Vision: active optimization of visual information during eye movements

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A new study by Niemeyer et al. uses a rigorous approach to isolate the consequences of eye-movements on cortical visual processing. They show that our visual system does not shut down during saccades but specifically modulates sensitivity to selected stimuli.

Look at your left eye in a mirror. Then shift your gaze to the image of your right eye, making saccades back and forth. You will see your eyes alternatively staring back, but you will never catch them moving. Your inability to see your own eye-movements is an example of the "saccadic suppression" phenomenon. As XVII century philosopher Descartes observed, we fail to see the motion produced by our own eye-movements, but are readily aware of the motion produced by other sources, such as by gently tapping the corner of our eye. This means that the same motion signal on the retinae is perceived differently when it is produced by our own eye-movements or by other external sources, logically implicating a (pre-)motor signal in the modulation of visual sensitivity[1,2]. But the visual system cannot afford to miss such a large share of information with every saccade, and has developed a strategy to allow continuity of visual analysis during saccades. The new study by Niemeyer et al.[3], essentially applying the Descartes approach to compare sensitivity during real saccadic eye-movements and "simulated saccades" (where the same retinal motion is produced by rotating the display in front of steadily fixating eyes), demonstrates that saccadic suppression selectively affects some stimuli, while others are enhanced (Figure 1A).

The simulated saccades technique is not new, but Niemeyer et al. are the first to use it in combination with electrophysiological measurements of single cell recordings in primary visual cortex (V1) in behaving monkeys. V1 cells are often thought of as simple filters, essentially representing the visual image in terms of prevalent eye-of-origin, orientation, and spatiotemporal frequency at each location. Previous studies compared V1 cell responses when images were static vs. presented during saccades, revealing a biphasic pattern of modulation. This consists of a slight suppression followed by strong enhancement

of activity, common to V1 and its main subcortical input LGN[4,5]. However, these studies could not ascertain whether the initial suppression and later enhancement were mere consequences of the high-speed motion recorded by the retinae during the eye-movement. Transients and fast motion change the spatio-temporal distribution of the visual input, and this dramatically affects image visibility (Figure 1B). Niemeyer et al. never compared responses with a static image presentation, but only between real and simulated saccades. Because the retinal stimulus was always matched across conditions, differences in temporal frequency content or visual masking could not account for the changes in sensitivity, which must be driven by an active signal associated with the movement of the eyes: an *efference copy*[6] or cor*ollary discharge*[7].

Niemeyer et al.'s results fit with previous psychophysical evidence in humans and reiterates the three key features of saccadic suppression: that it is active, partial and selective[8,9]. "Active suppression" refers to the need for a (pre-)motor signal modulating sensitivity, reaching as early as in V1. This is in line with evidence that eye-position and eye-movements are represented in V1[10-12], and suggests that these signals can shape visual cortical processing at the very first stage. Past studies opposing this view claimed that sensitivity changes during real and simulated saccades are qualitatively similar and may be explained by masking from the high-speed motion during the saccade, or the stable images preceding and following the saccade[13]. However, finding similarities between saccades and simulated saccades will not help understand saccadic suppression, simply because these two conditions are glaringly different in perception [14] – while we fail to notice our own saccades, we have no difficulty detecting a simulated saccade, as in Descartes' original observation.

"Partial suppression" means that vision does not shut off completely during saccades, as in a grey-out of input. Rather, sensitivity is reduced (not eliminated) in a way that counterbalances the redistribution of stimulus energy during the high-speed motion imposed by saccades (Figure 1). Relatedly, "selective suppression" means that, while lower spatial frequencies and motion signals are strongly affected[9,14,15] high spatial frequencies (and colors) are not suppressed[9,16]. This suggests that the parvocellular pathway is relatively unaffected by saccadic suppression – a proposal borne out when visual stimulation is carefully controlled, as in Niemeyer et al's study.

It appears that the primary goal of saccadic suppression is to optimize the encoding of available visual information, discarding the redundancies intrinsic to natural images. Eye-movements in general serve this purpose[17], as the retinal motion they produce redistributes the static energy in the natural image spectrum over space and time, hence "whitening" (flattening) it. This corresponds to attenuating the low spatial frequencies and preserving the high, which contain more important information for perception. Whitening is efficient for very slow and very small eye movements, particularly drift. But for jerky, faster, and larger eye-movements like saccades the whitening effect is weak, and limited to a small range of very low frequencies (Figure 1B). It is possible that the reason the brain implements such sophisticated sensory-motor control is to endorse a selective saccadic suppression of the (still prevalent) low spatial frequency content and to reestablish whitening of the incoming visual signals (Figure 1C). The high spatial frequency enhancement contributes to the same goal, flattening the energy spectrum of natural images (Figure 1C). The parvocellular system could be ideally suited to carry the resulting

whitened spectrum across saccades, integrating information relevant for object identification across different fixations.

