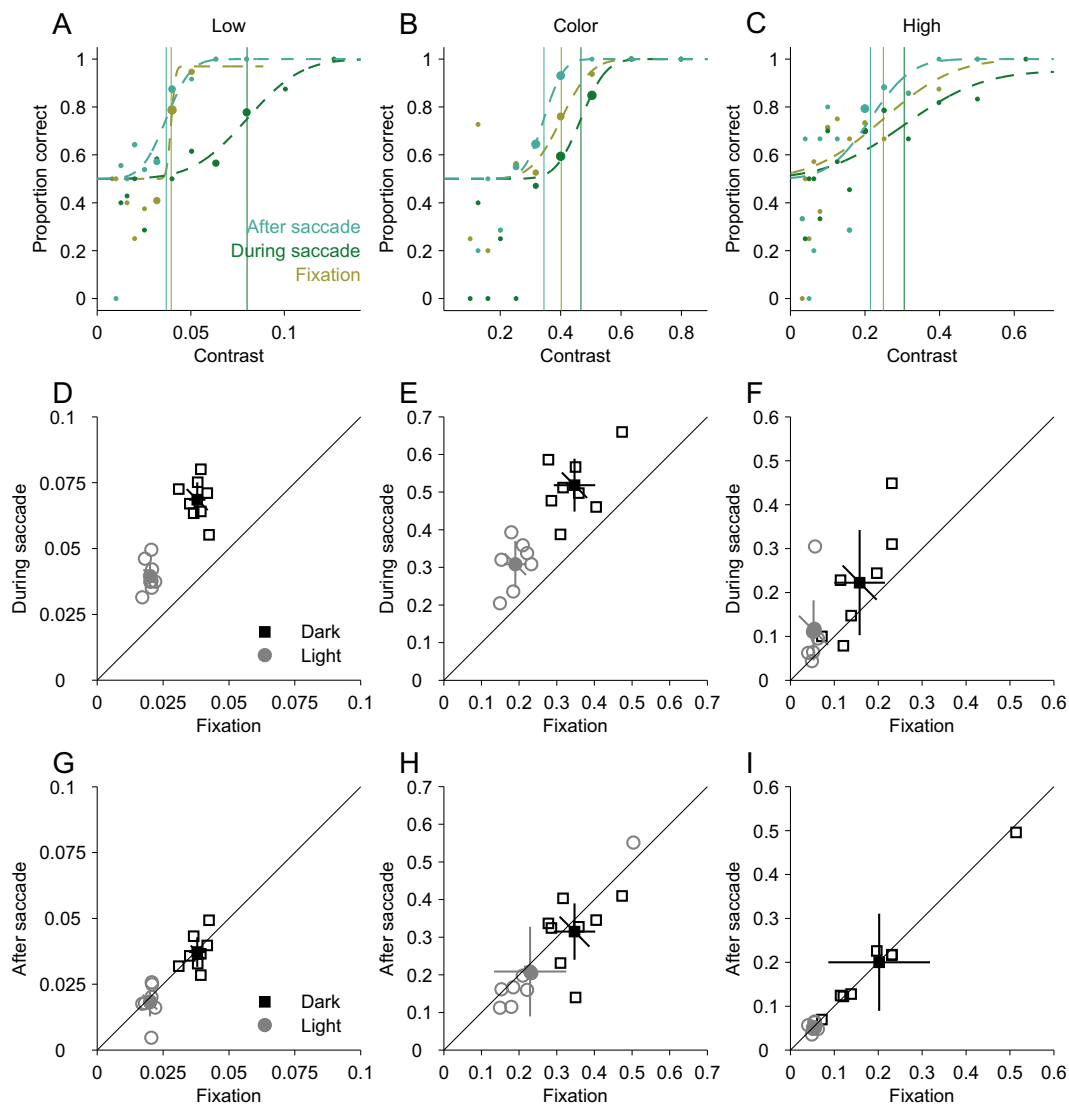


Fig. 6. Experiment 2, contrast thresholds during and after saccades for different stimulus types. (A, D, G) Low-spatial frequency luminance. (B, E, H) Low-spatial frequency color. (C, F, I) High-spatial frequency luminance. (A–C) Psychometric functions in the dark for a typical observer. (D–F). Contrast thresholds during saccades and fixation for all observers. Black and gray indicates dark and light conditions, respectively. Open symbols indicate individual observers, filled symbols the mean across observers. Error bars indicate 95% confidence intervals. (G–I) Contrast thresholds after saccades and during fixation for all observers. Conventions are the same as in D–F. (A–C) Yellow, green and cyan indicate fixation, saccade and post-saccadic conditions, respectively.

