



Spatial perception during pursuit initiation

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ABSTRACT

Spatial perception is modulated by eye movements. During smooth pursuit, perceived locations are shifted in the direction of the eye movement. During active fixation, visual space is perceptually compressed towards the fovea. In our present study, we were interested to determine the time course of spatial localization during pursuit initiation, i.e. the transition period from fixation to steady-state pursuit. Human observers had to localize briefly flashed targets around the time of pursuit initiation. Our data clearly show that pursuit-like mislocalization starts well before the onset of the eye movement. Our results point towards corollary-discharge as neural source for the observed perceptual effect.

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1. Introduction

Localization of targets in the environment is of ultimate importance in everyday life. Eye movements challenge this task because they continuously induce a shift of the retinal image of the outside world. Nevertheless we perceive the world as being stable. Different from introspection, however, visual stability is not perfect. In recent years, many studies have demonstrated spatial mislocalization of stimuli flashed during eye movements. During saccades localization errors follow a characteristic spatio-temporal pattern, which heavily depends on experimental conditions. In complete darkness, transient stimuli are mislocalized in the direction of the eye movement from about 100 ms before the eyes start to move (shift) (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Honda, 1989). The maximum shift is observed around saccade onset. Mislocalization is then inverted and stimuli are perceived as being shifted opposite to the saccade direction for up to 100 ms. In contrast, when visual references are available, the mislocalization strongly depends on the position of the target relative to the saccade goal and stimuli are perceptually shifted towards the landing point of the eye. This results in a perceptual compression of visual space (Kaiser & Lappe, 2004; Lappe, Awater, & Kregelberg, 2000; Ross, Morrone, & Burr, 1997).

During smooth pursuit briefly flashed stimuli are mislocalized in the direction of the eye movement. The magnitude of the error depends on the position of the target relative to the fovea (Koenigs & Bremmer, 2010; van Beers, Wolpert, & Haggard, 2001). The error is largest in the hemifield the eye is heading for and it is smallest in

the opposite hemifield. Optokinetic nystagmus (OKN) is a reflexive eye movement consisting of an alternating pattern of slow and fast phases. Fast phases share functional properties with saccades (Kaminiaz, Konigs, & Bremmer, 2009), while the slow phases are considered smooth eye movements like pursuit (Carpenter, 1988). During the slow phase of OKN, briefly flashed targets are spatially mislocalized. Different from pursuit, however, the mislocalization is rather constant across the visual field (Kaminiaz, Kregelberg, & Bremmer, 2007; Tozzi, Morrone, & Burr, 2007). Interestingly, stimuli are also mislocalized during the slow phase of the optokinetic after-nystagmus (OKAN). OKAN is also a reflexive eye movement and is induced by prolonged performance of OKN. The error pattern observed during OKAN, however, is different from the one observed during OKN or pursuit (Kaminiaz, Kregelberg, & Bremmer, 2008). In both hemifields, stimulus locations are perceived more eccentric than they are, resulting in a perceptual expansion of space. Two issues are important to notice: firstly, OKAN is a so-called open-loop eye movement, i.e. the eyes move without a driving visual signal. Secondly, OKAN is driven by subcortical rather than cortical oculomotor structures (Konen, Kleiser, Seitz, & Bremmer, 2005).

Fixation is considered to be a distinctive class of eye movements (Carpenter, 1988). Interestingly, even during fixation localization is not veridical. Like for saccades, the exact experimental conditions strongly influence the perceptual error pattern during fixation. In complete darkness, perceived locations are more eccentric than they are. During active fixation of a target, however, perceived stimulus locations are shifted towards the fovea resulting in a global compression of space (Kaminiaz et al., 2007; Mateeff & Gourevich, 1983; Sheth & Shimojo, 2001).

Pursuit initiation is a transition from active fixation to active tracking of a target. Perceptually, fixation of a target induces a compression of space while pursuit induces a shift in the direction

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of the eye movement. Hence, the interesting question arises, *when* relative to eye-movement onset, the spatial perception shifts from fixation-like to pursuit-like. In addition, clarifying the time course of mislocalization during pursuit (onset) might also allow narrowing down its possible neural basis.

Pursuit-initiation, like OKAN, is an open-loop eye movement. Unlike steady-state pursuit, the pursuit target is not placed in or around the fovea during this short period of time. Different from OKAN, however, pursuit and its initiation are under cortical control (Ilg, 1997, 2003; Komatsu & Wurtz, 1989; Konen et al., 2005; Lynch, 1987). Accordingly, a second question was addressed in our study, i.e. whether the spatial perception during pursuit initiation would be similar to the one observed during steady-state pursuit or during OKAN. We therefore asked human observers to localize visual targets that were briefly flashed around the time of pursuit initiation. Results clearly indicate a pursuit-like perceptual error. Interestingly, this mislocalization starts well before the onset of the eye movement.

2. Materials and methods

2.1. Behavioral paradigm

Six healthy adults, (three male, three female), aged 22–27 with normal or corrected to normal vision, participated in this study. Four of the subjects were naïve as to the purpose of the experiment with one having previous experience with psychophysical experiments. Two of the subjects are authors (L.H. and M.B.). Each subject gave informed written consent prior to the experiment. All procedures used in this study conformed to the Declaration of Helsinki.