To be efficient and ensure continuity of visual analysis, the whitening process should be precisely locked to saccadic time, requiring precise synchronization of the (pre-)motor signal regulating suppression with the saccade execution. Niemeyer et al. found a trace of this sensory-motor signal in the correlated noise in pairs of V1 cells, which peaked exactly at the time of a real saccade, but occurred at a much later and wider temporal window with simulated saccades. This raises the question: what kind of mechanism could ensure such sharp temporal alignment between functions mediated (pre-) motor and visual cortex? Recent studies implicate endogenous rhythms as the key to synchronizing sensory-motor function[18].

Image motion is a major challenge for vision during saccades, but it is not the only problem they pose: another major issue is object localization, which needs to remain stable in the face of the displacement of retinal images across saccades. Just as motion and displacement are separate aspects of perception, supported by distinct mechanisms, so are the mechanisms dealing with the motion and the displacement of retinal images produced by eye-movements. Both contribute to perceptual stability, and both may be supported by active (pre-)motor signals, but their specifications and implementation could be different. While this study is an important step towards unravelling the mysteries of perception at the time of saccades, there remain enough unexplained problems to keep researchers busy for many years to come.
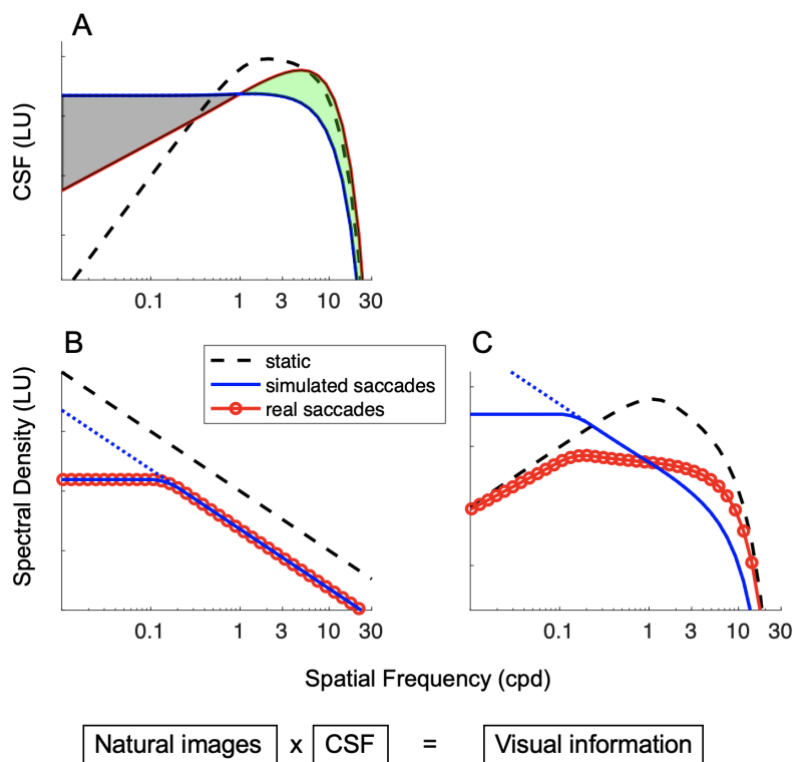
Figure 1: Visual processing during saccades is affected by high-speed motion and by the active modulation of the Contrast Sensitivity Function (CSF).

A. CSF for static images (black dashed curve), for moving images (blue curve) and during saccades (red curve). The low spatial frequencies of static images are largely invisible in fixation. However, motion changes the CSF into a low-pass filter[19] *and this boosts the visibility of the low spatial frequencies. Saccadic suppression recovers the band-pass characteristics of the filter by suppressing sensitivity in this frequency range (grey shaded area) and enhancing sensitivity for spatial frequencies above about 1 cpd (green shaded area, estimated from Figure 2B of Niemeyer et al.).*

B. Spectral energy of natural images (dashed line), which follows the 1/f law. The motion associated with a saccade (real or simulated) redistributes the energy of the static images over a large range of temporal frequencies (dashed blue line); in addition, it induces a small attenuation of the lowest spatial frequencies[17] (continuous blue curve).

C. Spectral energy of natural images filtered by the CSF in the three conditions in A: fixation, motion, saccades. For static images, the dominance of low spatial frequencies in the 1/f spectrum is eliminated by the band-pass characteristics of the CSF. During simulated saccades, the low-pass CSF makes the low spatial frequencies more visible than during fixation (dashed blue line); the partial whitening effect produced by retinal motion is insufficient to counterbalance the effect (continuous blue line). This might be the reason why the CSF needs to be actively modulated during real saccades (red): attenuated at low spatial frequencies and enhanced at high spatial frequencies, redistributing spectral energy to be similar as in steady-fixation conditions, hence optimizing the extraction of information from the retinal signal.

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