of stimuli: flashed luminance lines of low-spatial frequency, of high-spatial frequency and chromatic lines of low-spatial frequency. Since it has been shown that the surround can influence visual sensitivity by masking (Diamond, Ross, & Morrone, 2000), contrast thresholds were measured under two different illumination conditions, either in a dark room or in an illuminated room with a white cardboard covering the monitor frame to reduce possible masking effects. To match the luminance of monitor and white cardboard, the monitor luminance was reduced and the ceiling lights of the experiment room were turned on.

Fig. 6A–C shows psychometric functions of one observer in the dark for the detection of high- and low-spatial frequency luminance and low-spatial frequency color stimuli, during fixation, 15 ms or 300 ms after saccade onset. During saccades, contrast thresholds were increased, as evidenced by a rightward shift of all psychometric functions compared to the fixation condition. After saccades, contrast thresholds were slightly reduced, as evidenced by a leftward shift of all psychometric functions.

Across all observers, contrast thresholds were higher in the dark compared to thresholds with a homogenous monitor surround and illuminated room ($F(1,7) = 62.51$, $p < 0.001$). This decrease of thresholds is most likely caused by the homogeneity of monitor and surround (Craik, 1938).

When we compared thresholds during fixation and saccades (Fig. 5D–F), there was a significant interaction between eye movement and stimulus condition ($F(2,84) = 5.39$, $p = 0.0063$): contrast thresholds were increased for low-frequency luminance stimuli (dark: 82.9%, $t(7) = 9.09$, $p < 0.001$; light: 98.8%, $t(7) = 9.38$, $p < 0.001$) and for chromatic stimuli (dark: 52.3%, $t(7) = 6.03$, $p = 0.001$; 64.2%, light: $t(6) = 5.09$, $p = 0.002$). There were no significant modulations for high-spatial frequency luminance stimuli (dark: 37.6%, $t(6) = 2.04$, $p = 0.087$; light: 111.6%, $t(7) = 2.17$,

$p = 0.067$). However, only one observer under dark and light conditions each showed enhancement instead of suppression. Therefore, these modulations were not significant because of the large variability in the magnitude of suppression (between 6 and 400%).

Another effect of saccades on visual sensitivity is the so-called post-saccadic enhancement, a higher sensitivity after the execution saccades (Burr et al., 1994; Knöll et al., 2011). 300 ms after saccade onset, we found no evidence for a sensitivity improvement for dark and light conditions (Fig. 5G–I) (all $T_s \leq 1.58$; all $p_s \geq 0.159$).

3.3. Experiment 3: Contrast sensitivity for luminance and color during steady-state pursuit

The effect of pursuit on visual sensitivity was also tested in a dark or a lit room during steady-state pursuit at a fixed point in time, i.e. 300 ms after pursuit onset. As for saccades we compared visual sensitivity for the three different stimuli during fixation and pursuit. Fig. 7A–C shows psychometric functions of one observer in the dark: For low-spatial frequency luminance stimuli, contrast threshold was increased during pursuit, as evidenced by a rightward shift of the psychometric function. For color and high-spatial frequency stimuli, contrast thresholds were slightly reduced during pursuit, as evidenced by a leftward shift of psychometric functions.

