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CHAPTER 5.13

Tracking in 3-D space under natural viewing condition

H.A. Rambold[1,2,*], T. Sander[1], A. Sprenger[1] and C. Helmchen[1]

[1]*Department of Neurology, University of Lübeck, Lübeck, Germany*
[2]*Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, MD, USA*

Abstract: To track a small visual target in 3-D space, the two eyes have to move in different directions and/or at different velocities. This tracking might be accomplished by a disjunctive pursuit system, which uses separate motion processing of each individual eye but no disparity signal (hypothesis 1), or by the conjugate pursuit and the vergence system (hypothesis 2). To test the validity of the two hypotheses we recorded eye movements in five healthy human subjects with the scleral search-coil method. A small dim laser stimulus was presented on an earth horizontal platform. A position-ramp stimulus was presented in eight different directions: rightward or leftward, convergence or divergence, or a combination of them. We compared a fusible with an un-fused and a monocular viewing condition to assess whether a disparity signal is needed for 3-D tracking. Fusion was prevented by a vertical prism. We compared the monocular with the prism viewing condition to examine the effect of retinal motion signals of either one or both eyes on the tracking performance in the absence of disparity signals. Results revealed severe impairment of tracking in depth, while tracking in pure horizontal directions remained unaffected during the prism and monocular as compared to the binocular viewing condition. These data support hypothesis 2.

Keywords: vergence; eye movements; smooth pursuit

Introduction

Tracking a target in natural space, which includes different depth planes, requires disjunctive eye movements. The two eyes might move in different directions and/or at different velocities. Controversy still surrounds the questions of how these eye movements are generated and what signals are used. Two major hypotheses are put forward: (1) the disjunctive pursuit hypothesis proposes that retinal motion signals of the two eyes are processed independently for the right and the left eye (King and Zhou, 1995). (2) Hering's hypothesis predicts that tracking in space is accomplished by two independent eye movement systems, the conjugate smooth pursuit and the disparity vergence system (Maxwell and King, 1992; Semmlow et al., 1998). The latter hypothesis is supported by a study using large un-fuse images which impaired vergence eye movements (Erkelens and Collewijn, 1985). A study using un-fused slowly moving small targets in 3-D space in humans has not yet been conducted. This study is designed to elucidate whether either hypothesis can account for visual tracking in 3-D space.

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*Corresponding author. Tel.: +301 496 9080;
Fax: +301 402 0511; E-mail: ramboldh@nei.nih.gov

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Methods

Binocular recordings were obtained from five healthy subjects (five males), aged 28–44 years, in accordance with the Declaration of Helsinki (1994) and the local ethics committee. All subjects had normal vision and stereovision (Stereo Optical Co., Inc., Chicago, OH, USA). Binocular eye movements were recorded with the Scleral Search Coil System (Remmel Labs, MD, USA). The search coils were calibrated using a combined offline in vitro and in vivo calibration, as described elsewhere (Eggert et al., 1999; Rambold et al., 2002). Single laser targets (spot diameter 0.1°, 635 nm, LISA laser products OHG, Katlenberg-Lindau, Germany) were projected on a horizontal plane in an otherwise dark surrounding (Rambold et al., 2006). This plane was located 5 cm below the level of the eyes and was slightly tilted towards the subject by 5° (Rambold et al., 2006). For binocular stimulation the stimulus was aligned as exactly as possible in the mid-sagittal plane in between the eyes.

Ramp stimuli with a constant velocity were used in eight different directions starting from the mid-sagittal plane at an initial vergence angle of 7°. The stimulus moved in the plane of fixation on an isovergence line to the right or to the left (rightward or leftward condition), in a sagittal plane towards or away from the subject's nose (vergence condition) or in combination of both stimulus directions (oblique condition). Stimulus velocity was 10°/s angular velocity for the horizontal (isovergence) directions (calculated for a cyclopean eye) and 3°/s vergence velocity for vergence directions. The directions were randomized, and 20–30 repetitions were performed for each motion direction. In a first experiment, a vertical prism of 6 prism dioptre (pd) base down was mounted in front of one eye to examine retinal slip in the two eyes without horizontal fusion. The stimuli were repeatedly presented in three experimental conditions: prism in front of the right eye, prism in front of the left eye, and viewing with no prism. In a second experiment the eye was covered to serve as control for estimating the residual vergence movements caused by different cues during monocular viewing. Similarly, this stimulus condition was repeated three times, with the right eye or the left eye covered, or with no eye covered.

