



Dynamic integration of information about salience and value for smooth pursuit eye movements



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ABSTRACT

Eye movement behavior can be determined by bottom-up factors like visual salience and by top-down factors like expected value. These different types of signals have to be combined for the control of eye movements. In this study we investigated how smooth pursuit eye movements integrate salience and value information. Observers were asked to track a random-dot kinematogram containing two coherent motion directions. To manipulate salience, the coherence or the density of one of the motion signals was varied. To manipulate value, observers won or lost money in a separate experiment if they were tracking one or the other motion direction. Our results show that pursuit direction was initially determined only by salience. 300–400 ms after target motion onset, pursuit steered towards the rewarded direction and the salience effects disappeared. The time course of this effect depended crucially on the difficulty to segment the two signal directions. These results indicate that salience determines early pursuit responses in the same way as saccades with short latencies. Value information is processed slower and dominates pursuit after several 100 ms.

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1. Introduction

Humans use saccadic eye movements to foveate objects of interest and smooth pursuit eye movements to stabilize moving objects on the fovea. Of course, natural environments contain several targets at the same time, so that selection is an integral purpose of eye movements. Target selection for saccades has been studied intensively and a variety of different signals that can guide saccades have been identified (Schütz, Braun, & Gegenfurtner, 2011): Amongst others, saccades are executed towards salient image locations (Itti & Koch, 2000; Kienzle et al., 2009), towards objects (Einhäuser, Spain, & Perona, 2008; Nuthmann & Henderson, 2010), towards locations that maximize the expected value (Schütz, Trommershäuser, & Gegenfurtner, 2012) and are also controlled by current action planning (Ballard, Hayhoe, & Pelz, 1995; Johansson et al., 2001). The integration of these different types of signals is further complicated by the different time course of each of these signals. Recently we showed that salience and value information receive different relative weights depending on the saccade latency: saccades with latencies shorter than 180 ms favor salience, whereas saccades with latencies longer than

180 ms favor value (Markowitz et al., 2011; Schütz, Trommershäuser, & Gegenfurtner, 2012).

Compared to saccades, signals that affect smooth pursuit target selection are less well studied. In general, smooth pursuit can only be executed with a high gain in response to visual motion (Berryhill, Chiu, & Hughes, 2006). In the presence of two moving targets, the initial pursuit response is typically a vector average of both motion directions (Lisberger & Ferrera, 1997). Similar to saccades, smooth pursuit prefers stimuli with higher salience, such as higher contrast (Liston & Krauzlis, 2003) or stronger motion energy (Krauzlis & Adler, 2001; Schütz, 2011). Interestingly, smooth pursuit shows a stronger preference for luminance contrast compared to color contrast than saccades (Spering, Montagnini, & Gegenfurtner, 2008), which means that salience processing might not be identical for different types of eye movements. Besides low-level motion processing factors, there are also high-level factors influencing pursuit. Predictive onset and direction of motion can lead to anticipatory pursuit (Kowler, 1989). Similar to saccades, instructions and reward can bias the target selection for smooth pursuit. When two targets differ in their reward and a cue informs about the motion direction of the two targets, pursuit initiation is biased towards the rewarded motion direction (Ferrera, 2000; Joshua & Lisberger, 2012). Non-visual feedback can also increase pursuit gain during transient target blanking (Madelain & Krauzlis, 2003). A still remaining question

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is how different types of signals are traded off in the control of pursuit movements. For instance in a landscape one might encounter two flying birds, a duck and a kingfisher. The duck is certainly more salient because of its size, whereas the kingfisher might be more valuable to look at, because of its beauty. The brain has to resolve this conflict and select one of the two birds for pursuit. A previous study showed that top-down knowledge about the two-dimensional motion direction of a tilted bar does not allow to compensate for the biased one-dimensional edge motion (Montagnini, Spering, & Masson, 2006). This finding suggests that bottom-up stimulus information can even override top-down expectations.

Here we investigated how salience and value information are traded off in the control of smooth pursuit eye movements. Smooth pursuit eye movements are especially interesting in this respect, because each single smooth pursuit trace provides a continuous read-out of this integration process. The previous results on saccades (Schütz, Trommershäuser, & Gegenfurtner, 2012) suggest that the relative weighting of salience and value is not constant, but changes over time.

2. Methods

2.1. Subjects

The author FL and seven naïve observers participated in these experiments. Six observers participated in the first experiment; three observers participated in the second experiment. We had to exclude the data of one observer in the first experiment, because she/he was not able to segment the two motion directions at all. Experiments were in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and approved by the local ethics committee LEK FB06 at the University Giessen (proposal number 2009-0008). Written informed consent was obtained from all observers.