Across all observers, contrast thresholds were differently affected by pursuit for the different stimuli ($F(2,22) = 14.02$, $p < 0.001$). Contrast thresholds for low-spatial frequency luminance stimuli were slightly increased during pursuit, but this difference was not significant (dark: 12.5%, $t(11) = 0.88$, $p = 0.399$; light: 10.8%, $t(11) = 1.04$, $p = 0.320$). For color stimuli, thresholds were significantly reduced

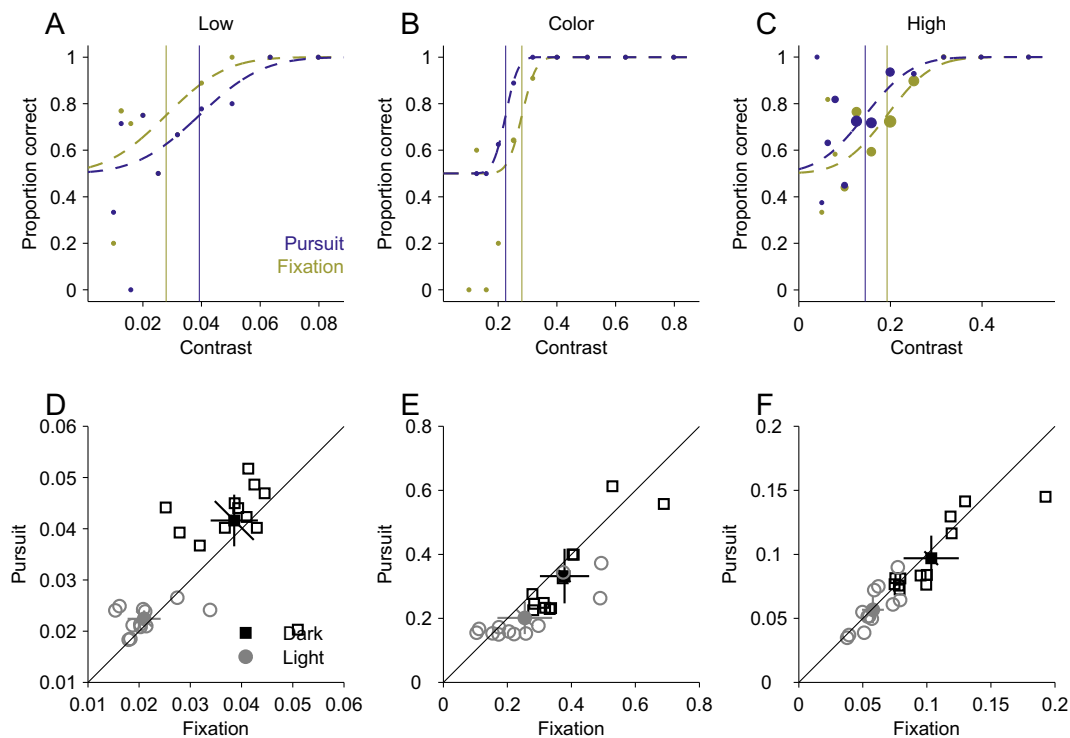


Fig. 7. Experiment 3, contrast thresholds during steady-state smooth pursuit for different stimulus types. (A, D) Low-spatial frequency luminance. (B, E) Low-spatial frequency color. (C, F) High-spatial frequency luminance. (A–C) Psychometric functions in the dark for a typical observer. (D–F) Contrast thresholds during pursuit and during fixation for all observers. Black and gray indicates dark and light conditions, respectively. Open symbols indicate individual observers, filled symbols the mean across observers. Error bars indicate 95% confidence intervals. (A–C) Yellow and blue indicates fixation and smooth pursuit, respectively.

during smooth pursuit (dark: -13.6% , $t(11) = -2.76$, $p = 0.019$; light: -10.8% , $t(11) = -2.28$, $p = 0.044$). Contrast thresholds during pursuit were also slightly lower for high-spatial luminance stimuli, but this difference was not significant (dark: -4.9% , $t(11) = -1.34$, $p = 0.206$; light: -2.2% , $t(11) = 0.39$, $p = 0.707$).

4. Discussion

In three experiments we investigated visual sensitivity for color and luminance during smooth pursuit and saccades. In the first experiment, the time course of detection performance for flashed isoluminant chromatic line stimuli was measured during smooth pursuit and saccades to moving and static targets. Chromatic detection performance increased around pursuit onset (Schütz et al., 2008), whereas it dropped before saccades and reached its minimum at saccade onset. The time course of this perisaccadic sensitivity reduction was not modified by subsequent pursuit movements. This indicates that saccadic suppression cancels a potential pursuit enhancement for color when combined. We also observed large differences in the temporal profiles of detection performance for two contrast levels tested, which emphasizes the limited validity of detection rate data.