Horizontal and vertical vergence was calculated as left minus right horizontal eye position. Positive values indicated a rightward, upward, and convergence eye movement direction. All data were low-pass filtered by a median (20 samples) and a Gaussian filter (cut-off frequency at 30 Hz) and further processed as described elsewhere (Rambold et al., 2006). The eye velocity was analysed for each trial. Subsequently vergence velocities were averaged and analysed. Latency and the initial acceleration of the open loop period were quantified according to the algorithm described (Carl and Gellman, 1987). The steady-state velocity was analysed by averaging a 100 ms interval 350 ms after target onset. Statistical differences were significant for $p < 0.05$.

Results

Eye positions

Figure 1A shows representative traces of the vergence (ordinate) and version (abscissa) position, in the binocular viewing condition, for different target directions for one subject (no. 1). During tracking conditions the eye position was variable but generally matched the target trajectory. A vertical prism before one eye (Fig. 1B) or covering one eye (Fig. 1C) impaired tracking in depth, whereas conjugate components were preserved. Data for right and left eye in comparable conditions (covered, uncovered, prism viewing, and non-prism viewing) were not different and the data were pooled and presented as if the right eye was viewing or the prism mounted in front of the right eye.

The effect of fusion: prism versus binocular viewing

Movements in one depth plane (rightward and leftward, isovergence viewing condition)

Figure 1D–F shows averaged eye velocities for the left (dashed) and right eye (black line) for rightward moving targets (black rectangular line) in the binocular, prism, and monocular viewing conditions for one subject (no. 1). The eyes were conjugate and had a latency of on average