2.2. Equipment

Observers were seated in a dark room facing a 21-in. SONY GDM-F520 CRT monitor driven by an Nvidia Quadro NVS 290 graphics board with a refresh rate of 100 Hz non-interlaced. At a viewing distance of 47 cm, the active screen area subtended 45 degrees of visual angle in the horizontal direction, and 36 degrees of visual angle vertical on the subject's retina. With a spatial resolution of 1280×1024 pixels this results in 28 pixels/degrees of visual angle. The observers's head was stabilized by a chin and a forehead rest and the display was viewed binocularly. Eye position signals of the right eye were recorded with a video-based eye tracker (EyeLink 1000; SR Research Ltd., Kanata, Ontario, Canada) and were sampled at 1000 Hz. Stimulus display and data collection were controlled by a PC.

2.3. Visual stimuli

All stimuli were presented on a gray background with a luminance of 14.6 cd/m^2 . Two random dot kinematograms (RDKs) appeared within a circular aperture of 20 degrees of visual angle radius. This aperture was slightly cropped at the bottom and top because the height of the monitor was only 36 degrees of visual angle. Individual dots were displayed in white (87 cd/m^2) or black (0.04 cd/m^2) and had a size of 0.14×0.14 degrees of visual angle. The dots had a life time of 200 ms and at the end of their life time they were positioned at a random position in the aperture. Each dot kept its motion direction for the whole 200 ms, such that signal dots could be segmented from noise dots, leading to the appearance of transparent motion (Schütz et al., 2010). The motion speed

was 10 degrees of visual angle/s. The overall motion direction was either leftward or rightward with the motion directions of the two RDKs deflected upward or downward from horizontal by 10° . We used RDKs with a limited dot-lifetime to study smooth pursuit in isolation without intervening saccades. Although saccades and smooth pursuit typically share a common target selection mechanism (Case & Ferrera, 2007; Krauzlis, Dill, & Fowler, 2012), they differ in salience computations (Spering, Montagnini, & Gegenfurtner, 2008) and also might differ in reward processing. We could show that a RDK elicits only few saccades (Schütz et al., 2010).

2.4. Experimental procedure

At the beginning of each trial a bull's eye with an outer radius of 0.3 degrees of visual angle and an inner radius of 0.075 degrees of visual angle appeared at the screen center. The observers had to fixate the bull's eye and press a button to start the trial, at which time the EyeLink 1000 System performed a fixation check. If the fixation check succeeded, the initial bull's eye disappeared and the random-dot kinematogram appeared. Motion started as soon as the dots appeared. The random-dot kinematogram was presented for 2000 ms (Fig. 1A).

2.5. Salience and value conditions

Observers participated in two different conditions: in the salience condition, there was no reward or penalty. The salience condition also consisted of single-target trials with only one RDK to measure the variability of smooth pursuit direction in the absence of a target conflict. In the value condition, observers could win up to 100 points per trial if they followed the white RDK and could lose up to 100 points if they followed the black RDK. After each trial we calculated the eye movement direction in a time window from 150 to 1500 ms after target motion onset. If the eye movement direction was within 10° of the direction of the white RDK in the whole time window, the observers won 100 points for one trial. If the eye movement direction was within 10° of the direction of the black RDK during the whole time window, the observers lost 100 points. The points in one trial were calculated according to the proportion of time that the eyes were moving in the rewarded or punished direction. The points earned during the trial and the total sum of points was displayed after each trial. Points were transformed into money at the end of the experiment, such that observers could maximally win 3 € in addition to the regular compensation of 8 € per hour.

2.6. Eye movement analysis

Eye velocity signals were obtained by digital differentiation of eye position signals over time. The eye position and velocity signals were filtered by a Butterworth filter with cut-off frequencies of 30 and 20 Hz, respectively. Saccade onset and offset were determined with the EyeLink saccade algorithm. This algorithm uses a velocity threshold of 22 degrees of visual angle/s to which the average velocity over the last 40 ms is added and an acceleration threshold of 3800 degrees of visual angle/s². Saccades were removed from the velocity traces by linear interpolation. All traces were rotated such that the overall target motion was to the right and the motion of the white and black RDK was upwards and downwards, respectively. Since left and right motion and up- and downward motion were balanced, any potential bias towards one of these directions cannot contaminate our results. We also did not observe any systematic direction biases in single-target trials. For each trace, the angular direction of the eye velocity was calculated in 100 ms wide time intervals, starting 200 or 900 ms after target motion onset. We only analyzed directions within -25° to 25° . Circular statistics

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