To overcome these limitations we also measured contrast sensitivity for chromatic and luminance stimuli of low- and high-spatial frequencies at fixed points in time during fixation, pursuit, saccades and shortly after saccades. A significant perisaccadic reduction of contrast sensitivity was present for low-spatial frequency stimuli modulated in luminance and again for color. For high-spatial frequency luminance stimuli, there was only a non-significant trend for suppression. We did not find any significant enhancement of sensitivity 300 ms after saccades. During steady-state pursuit, color sensitivity was enhanced relative to fixation, as has been shown previously (Schütz et al., 2008). There were no significant modulations for low- and high-spatial frequency luminance stimuli. In the following sections, we will discuss sensitivity modulations by the different eye movement types separately.

4.1. Sensitivity during pursuit

The comparison of detection rates for chromatic lines flashed at two contrast levels before and after pursuit onset showed a significant improvement during pursuit. This effect was also present when potential masking effects of the screen borders are eliminated by a large cardboard surrounding the screen. These results replicate our previous findings (Schütz et al., 2008, 2009a) and provide further evidence that this enhanced chromatic sensitivity during the execution of smooth pursuit is not caused passively by changes in retinal stimulation. Comparing sensitivity thresholds for luminance and chromatic stimuli with low-spatial frequencies, it is obvious that they were modulated by pursuit in opposite directions: for luminance stimuli they were slightly suppressed while for chromatic stimuli they were enhanced. However, contrary to previous results (Schütz et al., 2008, 2009b), this enhancement during pursuit was not significant for high-spatial frequency (10 cpd) luminance stimuli. Several reasons might explain this discrepancy: First, there are a couple of differences regarding the stimuli. The previous results were obtained either with a similar line pattern, but at a higher spatial frequency of 14 cpd (Schütz et al., 2008) or with a foveal Gabor stimulus for spatial frequencies between 3 and 7 cpd (Schütz et al., 2009b). Since we don't know the spatial distribution of the enhancement across the retina, it might be that the magnitude of enhancement varies with spatial frequency and retinal location. Second, we presented the stimulus 300 ms after target motion onset, which is earlier than in previous

studies. It might be that enhancements for color and high-spatial frequencies follow different time courses and that the enhancement for high-spatial frequencies has not reached its maximum yet at 300 ms after pursuit onset.

4.2. Interaction of saccades and smooth pursuit

The temporal profiles of detection rates in Experiment 1 showed a clear suppression during both, saccades to static and saccades to moving targets and no apparent difference in the magnitude of suppression or dynamics for the two conditions. This result can be interpreted in two ways: First, the enhancement of color sensitivity observed before and during the execution of pursuit actually may be suspended during the execution of saccades. Second, it might be that the smaller effect of pursuit is merely overshadowed by the stronger saccade effect. Looking at the more detailed contrast threshold measurements from Experiments 2 and 3, it is clear that the modulations by saccades (about 58% suppression for color) were indeed much stronger than the modulations by smooth pursuit (about 12% enhancement for color). However, in a previous study we found that suppressive effects of saccades and smooth pursuit for luminance signals are added during the execution of saccades to moving targets (Schütz et al., 2009a, 2009b). Although the pursuit effects were much smaller than the saccade effects, there was a clear difference between saccades to static and saccades to moving targets. In light of this previous study, a difference between saccades to static and moving targets should have been measurable. This suggests that the improvement of color sensitivity during pursuit is actually suspended during the execution of catch-up saccades rather than merely overshadowed by the larger saccade effects.