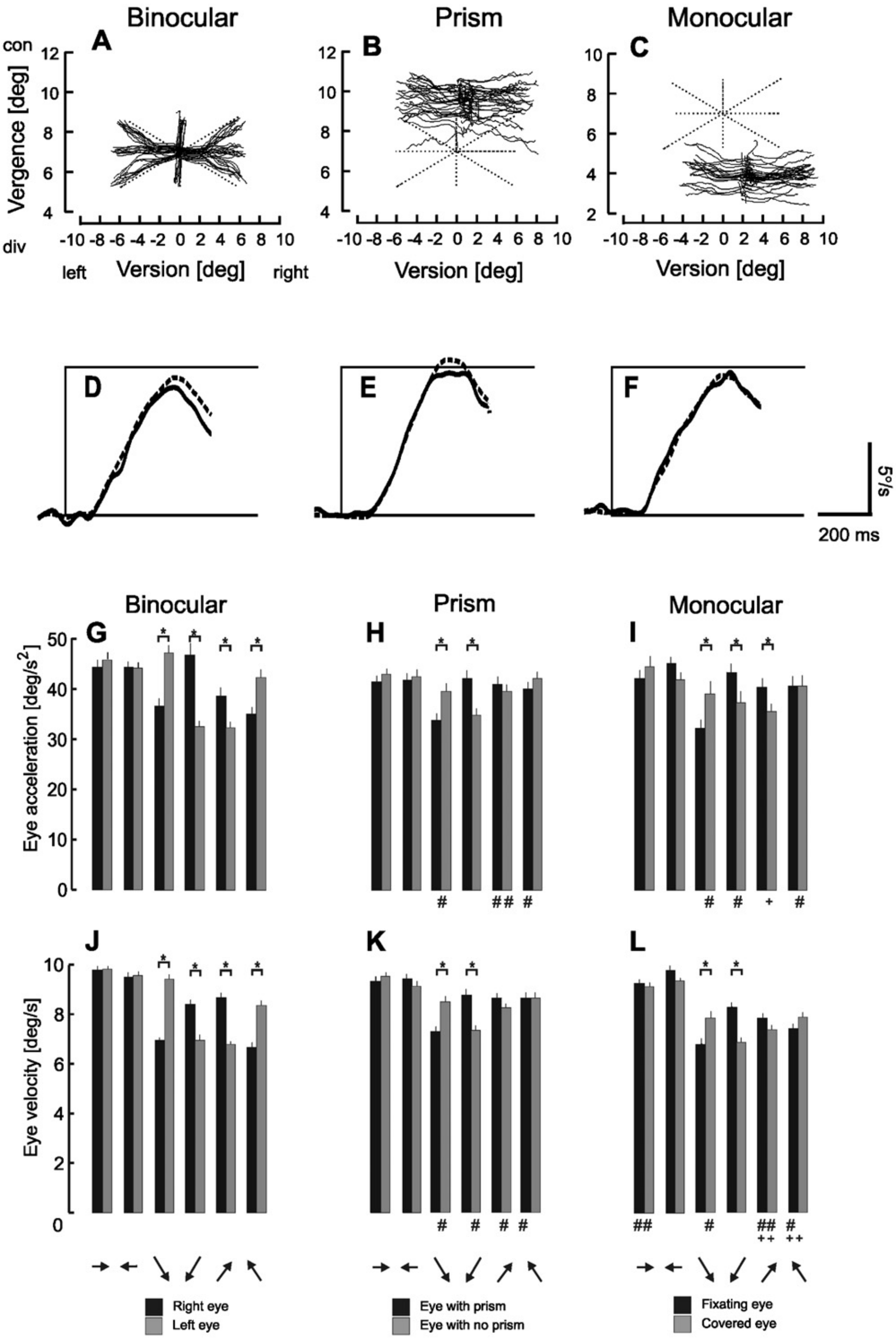

Fig. 1. Version (mean of the two eyes) and vergence (left minus right eye) positions (solid lines) are plotted for one subject (no. 1) in the three different viewing conditions. (A) Binocular viewing; (B) prism; (C) monocular viewing condition. Target trajectories are shown in dotted lines. In the prism (B) and monocular (C) viewing condition there is nearly no depth component and the vergence starting position is shifted (convergence: con; divergence: div). Horizontal right (solid line) and left eye (dashed line) velocities for rightward directions are shown for the binocular viewing condition (D), the prism (E), and the monocular viewing condition (F) in subject no. 1. Additionally, the zero and the target velocities are indicated by horizontal and vertical black lines. The initial eye acceleration (G–I), and steady-state eye velocity (J–L) are shown as group means ± one standard error (error bars) for the different viewing (binocular, prism, and monocular) conditions. The stimulus directions are indicated by arrows below (see also Fig. 2). Statistically significant differences ($p<0.05$) are indicated by different symbols: differences between the two eyes are indicated by a bracket and (∗, above the bars) difference between the monocular or the prism condition and the binocular condition by # (below the bars), and differences between the monocular and the prism condition by (+) (below the bars).

138 ± 32 ms. Generally, there was no difference for individual subjects and the group data for the rightward and leftward stimulus direction with respect to eye latency, initial eye acceleration (open loop), and steady-state eye velocity (closed loop), neither in the binocular, prism, or monocular viewing condition (Fig. 1G–L).

Movements in the depth (vergence condition)

In the prism viewing condition (Fig. 2B) eye velocities were decreased compared to the binocular viewing condition (Fig. 2A). There was no difference in initial acceleration and steady-state velocity between the right and left eye in the prism condition. The steady-state eye velocity, however, was decreased in the prism condition (1.2 ± 0.5°/s) compared to binocular viewing without the prism (1.6 ± 0.3°/s).

Vergence latency was increased (prism: 202 ± 50 ms; binocular: 153 ± 39 ms) and the initial vergence acceleration decreased (prism: 13.1 ± 9.0°/s^2; binocular: 30.0 ± 20.0°/s^2) in the prism condition compared to binocular viewing without prisms. The vergence steady-state velocity was decreased by 61 ± 12% compared to the binocular no-prism condition (Fig. 2D).

