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Alteration of the perceived path of a non-pursued target during smooth pursuit: Analysis by a neural network model

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Abstract

During pursuit of a circularly moving target, the perceived movement of a second circularly moving target is altered. The perceived movement of the non-pursued target is different from both its real movement path and its retinal path. In the present paper this phenomenon is studied using a physiologically based neural network model. Simulation results were compared to psychophysical findings in human subjects. Model simulations enabled us to suggest an explanation for this phenomenon in terms of underlying physiological mechanisms and to estimate the contribution of the efferent eye-movement signal to the perceptual process.

Keywords: Pursuit eye movement; Neural network; Motion perception; Area MST

1. Introduction

The highly developed smooth pursuit system enables primates and humans to keep the image of a moving object on the fovea at objects speed up to 30°/s. During pursuit, objects movements on the retina are different from their real world movements, forcing the visual system to use some kind of eye-movements compensation to enable us to perceive, for example, a pursued object as moving, although its retinal image is nearly stable.

Early theories of eye-movement compensation (Gregory, 1958; Von Helmholtz, 1909; Von Holst, 1954), suggested that extraretinal information, a copy of the motor command sent to the eyes, is subtracted from the retinal information on target velocity. Various physiological and psychophysical studies are consistent with this mechanism, and it is thus commonly assumed that perception during pursuit eye movements involves a combination of afferent (visual) and efferent (motor) signals.

Basic perceptual phenomena related to pursuit were successfully addressed by theoretical studies of the subject (see Pack, Grossberg, & Mingolla, 2001). More complex phenomena (see below), however, still lack theoretical analysis. In Furman and Gur (2003) we described a physiologically based neural network model for motion processing in the cortex during pursuit. The model was based on single cell properties and on organization of relevant cortical areas. The model analyzed integration of afferent and efferent signals within a broad context including a full representation of directions and velocities of movement, and complex retinal images. Therefore our model enables, for the first time, analysis of complex perceptual phenomena related to pursuit. Section 3 gives a brief description of the model.

This work deals with two issues not treated by previous models; the effectiveness of efferent vs. afferent signals and the physiological mechanisms underlying complex perceptual phenomena related to smooth pursuit.

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There is an ongoing debate on the degree of effectiveness of the efferent signal in the perceptual process. It is commonly assumed that the efferent signal is less effective than the afferent one, as demonstrated, for example, by the underestimation of target speed during pursuit (the *Aubert–Fleich phenomenon*, Aubert, 1886) and the perceived movement of a stationary background (the *Filehne effect*, Filehne, 1922). Some researchers suggested that the efferent signal participates in a significant manner in the perceptual process (e.g. Carr, 1935; Mack & Herman, 1972), while others claimed that the efferent signal contribution is marginal (e.g. Dodge, 1910; Festinger, Sedgwick, & Holtzman, 1976; Stoper, 1973).

That there is a complex interaction between efferent and afferent signals during pursuit is evident in a family of perceptual phenomena: The alteration in the apparent trajectory of a moving target while a second one is being pursued (Dodge, 1904, 1910). The present work focuses on the perceived path of a circularly moving target during pursuit of another, circularly moving, one. This phenomenon was first described by Kano and Hayashi (1981) who reported that the perceived path of the non-tracked spot differed dramatically from its retinal path—particularly for spots moving, out of phase, in opposite directions.

To enable a more detailed and quantitative comparison between simulation results and experimental data, we studied the phenomenon described by Kano and Hayashi (1981) for a greater number of subjects and different parameter values.

We show that the model suggests an explanation for the perceptual phenomena in terms of physiological mechanisms, and accounts for experimental data if the efferent signal is assumed to significantly participate in the perceptual process, at about 80% strength relative to the visual signal.

2. Experimental methodology

2.1. Subjects

Eight subjects (4 males, 4 females, ages 24–57), including the 2 authors, took part in all experiments. All had normal or corrected-to-normal vision. Three subjects were naive about the purpose of the experiment.

2.2. Apparatus

Stimuli were generated using a 1.80 GHz Pentium PC and displayed on an SVGA monitor with a 600×800 pixel resolution at a 85 Hz frame rate. The monitor was viewed binocularly at a distance of 70 cm in a darkened room. A chin rest restricted the subjects' head movements.

2.3. Stimuli

Each test stimulus consisted of a pair of circularly moving spots. The 3 mm diameter spots were moderately dim but distinctly visible. Both spots moved at the same angular velocity (3.5 rad/s), along equi-diameter (9 cm) circles whose centers were separated by 12 cm in the horizontal direction. At the beginning of each stimulus, the left spot (target A) appeared first, moving clockwise. After completing one cycle, the right spot (target B) appeared and moved with target A until completing 4 additional cycles. Target B moved either in the same direction as target A (clockwise) or in the opposite direction (counterclockwise). Phase differences between targets were 0°, 60°, 120°, or 180°. The eight combinations of movement directions and phase differences were presented in a random order.

An additional stimulus was used as a reference; it consisted of a stationary spot (target A) and a circularly moving spot. The spots' characteristics were as described above, only that target A was now stationary at the center of its previous path.

2.4. Procedure

When viewing the two moving spots, each subject was instructed to track target A as accurately as possible during the whole presentation and memorize the perceived path of target B. After the presentation, the subject was requested to verbally report the shape of target B perceived path (e.g. a tilted elongated ellipse) and then a small circle appeared around the center of target B path. Control keys enabled the subject to change the circle size, or to transform it to an ellipse of varying size, axes ratio, and inclination. The subject thus adjusted the curve presented on the screen according to the memorized target B path. The subject could choose to repeat the last stimulus presentation and in this case, after the presentation, the ellipse appeared as last modified by him. The subject could then modify it further, or leave it as is, and move to the next trial or repeat the procedure. A record of the last ellipse estimation (axes and inclination) at each session was stored.

To use the reference stimulus, depicting a stationary target A with a moving target B, the subjects were instructed to fixate on the stationary target during the whole presentation and memorize the perceived path of the moving one. After the presentation the subjects recorded the perceived path of the non-pursued target by the above described procedure.

2.5. Eye-movement monitoring

A control experiment with 4 of the 8 subjects was performed to monitor the subjects' eye movement during pursuit. The viewing conditions and experimental setup