4.3. Sensitivity during saccades

Previous studies found that only low-spatial frequency luminance stimuli are suppressed during saccades, while color and high-spatial frequency stimuli are spared from suppression (see review, Morrone, 2014). This dissociation between different types of stimuli led to the hypothesis that saccadic suppression acts on the magnocellular pathway only (Bruno, Brambati, Perani, & Morrone, 2006; Burr et al., 1994; Diamond et al., 2000; Ross et al., 1996, 2001; Knöll et al., 2011). The significant reduction of chromatic sensitivity around saccade onset found in Experiment 1 and 2 partially disagrees with these previous findings. The temporal profiles of detection rates for chromatic stimuli as measured in Experiment 1 started to decrease shortly before and reached their minima (a loss of 10–30%) at saccade onset as. The shapes of these profiles (see Fig. 4) are similar to the temporal profiles of luminance sensitivity measured during saccades, as shown in the studies by Diamond et al. (2000) or Knöll et al. (2011). Rolfs and Castet (2014) reported results similar to ours in abstract form. They compared perisaccadic reduction of visual sensitivity for flashed luminance and isoluminant red-green sinusoidal gratings of low spatial frequency (0.25 cpd) and found a similar perisaccadic reduction for luminance and color.

Our extensive contrast sensitivity measurements during saccades in Experiment 2 showed distinct differences between different types of stimuli. Although saccadic suppression was present for low-spatial frequency luminance and color stimuli, the suppression was much larger for luminance than for color. For high-spatial frequencies, there was no significant suppression of sensitivity, replicating previous studies (Burr et al., 1994). These differential effects support previous findings that suppression is not a general mechanism that affects all kinds of stimuli in the same way. The fact that color sensitivity is spared from saccadic suppression in some cases and subject to suppression in other

Table 2
Summary of similar studies of saccadic suppression in humans.

Study	Display	Surround	Obs.	Sac. Amp.	Detection Stimulus	Spat. freq.	Dur. ms	Position	Task	Suppression
Latour (1962)		Dark room	1	~40°	L: light flashes				Yes/no	Pc –90%
Volkmann et al. (1978)	Ganzfeld	Ganzfeld	3	6°	L: grating 9.5°	0.21	10	Center	Yes/no	Cs/5
	Ganzfeld	Ganzfeld	3	6°	L: grating 9.5°	0.65	10	Center	Yes/no	Cs/2
	Ganzfeld	Ganzfeld	3	6°	L: grating 9.5°	1.85	10	Center	Yes/no	Cs/2
	Ganzfeld	Ganzfeld	3	6°	L: grating 9.5°	4.5	10	Center	Yes/no	Cs/1.3
Uchikawa and Sato (1995)	Ganzfeld 106 cd/m ²	Ganzfeld	2	6°	418–665 nm 12° patch		10	Center	Yes/no	Cs/10 (lum) 569 nm Cs/3 (color) 530 nm
Sato and Uchikawa (1999)	Ganzfeld 62 cd	Ganzfeld	4	~12°	421–667 nm		10	Center	Yes/no	Pc –70% (lum) 569 nm Pc –70% (color) 505 nm
Burr et al. (1994)	Color monitor yellow 10 cd/m ²	Dim & lit card	3	40°	L: yellow/black grating	0.02–5	17	Center	2 AFC	Cs/10 for 0.02, Cs/1.1 for 1
Diamond et al. (2000)	Yellow 10 cd/m ²	Dim & lit card	3	40°	C: red/green grating	0.02–2	17	Center	2 AFC	0
	Color monitor	dim & lit card	2	12°	L: yellow/black grating 4.8°	0.04	8	Hor. midline	Yes/no	Cs/10
	Yellow 17 cd/m ²									
	Yellow 0.17 cd/m ²	Dim & lit card	2	12°	L: yellow/black grating 4.8°	0.04	8	Hor. midline	Yes/no	Cs/3
Bruno et al. (2006)	Yellow 17 cd/m ²	Dim & lit card	2	12°	C: red/green grating (flicker)	0.04	8	Hor. midline	Yes/no	Cs/2
	Color monitor	Dim room	10	16°	L: yellow/black Gabor	0.15	5	Center	2 AFC	Cs/5.5
	yellow 28 cd/m ²				35 × 24.5°		25			
	Yellow 28 cd/m ²	Dim room	10	16°	C: red/green Gabor 35 × 25° (flicker)	0.15	25	Center	2 AFC	Cs/1.2
Knöll, et al. (2011)	Color monitor	Dim room	5	15°	L: 2D Gaussian blob 1°	1	10	Hor. meridian	Yes/no	Cs/3
	Gray 12 cd/m ²									
	Color monitor	Dim room	2	15°	C: red/green 2D Gaussian blob 1° (flicker)	1	10	3°	Yes/no	Cs/1.5 (Fig 5C)
Dorr and Bex (2013)	ViewSonic 35°x25° nature videos	Dark room	4	~7.8°	0.5°x0.5° patches on video	0.375–0.75	18–26	2° from fovea	4 AFC	Pc: –50/–30%
	ViewSonic 35°x25° nature videos	Dark room	4	~7.8°	0.5° × 0.5° patches on video	1.5–3	18–26	2° from fovea	4 AFC	Pc: –50%
Our study	Color monitor	Dark room	8	10°	L: gray line	0.3	8	2° above/below midline	2 AFC	Cs/1.8
	Gray 103 cd/m ²									
	Gray 103 cd/m ²	Dark room	8	10°	L: gray line ver. 1.2	10	8	0.6° above/below mid.	2 AFC	n.s.
	Gray 103 cd/m ²	Dark room	8	10°	C: red (DKL)	0.3	8	2° above/below mid.	2 AFC	Cs/1.5
	Gray 46 cd/m ²	Lit & card	8	10°	L: gray line	0.3	8	2° above/below mid.	2 AFC	Cs/1.8
	Gray 46 cd/m ²	Lit & card	8	10°	L: gray line	10	8	0.6° above/below mid.	2 AFC	n.s.
	Gray 46 cd/m ²	Lit & card	8	10°	C: red line (DKL)	0.3	8	2° above/below mid.	2 AFC	Cs/1.3