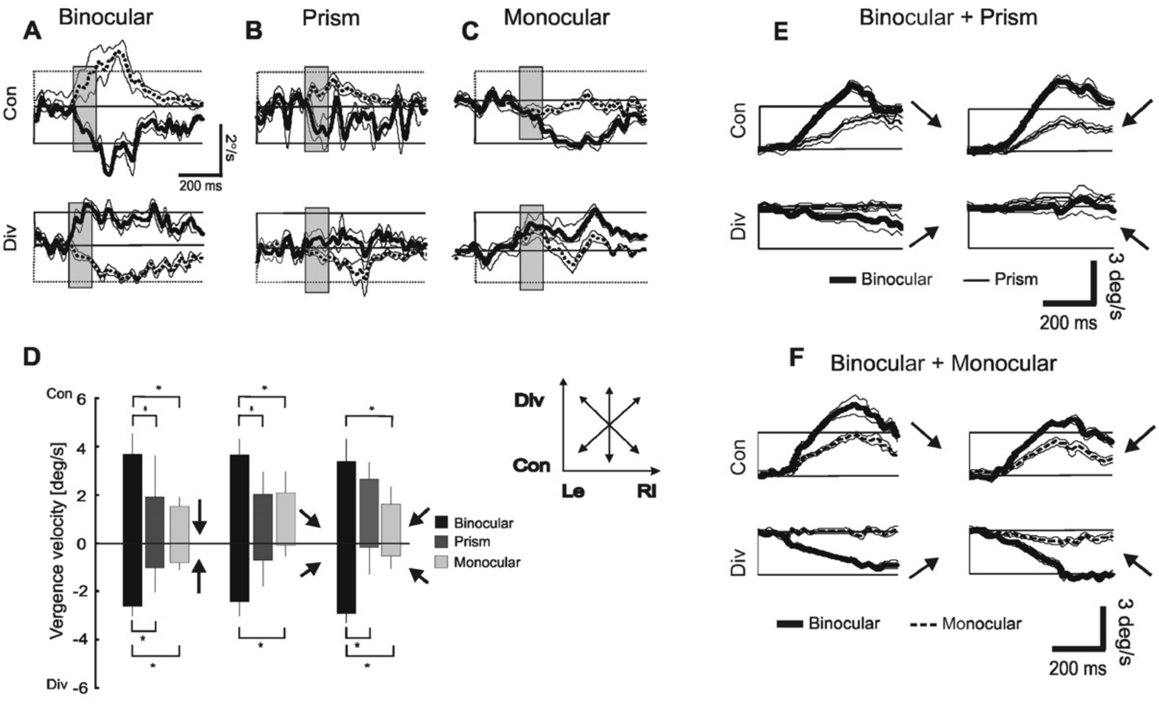

Fig. 2. Horizontal right (RE; solid line) and left eye velocity (LE; dashed line) in the convergence (Con) and divergence (Div) direction are shown for the binocular condition (A), the prism (B), and monocular viewing condition (C). Target velocities are indicated by horizontal black lines for each eye (right eye: solid line; left eye: dashed line). The first 100 ms after eye movement onset (open loop period) are indicated by a grey rectangle. Group means ± one standard deviation (error bars) for vergence steady-state velocity is shown in D. The stimulus directions are indicated by the small arrows next to the bars as defined in the schematic drawing. Significant differences are indicated by asterisks ($p < 0.05$). In the monocular and the prism viewing conditions there is a significant decrease in vergence velocity when compared with the binocular viewing condition (convergence: Con; divergence: Div; rightward: Ri; leftward: Le). Averaged vergence velocity traces (± one standard error, thin lines) are shown for subject no. 1 for the prism (E) and the monocular viewing condition (F) and compared with the binocular condition (thick black trace). Vergence velocity is decreased in the monocular and prism compared to the binocular viewing condition (convergence: Con; divergence: Div).

Movements in depth (oblique condition)

The differences in initial eye acceleration and the steady-state eye velocity between the left and right eye were smaller in the prism and monocular viewing condition as compared to the binocular condition (Fig. 1G–L). The vergence component was nearly absent in the oblique-divergence and reduced in the oblique-convergence condition (Fig. 2E). Vergence latency was increased in the prism viewing condition (prism: 203 ± 43 ms; binocular: 142 ± 41 ms). Vergence acceleration (prism: 11 ± 10 °/s^2; binocular: 28 ± 15°/s^2) and vergence steady-state velocity were decreased (by 68 ± 28%) when prism and binocular conditions were compared (Fig. 2D).

The effect of monocular versus binocular retinal image motion

Movements in depth (vergence condition)

When one eye was occluded divergence and convergence eye velocities were decreased when compared to the binocular viewing condition (Fig. 2A, C). However, a small disconjugate component remained. There was no difference in steady-state velocity of the viewing eye between the monocular (1.2 ± 0.5°/s) and prism condition (1.2 ± 0.5°/s). The initial eye acceleration (8.3 ± 4.0°/s^2) in the monocular condition did not differ from the prism condition (8.3 ± 3.5°/s^2). Vergence latencies (monocular: 182 ± 56 ms; prism: 201 ± 45 ms), initial vergence acceleration (monocular: 13.1 ± 9.3°/s^2; prism: 13.2 ± 9.0°/s^2), and the vergence steady-state velocity were not significantly different in the monocular and prism condition.

Movements in depth (oblique conditions)

In general, there were no differences of the oblique tracking eye movements in the prism and monocular condition with respect to steady-state eye velocity, latency, and initial acceleration, except for small differences in the divergence directions as indicated by (+) in Fig. 1I, L.

Vergence latencies (monocular: 185 ± 98 ms; prism: 203 ± 50 ms), vergence acceleration (monocular: 11.0 ± 10°/s^2; prism: 11.0 ± 10°/s^2), and steady-state vergence velocity (Fig. 2D) were not different in the monocular and prism condition. There was a consistent small vergence component (Fig. 2F) during monocular tracking in the depth. Our data show that the tracking behaviour was not improved by providing the second eye with a motion signal.

