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Are the visual transients from microsaccades helpful? Measuring the influences of small saccades on contrast sensitivity

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ABSTRACT

Like all saccades, microsaccades cause both spatial and temporal changes in the input to the retina. In space, recent studies have shown that these small shifts precisely relocate a narrow (smaller than the foveola) high-acuity retinal locus on the stimulus. However, it has long been questioned whether the temporal modulations resulting from microsaccades are also beneficial for vision. To address this question, we combined spectral analysis of the visual input to the retina with measurements of contrast sensitivity in humans. Estimation of how different types of eye movements redistribute the power of an otherwise stationary stimulus shows that small saccades contribute more temporal power than ocular drift in the low-frequency range, suggesting a specific role for these movements in the encoding of low spatial frequencies. However, an influence on contrast sensitivity was only found for saccades with amplitudes larger than 30′. Contrast thresholds remained highly similar in the presence and absence of smaller saccades. Furthermore, saccades of all amplitudes, including microsaccades, were strongly suppressed during exposure to the stimulus. These findings do not support an important function of the visual transients caused by microsaccades.

1. Introduction

The visual functions of microsaccades have long been debated (Collewijn & Kowler, 2008; Rolfs, 2009). Several recent findings provide evidence that microsaccades, like saccades with larger amplitudes, serve important *spatial* functions. Studies with accurate localization of the line of sight have shown that, during examination of fine spatial detail, microsaccades precisely shift gaze among nearby objects of interest (Ko, Poletti, & Rucci, 2010). This strategy appears to take advantage of a small preferred retinal locus of fixation which enhances performance in high-acuity tasks (Poletti, Listorti, & Rucci, 2013). In addition, microsaccades also seem to be part of the normal oculomotor strategy by which humans maintain their gaze spatially close to a marker when requested to do so (Cornsweet, 1956; Engbert & Kliegl, 2004; Cherici et al., 2012), even though strict fixation can also be maintained by means of ocular drift alone (Steinman et al., 1973).

Besides these spatial effects, it has long been argued that microsaccades may also serve important *temporal* functions. According to a popular proposal—but subject to sharp disagreement (*e.g.*, Collewijn & Kowler, 2008)—the visual transients caused by microsaccades are necessary for preventing the progressive fading experienced when stimuli are artificially immobilized on the retina (Ditchburn, Fender, & Mayne, 1959; Martinez-Conde et al., 2006). Furthermore, contrast thresholds to stationary low-frequency gratings have been found to be lower in a relaxed fixation condition with small saccades than under strict fixation (Deubel & Elsner, 1986), suggesting that temporal modulations resulting from microsaccades may enhance sensitivity to low spatial frequencies.

Since recent studies have shown that the input luminance fluctuations resulting from ocular drift amplify high spatial frequencies (Rucci et al., 2007), a microsaccade enhancement of low spatial frequencies raises the interesting hypothesis that ocular drift and microsaccades may serve complementary functions in transforming spatial information into temporal modulations. Complementary roles for microsaccades and drift are supported by neurophysiological findings, which have suggested the existence of distinct neuronal populations that selectively respond to the input signals elicited by ocular drift and microsaccades (Riva Sanseverino et al., 1979; Kagan, Gur, & Snodderly, 2008). However, the effect opposite to that described by Deubel and Elsner (1986)—*i.e.*, an adverse consequence of microsaccades on visual sensitivity—has also been reported (Ditchburn, 1955; Beeler, 1967; Zuber & Stark, 1966; Hass & Horwitz, 2011; but see Krauskopf, Graf, & Gaarder, 1966) with a reduction in contrast sensitivity at the time of microsaccades

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similar to the "saccadic suppression" of larger saccades (Volkmann et al., 1978; Ross et al., 2001).

Surprisingly, no previous study has examined the actual information content of the input transients caused by microsaccades, nor specifically isolated the influences of these transients on contrast sensitivity thresholds in human observers. To start filling this gap, here we coupled spectral analyses with measurements of human contrast sensitivity. We (a) examine how the abrupt changes in the retinal stimulus caused by microsaccades and small saccades transform the spatial frequency content of a static stimulus into a spatiotemporal frequency distribution on the retina; and (b) assess the impact of these transformations on visual sensitivity at low and high spatial frequencies.

2. Materials and methods

2.1. Subjects

Five subjects (all females, age range: 21–31 years) with normal vision participated in this study. All observers, with the exception of one of the authors (NM), were naïve about the purpose of the experiment and were compensated for their participation. All participants gave their informed consent following the procedures approved by the Boston University Charles River Campus Institutional Review Board. The work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus

Stimuli were displayed on a fast phosphor monitor (Iyamaya HM204DT) at a resolution of 800 × 600 pixels and vertical refresh rate of 200 Hz in a dimly illuminated room. The monitor was calibrated to linearize the relationship between the input gray level and the displayed luminance. Subjects looked at stimuli from a fixed distance of 126 cm from the monitor. A dental-imprint bite bar and a head-rest restricted head movements. Stimuli were observed monocularly with the right eye, while the left eye was patched.