A direct comparison between the given studies is difficult because of the differences regarding the used experimental conditions and tasks. The values are taken from the method sections of the studies. The data for luminance (L) or chromatic (C) detection stimuli are given in separate rows. The strength of suppression is given either as percentage correct (Pc) or as factor of the contrast sensitivity (Cs) reduction compared to fixation. They are either taken from the given results or estimated from figures of the studies.

cases suggests that the exact stimulus properties might have a large influence on the results. It also suggests that the neurophysiological basis of saccadic suppression might be more complex than previously assumed. This is in line with quite variable results from electrophysiological recordings (for recent review see Krock & Moore, 2015).

Different results regarding the reduction of visual sensitivity for chromatic stimuli during saccades may therefore depend on the specific experimental conditions, e.g. contrast and size of visual stimuli, luminance or color of the background, light level of the experimental room, and masking effects (Table 2). The early experiments of saccadic suppression of Latour (1962) and Zuber and Stark (1966) were conducted in complete darkness. Burr et al. (1982) reported a shift of perisaccadic contrast sensitivity depending on the luminance level and a reduction of the saccadic suppression effect with lower luminance levels. Also Diamond et al. (2000) found that during saccades the loss of contrast thresholds for luminance was stronger at a luminance level of 17 cd/m² compared to 0.17 cd/m². Our own measurements of contrast sensitivity under two different illumination conditions also show small effects of the testing conditions, i.e. dark/lit room and screen luminance. Suppression was stronger in the lit room on the slightly darker monitor, however the suppression effects for luminance and chromatic stimuli were both present and similarly increased. Therefore, we can exclude that our results regarding color suppression are caused by illumination or masking effects alone. Different from Diamond et al. (2000) and Knöll et al. (2011) we did not find any significant postsaccadic enhancement of visual sensitivity for color, neither in the period of 100–140 ms after saccades as measured continuously during the first experiment nor 300 ms after saccades onset as tested in the second experiment under different illuminations. Note, that there are two differences between our study and the earlier ones with respect to the color properties of the stimuli. Earlier studies presented red-green stimuli on a yellow background and used individual flicker photometry to estimate isoluminance. The gray background used in our experiments differs from the yellow background only in a constant and modest stimulation of S-cones, which is known as not to affect red-green detection thresholds (Gegenfurtner & Hawken, 1996; Stromeyer, Chaparro, Tolias, & Kronauer, 1997). Our estimate of individual isoluminance is also not very different from photometric isoluminance and most previous estimates, but by using the detection contour approach we could use stimuli with the same spatiotemporal properties as in the detection experiment. Furthermore, the analysis of the detection contours essentially guarantees that our stimuli are indeed detected by a chromatic mechanism.

