



Receptive fields for smooth pursuit eye movements and motion perception

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ARTICLE INFO

Article history:

Received 18 June 2010

Received in revised form 28 September 2010

Keywords:

Smooth pursuit
Motion perception
Random-dot kinematogram
Motion integration
Motion segmentation
Motion perturbation
Oculometric function
Psychometric function

ABSTRACT

Humans use smooth pursuit eye movements to track moving objects of interest. In order to track an object accurately, motion signals from the target have to be integrated and segmented from motion signals in the visual context. Most studies on pursuit eye movements used small visual targets against a featureless background, disregarding the requirements of our natural visual environment. Here, we tested the ability of the pursuit and the perceptual system to integrate motion signals across larger areas of the visual field. Stimuli were random-dot kinematograms containing a horizontal motion signal, which was perturbed by a spatially localized, peripheral motion signal. Perturbations appeared in a gaze-contingent coordinate system and had a different direction than the main motion including a vertical component. We measured pursuit and perceptual direction discrimination decisions and found that both steady-state pursuit and perception were influenced most by perturbation angles close to that of the main motion signal and only in regions close to the center of gaze. The narrow direction bandwidth (26 angular degrees full width at half height) and small spatial extent (8 degrees of visual angle standard deviation) correspond closely to tuning parameters of neurons in the middle temporal area (MT).

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1. Introduction

Smooth pursuit eye movements have for the most part been studied using small (<1 degree of visual angle (DVA)) foveal targets against a uniform featureless background (e.g. Rashbass, 1961). This approach underestimates the abilities of the pursuit system to: (a) integrate motion signals in order to follow large field targets and (b) isolate and follow some motion signals while ignoring others. Integration and segmentation processes have received more attention in recent literature. For instance, several studies have investigated the influence of additional motion signals on pursuit as well as perception (for a review see: Spring & Gegenfurtner (2008)), and some show that peripheral motion can modulate perception and pursuit in different ways (e.g. Spring & Gegenfurtner, 2007a).

Earlier studies used clearly distinct pursuit targets with different motion signals, such as multiple moving objects (e.g. Ferrera & Lisberger, 1997; Lisberger & Ferrera, 1997; Spring, Gegenfurtner, & Kerzel, 2006), a moving object and an independently-moving context (Miura, Kobayashi, & Kawano, 2009; Spring & Gegenfurtner, 2007a, 2007b), or a small target moving in front of a large-field background (e.g. Kodaka, Miura, Suehiro, Takemura, & Kawano, 2004; Lindner, Schwarz, & Ilg, 2001; Masson, Proteau, & Mestre, 1995). On the other hand, only a handful of studies measured spatial integration of pursuit eye movements to uniform, but spatially extended targets.

Heinen and Watamaniuk (1998) used coherently-moving random-dot kinematograms (RDK) at a fixed width of 10 DVA and showed that increasing RDK aperture height from 0.5 DVA to 10 DVA increases pursuit acceleration and decreases pursuit latency. When different motion vectors across a large field in a RDK do not share the same direction, but are distributed across a narrow bandwidth of directions, those vectors with similar directions are integrated for pursuit (Watamaniuk & Heinen, 1999), and perception (Watamaniuk, Sekuler, & Williams, 1989).

In the present study we asked two questions: (1) How does the pursuit system treat multiple motion vectors that are presented in different spatial locations across the visual field? (2) Are pursuit and perception equally sensitive to extrafoveal motion signals? The ultimate goal of this study was to map a receptive field for smooth pursuit eye movements, which we are calling an 'oculoceptive field', akin to receptive fields for visual neurons. We asked observers to pursue the large-field coherent motion signal inside a RDK. The coherent signal could be perturbed by shifting some of the dots in a direction offset obliquely from that of the signal, thus creating a secondary extrafoveal motion signal throughout pursuit. The perturbations were presented in several gaze-contingent regions around gaze position. We measured the effects of the direction of perturbations, and also the effects of the spatial size and position of the perturbation regions relative to gaze, on the direction of the pursuit response. In all five experiments presented here, we also asked observers to report perceived motion direction after each trial so that we could compare pursuit response to the perceived direction. We used the perceptual

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responses to map a ‘perceptive field’, which we compared to the oculocceptive field.

2. Methods

2.1. Overview of experiments

We conducted five experiments to map an oculocceptive field for pursuit, and a perceptive field for perception. We did this by presenting coherently moving dots (masked by noise) as a signal for pursuing while perturbing regions around the gaze position by changing the direction of a percentage of dots in the region. Observers were instructed to pursue the motion signal and to indicate at the end of each trial whether they perceived the overall motion direction to be up or down relative to horizontal motion.

2.1.1. Experiment 1: Oculometric and psychometric functions without perturbation

To determine the effect of signal angle on direction discrimination, we used a range of signal angles (0 angular degrees ($^{\circ}$), $\pm 2^{\circ}$, $\pm 5^{\circ}$, $\pm 10^{\circ}$). The 0° (horizontal) signal angle condition served as a baseline for oculometric analysis.

2.1.2. Experiment 2: Oculometric and psychometric functions with a 10° perturbation

We compared the effect of perturbation angles $\pm 10^{\circ}$ on pursued and perceived signal direction. Perturbation trials had signal angles of 0° , $\pm 2^{\circ}$, $\pm 5^{\circ}$ or $\pm 10^{\circ}$ with a perturbed region in front of the gaze position. We included unperturbed trials at a signal angle of 0° as a baseline.