A Generation 6 Dual Purkinje Image (DPI) eye-tracker (Fourward Technologies) was used to record eye movements. This system possesses a time delay of about 0.25 ms and an internal noise level of less than 20″ (Crane & Steele, 1985), yielding a resolution—measured by means of an artificial eye—of approximately 1′. Vertical and horizontal eye positions were sampled at 1 kHz and recorded for subsequent analysis.

2.3. Stimuli

Stimuli consisted of 2D Gabor patterns oriented at ±45° (Fig. 1A). Their contrast varied across trials following the Parametric Estimation by Sequential Testing (PEST) procedure (Taylor & Creelman, 1967), always starting from an initial contrast level at least one order of magnitude above threshold. The frequency of the Gabor grating was either 0.8 cycles/deg (low spatial frequency condition) or 10 cycles/deg (high spatial frequency condition). In both cases, the standard deviation of the Gabor was 2.25°. Stimuli were displayed over a uniform field with luminance of 21 cd/m^2. To minimize transients not resulting from eye movements, in each trial, the contrast of the stimulus first increased gradually from zero to the selected level over a period of 500 ms (ramp-up phase) and then remained at the constant value determined by the PEST procedure for another 500 ms (plateau phase), as shown in Fig. 1C.

2.4. Procedure

Data were collected in separate experimental sessions, each with approximate duration of 1 h. Every session started with

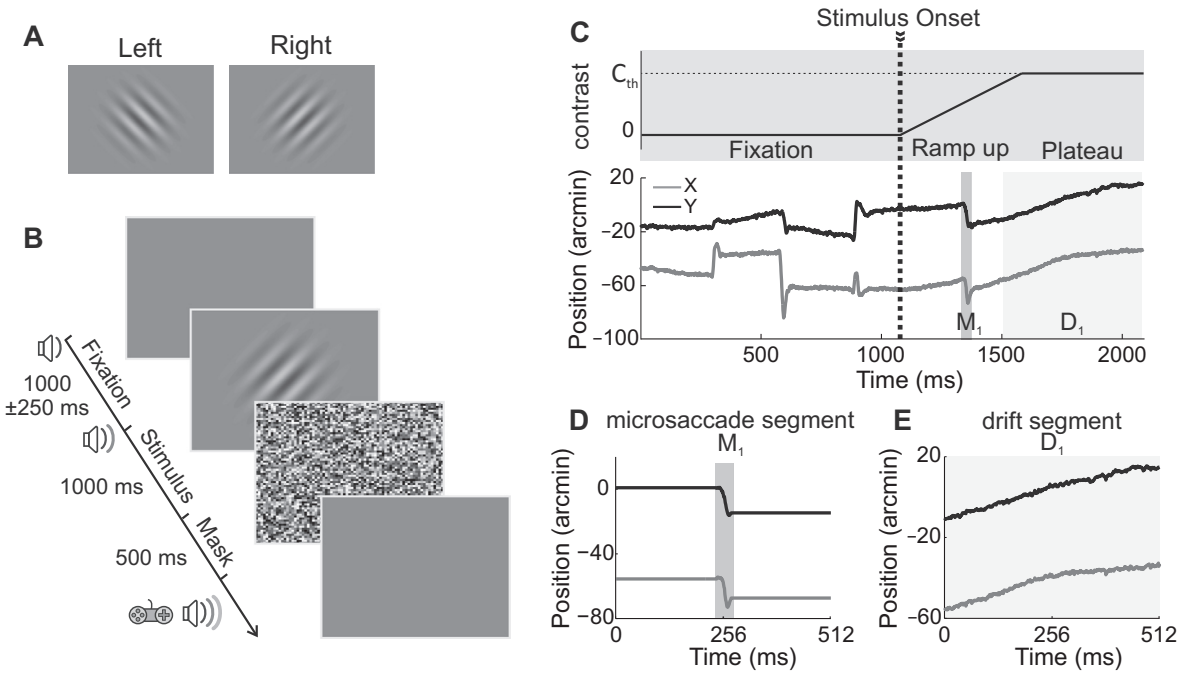

Fig. 1. Experimental design and methods. (A) Subjects reported whether a Gabor grating was tilted by 45° to the left or to the right. Stimuli were displayed at either 0.8 cycles/deg (low spatial frequency) or 10 cycles/deg (high spatial frequency). (B) Stimuli were presented for 1 s after a fixation period with random duration and were followed by a high-contrast mask. (C) Stimulus contrast increased gradually from zero to the desired level (C_{th}) in 500 ms (ramp-up phase) and then remained constant for another 500 ms (plateau phase). The dashed vertical line indicates the start of the stimulus presentation interval. An example of recorded eye movements in a trial is also shown (bottom traces) together with the selected periods used for the spectral analyses of the retinal input (shaded regions M_1 and D_1). (D–E) Examples of the microsaccade (D) and drift segments (E) used for the spectral analysis. Segments had duration of 512 ms and consisted of one isolated microsaccade/small saccade (D) or a period of continuous, uninterrupted drift (E). In D, pre- and post-saccadic drift modulations were eliminated from the trace to isolate the impact of the saccadic gaze shift.