4.4. Comparison to other studies

For comparison of the results of similar experiments regarding human visual sensitivity during saccades and the different test conditions, we listed in Table 2 the results of studies during the time period of 1978–2011. It shows that the design of many studies is quite similar, i.e. short presentation duration of a detection target, a yes/no-, 2-AFC detection or localization task, parallel orientation of detection stimulus and saccade direction to minimize effects of retinal smear and reduction of masking effects. Our study is actually most similar to the one by Bruno et al. (2006), who also tested contrast sensitivity of luminance and isoluminant stimuli during saccades with ten adult observers. Interestingly, their data also show a trend for an impairment in detecting isoluminant stimuli during saccades, even though the relative decrease in performance is smaller in their study compared to ours. Most other studies tested only very few observers, typically two or three. However, the variability of the color data is higher than that of the luminance data, and the suppression effect is also clearly

smaller than for low-spatial frequency luminance. A smaller suppression effect combined with larger inter-individual variability might explain the discrepant findings across different studies.

4.5. Comparison to neurophysiology

Effects of saccades on neuronal response behavior have been studied intensively in neurophysiology and for several cortical and subcortical areas a characteristic perisaccadic modulation was reported (Ibbotson & Krekelberg, 2011). Despite the numerous psychophysical and neurophysiological studies on visual sensitivity during saccades in humans and monkey and despite similarities regarding the time course of neuronal response modulations and behavioral responses in psychophysical studies the source of saccadic suppression remains unclear. In behaving monkeys several electrophysiology studies investigated perisaccadic response modulations along the dorsal and ventral visual pathways (for recent review see Krock & Moore, 2015). The general finding is, that mainly along the dorsal visual processing stream neuronal response amplitudes are modulated by different extents until saccade onset and increase again often to a higher level compared to the average firing rate during steady fixation. The dorsal pathway along the middle temporal area (MT) and median superior temporal area (MST) is important for motion processing and pursuit initiation (Newsome & Pare, 1988; Newsome, Wurtz, Dursteler, & Mikami, 1985). MT neurons respond optimally to luminance gratings of low-spatial and high-temporal frequencies (Hawken, Shapley, & Grosof, 1996; Movshon & Newsome, 1996) but less to color stimuli (Gegenfurtner & Hawken, 1996; Maunsell et al., 1990; Saito, Tanaka, Isono, Yasuda, & Mikami, 1989; Seidemann, Poirson, Wandell, & Newsome, 1999; Seymour, Clifford, Logothetis, & Bartels, 2009).

Similar to the different psychophysical results regarding the selectivity of saccadic suppression as discussed above, neurophysiological studies often disagree and do not support a selective suppression mechanism. For example in the lateral geniculate nucleus (LGN), the neuronal response modulations in behaving monkeys precede saccades by 100 ms, but different from the psychophysical results here only a weak suppression is found followed by a strong enhancement (Ramcharan, Gnadt, & Sherman, 2001) which is not always present in psychophysical studies. In the LGN suppression affects also either both, magno- and parvocellular cells (Reppas, Usrey, & Reid, 2002) or all processing streams even in absence of direct visual stimulation (Royal, Sary, Schall, & Casagrande, 2006). For neurons in the primary visual area (V1) perisaccadic response modulations were reported by some studies (Kagan, Gur, & Snodderly, 2008; MacEvoy, Hanks & Paradiso, 2008; Niemeier & Paradiso, 2017; Ruiz & Paradiso, 2012) while others found no change (Gawne & Martin, 2002; Judge, Wurtz, & Richmond, 1980; Wurtz, 1969). For example, Gawne and Martin (2002) found that responses of most neurons in V1, V2, V3V and V4V did not differ when a stimulus pattern was either flashed into the receptive field or brought into the field by a saccade. However, V1 response behavior is different when natural images are used as background (Ruiz & Paradiso, 2012). Specific perisaccadic response changes were found in area V3, MT and MST (Cloherty, Mustari, Rosa, & Ibbotson, 2010; Ibbotson, Price, Crowder, Ono, & Mustari, 2007; Thiele, Henning, Kubischik, & Hoffmann, 2002), ventral intraparietal area (VIP), lateral intraparietal area (LIP) (Bremmer, Kubischik, Hoffmann, & Krekelberg, 2009) and the parietal cortex (Duhamel, Colby, & Goldberg, 1992). Modulations are also found in the superior colliculus (SC) (Wurtz, Richmond, & Judge, 1980), the pulvinar (Berman & Wurtz, 2011) and the LGN (Ramcharan et al., 2001; Reppas et al., 2002; Royal et al., 2006). However, a precortical suppression of the dorsal pathway seemed unlikely since in awake behaving monkeys retinal visual motion caused