Discussion

Our study shows that disabling the fusional mechanism with a vertical prism impairs tracking of a small slowly moving target in 3-D space in the depth component but not in a conjugate pursuit (rightward, leftward) condition. A similar impairment was found in the monocular viewing condition, e.g., in the presence of only one retinal slip signal.

Hering's law of equal innervation states that eye movements result from a summation of conjugate version and vergence eye movements at the motoneuron level. While Hering's law has been shown to be valid for closed loop tracking eye movements (Rashbass and Westheimer, 1961; Miller et al., 1980; Semmlow et al., 1998; Maxwell and Schor, 2004), a disjunctive pursuit system has been proposed for the open loop period based on a non-human primate study (King and Zhou, 1995). In accord with the latter study eye acceleration (open loop phase) of the viewing eye in the monocular viewing condition of our study was not different from the binocular viewing condition. However, eye velocity trajectories in the open loop phase were different during disjunctive and conjunctive tracking, i.e., vergence velocity was severely decreased in the monocular and prism condition during tracking in depth (vergence) compared to the binocular viewing condition. In contrast, eye velocity during conjugate pursuit (isovergence) was not different from the binocular viewing condition.

In contrast to previous studies (Rashbass and Westheimer, 1961; King and Zhou, 1995) we additionally examined eye movements to slowly moving, small, un-fused targets. Pursuit movements to un-fused targets have previously been studied by Erkelens and Collewijn (1985) by sinusoidally moving half images of a larger random dot stereogram in the closed loop phase. In contrast to them, we analysed the open loop phase of eye movements following small un-fused targets with ramp stimuli: (i) to better dissociate Hering's hypothesis from the disjunctive pursuit model, and (ii) to compare the findings of Erkelens and Collewijn (1985) with stimulation conditions with single spot targets in 3-D space in humans.

We used a vertical prism mounted in front of one eye to disable fusion and to decrease the horizontal retinal disparity signal. This view is in accord with several studies showing that vertical disparity decreases horizontal disparity vergence (Mitchell, 1970; Boman and Kertesz, 1983; Yang and Miles, 2003). Our subjects might have seen two images. One of the two apparent stimuli was tracked with the fovea, while the other was tracked parafoveally which might led to a slight decrease in pursuit gain and initial acceleration (Tychsen and Lisberger, 1986; Carl and Gellman, 1987; Pidcoe and Wetzel, 2006). However, initial eye acceleration and velocity during tracking was not different between the two eyes (eye with vs. without prism) during our prism vergence and pursuit (isovergence) conditions. This indicates that parafoveal tracking probably does not account for the decrease in vergence velocity in the prism paradigm.

Alternatively, a change in motor strategy in the prism condition might take place if, instead of the two, only one target is selected and tracked (Erkelens and Collewijn, 1985; Ferrera and Lisberger, 1995). Some evidence against this hypothesis comes from our data in which vergence velocities gradually decreased with increasing power of the vertical prisms (unpublished data). This gradual decline contradicts an all-or-nothing principle as would be expected from a change in motor strategy and argues in favour of a decrease of disparity vergence.

Since the introduction of a prism severely reduced tracking in depth but not in one depth plane (isovergence) our data, obtained with un-fused targets, support Hering's hypothesis. Accordingly, both (disparity) vergence and conjugate pursuit seem to contribute to depth tracking in space. In contrast, according to a disjunctive pursuit model vergence velocity should not have been decreased in the prism condition (retinal slip presented to both retinas).

Our 3-D tracking in the monocular viewing condition shows some residual vergence. This small monocular disjunctive component was delayed compared to the binocular viewing condition and might be caused by different monocular cues: blur driven accommodative vergence (Hung et al., 1983), proximal vergence caused by the proximity of the target, looming, luminance gradient, kinetic depth effect (Erkelens and Regan, 1986; Enright, 1987a, b; McLin and Schor, 1988; Ringach et al., 1996), a learned association of vertical height and depth. However, cues for proximal vergence have little effect on vergence during closed loop accommodation or disparity vergence (Hung et al., 1994). The change in target blur or the change in target luminance which drives accommodative vergence was not large enough to explain the effects on vergence in our setup. There might be a learned association of vertical height and depth due to our target presentation in 3-D space. This factor could not be proved or disproved by our data and is a feasible explanation of our disjunctive vergence eye movements. We conclude that tracking a target in 3-D space can largely be explained by Hering's hypothesis.

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