Behavioural Brain Research 312 (2016) 246–252

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

Research report

Effect of heading perception on microsaccade dynamics

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HIGHLIGHTS

- Fixational eye movements such as microsaccades are related to perceptual/attentive mechanisms like heading perception.
- Microsaccade rate is modulated by the time course of the heading perception.
- Microsaccades show a longer duration and greater amplitude during the build-up of the correct perception.
- Microsaccades present a directional bias toward the opposite side of the perceived heading.
- Microsaccades may represent an efficient oculomotor strategy for spatial information acquisition.

ARTICLE INFO

Article history:
Received 26 April 2016
Received in revised form 13 June 2016
Accepted 14 June 2016
Available online 17 June 2016

Keywords:
Microsaccades
Optic flow
Saccadic reaction time
Visual perception

ABSTRACT

The present study shows the relationship between microsaccades and heading perception. Recent research demonstrates that microsaccades during fixation are necessary to overcome loss of vision due to continuous stimulation of the retinal receptors, even at the potential cost of a decrease in visual acuity. The goal of oculomotor fixational mechanisms might be not retinal stabilization, but controlled image motion adjusted to be optimal for visual processing. Thus, patterns of microsaccades may be exploited to help to understand the oculomotor system, aspects of visual perception, and the dynamics of visual attention. We presented an expansion optic flow in which the dot speed simulated a heading directed to the left or to the right of the subject, who had to signal the perceived heading by making a saccade toward the perceived direction. We recorded microsaccades during the optic flow stimulation to investigate their characteristics before and after the response. The time spent on heading perception was similar between right and left direction, and response latency was shorter during correct than incorrect responses. Furthermore, we observed that correct heading perception is associated with longer, larger and faster microsaccade characteristics. The time-course of microsaccade rate shows a modulation across the perception process similar to that seen for other local perception tasks, while the main direction is oriented toward the opposite side with respect to the perceived heading. Microsaccades enhance visual perception and, therefore, represent a fundamental motor process, with a specific effect for the build-up of global visual perception of space.

1. Introduction

Gibson was the first author to study the contribution of the optic flow to heading perception. He used the term "focus of expansion" (FOE) to define the source of the optic array surrounding a moving observer. Human subjects can perceive their direction of self-motion from such optical outflow patterns with an accuracy of 1° of visual angle [1]. When the observer moves forward, the optic flow pattern is expanding, if he/she moves backward the flow is contracting.

Because the eyes are moving continuously, the FOE is not stationary on the retina but its position varies due to eye movements, and could continuously shift due to fixational eye movements. These include tremors, drifts and microsaccades (MS). The effect of such small movements is to shift constantly the image minutely over the fovea so that the photoreceptors are dynamically stimulated. If this does not happen then the image of the object would fade. High frequency tremor causes the image of an object to stimulate cells in the fovea continuously. Drifts are slow movements away from a fixation point. MS are small and rapid eye movements (1–2/s) that reposition the eyes on the target. MS are associated with an enhancement of visual perception [2–4], and their function during visual fixation has been the subject of debate for many years. Predominantly these are corrective movements, compensating for

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http://dx.doi.org/10.1016/j.bbr.2016.06.030
0166-4328/

the off center foveal position produced by a drift eye movement. It was postulated that only MS might contribute significantly to the maintenance of vision, as drift velocities are too low, and the amplitude and frequency of tremor would make it more detrimental than beneficial [5–7]. It was proposed that MS could bring stationary stimuli in and out of receptive fields during viewing, and therefore produce transient neural responses [8]. Gur et al. [9] suggested that MS could account for much of the response variability of neurons in visual area V1 of the awake monkey. On one hand, receptive fields near the fovea might be so small that drifts and tremor are sufficient to prevent visual fading in the absence of MS [2]. On the other hand, receptive fields in the parafovea might be so large that only MS are large and fast enough (compared to drifts and tremor) to prevent visual fading, especially with low-contrast stimuli [9,10]. Moreover, recent studies by Costela et al. [11] and McCamy et al. [12] indicate that microsaccades also play a role in the prevention and reversal of foveal fading.

While there is agreement about a modulation of MS rate by the appearance of a visual stimulus [2], and due to the fixation target [13], there is little evidence on the relationship between MS and perception of complex stimuli, either local or global, as well as with the attentional load required by the visual detection processes. Many Authors have reported that there is a modulation of MS rate by static vs. dynamic backgrounds during the execution of a spatial discrimination tasks, suggesting that MS can represent a sampling strategy for spatial information acquisition [14–16]. They also suggest that MS occurrences are greatly affected by attentive processes devoted to gain spatial information during task execution more than purely visually driven effects. Moreover, MS presented a directional bias during detection tasks. Laubrock et al. [17] demonstrated a modulation of MS rate by apparent visual motion perception.