by saccades had a transient effect on the firing rate of MT neurons and depended on the direction preference and ongoing activity of the MT neuron (Bair & O'keefe, 1998). These authors concluded that the visual motion signals caused by saccades reached the cortical area MT and modify MT responses accordingly; they “may be a source rather than a target, for saccadic suppression (page 784).”

However, there is strong evidence for an active suppression mechanism, the corollary discharge circuit, which originates in the same superior colliculus (SC) neurons that program saccades (for review see Wurtz, 2008). Correct timing of perisaccadic sensitivity modulation and coordination is possible when a copy of the movement vector of a planned saccade is sent to the frontal eye field cortex (FEF) via the medial dorsal nucleus of the thalamus (Bruce & Goldberg, 1985; Sommer & Wurtz, 2004) which projects of the dorsal stream (Berman & Wurtz, 2011). The relative smaller suppression effect on color and high-spatial frequency vision may be based on the exclusive projections of the SC to the areas of the dorsal stream via the pulvinar but not to the ventral stream (Berman & Wurtz, 2011). Procession of color information involves more areas of ventral stream and seems to be more distributed compared to motion processing (Gegenfurtner & Kiper, 2003; Shapley & Hawken, 2011; Zeki, 1983). Regarding saccadic suppression effects, neurons of area V4 responded more variable during saccades (see review of Krock & Moore, 2014). Han, Xian, and Moore (2009) compared the dynamics of luminance and chromatic contrast sensitivity of area V4 neurons in monkey during saccades and found for luminance a general decrease in sensitivity but very heterogeneous effects for color.

In humans several fMRI studies investigated saccade related modulations in visual areas and both, positive (Paus, Marrett, Worsley, & Evans, 1995; Wenzel et al., 2000) and negative (Bodis-Wollner et al., 1997; Sylvester, Haynes, & Rees, 2005; Vallines & Greenlee, 2006) effects were found. In the human primary visual areas V1 and V2 bold signals evoked by achromatic and isoluminant chromatic gratings are reduced similarly during saccades (24% and 21%) (Kleiser, Seitz, & Krekelberg, 2004; see also Sylvester et al., 2005). For the higher cortical areas, hMT, V4 and V7, however, Kleiser et al. (2004) reported a stimulus selective suppression effect during saccades; for luminance stimuli perisaccadic BOLD response were reduced by 34% in hMT and by 50% in V4 compared to 5% and 4% for isoluminant stimuli. However, the location and function of the human area V4 is still under discussion as those of the distinct other color-selective regions in the human cortex (see Shapley & Hawken, 2011; Winawer & Witthoft, 2015).

5. Conclusion

We studied the effect of saccades and smooth pursuit on visual sensitivity in three experiments. Sensitivity modulations were clearly stimulus specific for both types of eye movements. Saccades suppressed low-spatial frequency luminance and color stimuli, with much stronger suppression for luminance, but had no effect for high-spatial frequencies. Smooth pursuit enhanced color stimuli and slightly suppressed low-spatial frequency luminance stimuli. This indicates that the sensitivity modulations of saccades and smooth pursuit might be more complex than previously thought and that the specific stimulus conditions affect the pattern of modulation. Saccades to static and moving targets resulted in identical suppression of chromatic sensitivity, which suggests that effects of saccades cancel out effects of pursuit.

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