Experiments were carried out in complete darkness. Computer generated stimuli were projected onto a large tangent screen by means of a CRT projector (Marquee 8000, Electrohome Inc.) running at a spatial resolution of 1152 by 864 pixels and a frame rate of 100 Hz. The screen was viewed binocularly at a distance of 114 cm, spanning 70° by 55° viewing angle. The subjects' head was supported by a chin rest. Eye position was sampled at 500 Hz using an infrared eye tracker (Eye Link 2, SR Research). Prior to each session the system was calibrated via a 3 by 3 target matrix. Drift correction was performed offline based on the fixation position at the beginning of a trial. Eye movement and behavioral data were stored on hard disk for offline analysis.

To induce smooth pursuit eye movements without catch-up saccades we employed the Rashbass paradigm (Rashbass, 1961). In this paradigm the pursuit target is initially at rest before stepping into the periphery. There it immediately starts to move at a constant velocity in the opposite direction, i.e. centripetally. In this study, the initial static presentation lasted randomly between 1000 and 1100 ms. The target then stepped horizontally into the periphery (2° or 2.2°, depending on the subject, see below) and started to move centripetally at 10°/s (see Fig. 1). Depending on the initial step the target crossed the starting point after 200 ms or 220 ms and continued its movement for another 2800 (2780) ms. The pursuit target was a dot of light (12 cd/m²) with a Gaussian luminance profile ($\sigma = 0.3^\circ$). A localization target (size: $[x, y] = [0.25^\circ, 2^\circ]$) was flashed for 10 ms at one of four possible positions $([x, y] = (5^\circ, 3^\circ), (-5^\circ, 3^\circ), (5^\circ, -3^\circ)$ or $(-5^\circ, -3^\circ)$) relative to the pursuit target. The time of flash presentation was varied randomly between 400 ms before and 800 ms after onset of the pursuit target movement. During the whole trial two sets of vertical reference bars were presented: one above and one below the horizontal meridian, i.e. the pursuit trajectory. Each set of reference bars were two narrow lines, extending 5° outward from a starting

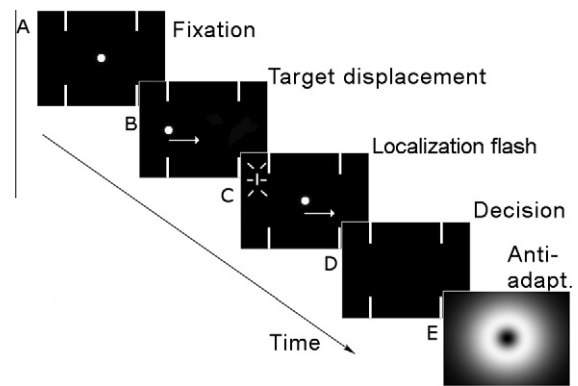


Fig. 1. Scheme of the experimental paradigm. (A) A fixation period of 1000–1100 ms precedes pursuit target movement onset. (B) The target is displaced by 2–2.2° into the periphery and starts to move in the opposite direction at 10°/s for 3000 ms. (C) The localization target is flashed at 700–1800 ms after fixation start, i.e. 400 ms before to 700 ms after pursuit target movement onset. (D) The decision period lasts until the subject's response is entered. (E) The presentation of an anti-adaptation stimulus prevents darkness adaptation and gives time for blinks. The next trial starts when the subject signals readiness by pressing a key.

point 5° above or below the pursuit trajectory. The horizontal position of these reference bars was such that one set of bars had a horizontal offset to the localization target of $\pm 3^\circ$, $\pm 1.25^\circ$, $\pm 1^\circ$, $\pm 0.75^\circ$, $\pm 0.5^\circ$ or $\pm 0.17^\circ$ (reference bar). The other set of bars mirrored the first set with respect to the pursuit target and served as a decoy, preventing anticipation of pursuit direction and localization target position. At the end of each trial the subjects had to indicate in which of three parts of the screen they had perceived the target: left from the leftmost bars (left), in between the bars (central), or right from the rightmost bars (right). This response was delivered via a standard PC keyboard using numbers 4, 5 or 6 for indicating *left*, *central* or *right*. The delivered answer was translated into a binary answer (left, right) with respect to the actual reference bar, ignoring the decoy reference. The trial ended when the subject hit the return key for confirming the response. Between trials a bright screen was shown to prevent dark adaptation of our subjects. The illumination profile of this anti-adaptation screen was defined by a difference of Gaussians having a dark center surrounded by a brighter ring which in turn was surrounded by darkness. This screen stayed on until the subject signaled readiness for the next trial by pressing a key.

Baseline trials were performed since fixation of a target without background reference is known to induce a subjective compression of space (Kaminiaz et al., 2007). To map each subject's perception of space during fixation a baseline paradigm was presented which was equal to the main experiment except that the "pursuit target" never moved.

The central goal of our study critically required pursuit initiation without catch-up or intermittent saccades. Accordingly, subjects were tested for this oculomotor ability prior to the main experiment. This pre-screening also allowed us to determine on an individual basis the spatial offset of the initial target step for the Rashbass paradigm. Only subjects who were able to initiate pursuit without catch-up saccade and who were able to perform stable pursuit without saccading to the flashed target in at least 50% of the trials were admitted to the main experiment. Subjects admitted to the main experiment were trained with three more sessions under full main experiment conditions before data were included in the analysis.

Experimental sessions lasted between 10 and 15 min depending on the subject. Subjects themselves determined when to take a break to maintain their ability to concentrate, which they usually did after three or four sessions.

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