More notably, MS rate and amplitude modulation driven by attentive load and task difficulty has been demonstrated for non-visual tasks, like mental arithmetic calculation [18,19]. It has been reported that MS rates decrease and amplitudes increase with increasing task difficulty. These reports highlight the involvement of MS with mental procedures beyond local visual stimulation, suggesting that more advanced neuronal functions such as detection of global visual stimuli and attentive load can affect MS ad possibly depend on them. Furthermore, it has been shown in a recent study of Troncoso et al. [20], that the stimulation of area V1 with microsaccades (i.e. self-generated motion) showed a biphasic neural response with an increased spiking rate followed by a suppression below baseline. This was different when compared to neural responses to simulated microsaccades (i.e. stimulus motions mimicking microsaccades, motion in the world) in which the Authors found an excitatory phase only. These findings indicate that V1 neurons can respond differently to self-generated motion and to equivalent motion in the world, expanding its potential role in information processing and visual stability during eye movements.

We wondered if MS are modulated by global spatial detection task, like heading perception based on optic flow. To address this question, we carried out an experiment of heading direction detection based on the distribution of velocity vectors of a radial optic flow. In this sort of retinal stimulation, one uses the global motion pattern instead of local motion cues [21]. Perception of self-movement by radial flow occurs in at least two stages of analysis: i) an early stage of local-motion analysis, with a time constant of about 200–300 ms, and ii) a later global-motion integration stage, with time constant about 3000 ms [22]. Because of this, different time course of MS modulation can be expected.

In this experiment, we presented an expanding optic flow in which the dot speed accelerated in the left or right hemifield, simulating a heading direction to the left or to the right of the vertical midline. Subjects had to signal the perceived heading direction by making a saccade toward a fixed target in the proper hemifield. Our aim was to verify the characteristics of MS generated before heading perception (i.e. MS made during fixation in the center of the screen – MSc) and MS made after heading perception (MS made during fixation in the peripheral position – MSp). Also, since after stimulus presentation MS usually show an inhibition epoch followed by a temporary enhancement [23–25], we investigated the time course of MS when participants perceived the optic flow direction, across the response saccade.

2. Methods

2.1. Participants

We tested 23 healthy volunteers, 12 males and 11 females, ranging from 20 to 29 years (average age was 22.58). Average height and weight with standard deviation for females were 166.8 ± 5.7 cm and 57.8 ± 5 kg, and for males 177.3 ± 5.4 cm and 79 ± 11 kg. All subjects had normal or corrected to normal vision and provided signed written informed consent to participate into the study. The experimental protocol was approved by the Ethics Committee of the University of Bologna. Recordings were performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.2. Optic flow stimuli

All experiments were performed in a dark room. Expanding optic flow stimuli were back-projected (Sony VPL EX3) full field onto a translucent screen positioned 415 cm away. The screen covered $135 \times 107^\circ$ of visual field and was placed 115 cm from the subjects' eyes. Optic flow stimuli were made by white dots 0.4° in width and of 1.3 cd/m^2 of luminous intensity. We presented two types of optic flow motion: in the first condition the dots speed accelerated to the left to simulate a left-heading, while in the second condition the speed accelerated to the right to simulate right-heading. To study the relationship of MS characteristics and optic flow direction perception, we presented the optic flow motion together with three steady points 0.8° in width (Fig. 1): one at the center of the screen, one to the right (20°) and one to the left (20°). As control stimulus, we showed the optic flow motion with all dots moving radially with symmetrical velocity gradient. At the stimulus onset, the participants had to fixate at the central point, keeping the fixation until they perceived a left or right self-movement direction. As soon as the direction was detected, they had to make a saccade to the point presented in the hemifield corresponding to the motion direction. For the control stimulus, they had to keep their gaze on the central point. Optic flow stimuli were made using Matlab psychophysical toolbox (Mathworks Inc.).

2.3. Apparatus and procedure

Eye movements were recorded binocularly by a video-based eye tracking system (EyeLink II; SR Research Ltd., Mississauga, Ontario, Canada). The system consisted of two miniature cameras mounted on a leather-padded headband. Pupil tracking was performed at 500 samples/s, with high spatial resolution ($<0.005^\circ$) and low noise ($<0.01^\circ$).

The eye tracker was calibrated at the beginning of the experiment and after every 4 optic flow stimulations. Then, we performed data validation and drift correction by applying a corrective offset to the raw eye position data after every movie. To start the experiment, participants had to fixate a white fixation point presented at the center of the screen. The stimulus appeared only if gaze position was detected in the fixation area. Each trial lasted 10 s and we