2.1.3. Experiment 3: Varying the perturbation angle

To measure the effect of the perturbation angle, unperturbed trials with signal angles 0° and $\pm 5^{\circ}$ were randomly interleaved with perturbation trials with signal angles 0° or $\pm 5^{\circ}$ and perturbation angles $\pm 5^{\circ}$, $\pm 10^{\circ}$, $\pm 15^{\circ}$, $\pm 20^{\circ}$, $\pm 25^{\circ}$, $\pm 45^{\circ}$, or $\pm 90^{\circ}$. Perturbations for this experiment were located in front of the gaze position. The mean within each signal angle group served as a baseline (same for experiments 4 and 5).

2.1.4. Experiment 4: Varying the perturbation location

To test the effect of perturbation location, perturbation trials (signal angles 0° or $\pm 5^{\circ}$, perturbation angles $\pm 10^{\circ}$) had a perturbation region that was presented above, below, in front of, or behind the gaze position. Perturbation trials were randomly interleaved with unperturbed trials at signal angles 0° or $\pm 5^{\circ}$.

2.1.5. Experiment 5: Varying the perturbation width and eccentricity

We varied the width and eccentricity of the perturbation region to quantify the extent of spatial integration of motion information for pursuit and perception. Perturbation trials (signal angle 0° , perturbation angles $\pm 10^{\circ}$) were randomly interleaved with unperturbed trials (signal angles 0° , $\pm 2^{\circ}$, or $\pm 5^{\circ}$). Only perturbation trials and signal-only trials with a 0° signal angle were analyzed in this experiment.

2.2. Observers

Participants were ten trained observers, seven females and three males (mean age 24 ± 4 yrs). Not all observers took part in all experiments: 10 participants took part in experiment 1, 8 in experiment 2, 7 in experiment 3, 8 in experiment 4, and 8 in experiment 5. For each condition, observers did 112, 72 and 960 trials for experiments 1–3 respectively. For experiment 4, observers did 360 trials for the condition with a perturbation, and 720 trials for the

condition without a perturbation. For experiment 5, observers did between 80 and 120 trials per condition. The variability in number of trials across experiments resulted from the way we later collapsed some of the conditions, since conditions reported here represent the grouped conditions shown in the figures of this study. Author K.D. participated in all experiments; all other observers were unaware of the purpose of the study. All observers had normal or corrected-to-normal visual acuity.

2.3. Equipment

Observers were seated in a dimly-illuminated room, with their head stabilized by a chin rest and a forehead support, in front of a 19" Sony Trinitron F520 CRT monitor, 40×31 cm (1280×1024 pixel resolution, 100 Hz refresh rate), driven by an Nvidia Quadro NVS 290 graphics board. The center of the monitor was at eye level and the viewing distance was 47 cm. The active screen area was circular, centered in the middle of the monitor, and subtended 40 DVA. Observers viewed the screen binocularly, while movements of the right eye were recorded at 2000 Hz (Eyelink 1000; SR Research Ltd., Mississauga, Ontario, Canada). We used standard procedures to calibrate the eye tracker and validate eye position. Stimulus display and data collection were controlled by a PC.

2.4. Visual stimuli

The central fixation spot was a bull’s-eye with an outer radius of 0.3 DVA and an inner radius of 0.15 DVA. The stimulus was a RDK that had white dots with a luminance of 87 cd/m^2 moving at 10 DVA/s and a limited lifetime of 200 ms, presented on a black background with a luminance of 0.04 cd/m^2 . When expired, each dot reappeared at a random position within the aperture for subsequent 200-ms lifetimes, so that the overall dot density of the aperture was kept constant at 2 dots/DVA. The phase of each dot’s lifetime cycles was shifted randomly to prevent all dots from being relocated at the same time. The RDK consisted of 20% signal dots, moving coherently in a common direction across lifetimes, thereby giving the impression of global motion across the aperture and providing a signal for pursuit. The remaining 80% of the dots were noise dots with a random initial direction of displacement every subsequent lifetime. The direction distribution of the noise dots at each lifetime was isotropic. Signal motion was rightward or leftward along the horizontal meridian or offset obliquely upwards or downwards from the horizontal in steps of 2° , 5° , and 10° . We decided to use a 20:80 signal-to-noise ratio since our own pilot studies indicated that observers reach close to 100% accuracy with a higher signal-to-noise ratio (data not presented here).

To perturb a region of the stimulus, 20% of the signal dots and 20% of the noise dots inside that region were turned into perturbation dots. Perturbation dots had the same characteristics as signal dots, but differed in motion direction. They moved obliquely upwards or downwards but in the same left/right general direction of (or, in the case of a 90° perturbation, perpendicular to) signal motion. For experiments 2–4, perturbations were presented in one of four regions inside a circular window around gaze position. The window was composed of two concentric circles (centered on the gaze position) with an inner-circle radius of 2 DVA and an outer-circle radius of 10 DVA. The resulting ring-shaped area between these two circles was divided into four regions: above, below, to the right, or left of gaze position. The four regions had borders along the crossing diagonals of the circular window, and were equal in size and shape (Fig. 1C). The borders of the perturbation regions were not visible to the observers. The regions were gaze-contingent and reacted to an eye movement with a latency of <10 ms. In experiment 5, perturbations were presented inside a gaze-contingent rectangular region of varying width (2–10 DVA)

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