



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



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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

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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. [Volkman, 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

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