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The influence of stationary and moving textured backgrounds on smooth-pursuit initiation and steady state pursuit in humans

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Abstract We investigated the effects of stationary and moving textured backgrounds on the initiation and steady state of ocular pursuit using horizontally moving targets. We found that the initial eye acceleration was slightly reduced when a stationary textured background was employed, as compared to experiments with a homogeneous background. When a moving textured background was introduced, the initial eye acceleration was significantly larger when the target and the background moved in opposite directions than when the target and the background moved in the same direction. The use of stationary and moving textured backgrounds resulted in comparable effects on the initial eye acceleration when they were presented either as a large field or as a narrow, horizontal small field, only covering the trajectory of the target. Moreover, small-field stationary backgrounds slightly reduced the eye velocity during steady state pursuit. A small-field background moving in the opposite direction to the target distinctly reduced eye velocity, while a target and a background moving in the same direction sometimes even improved pursuit performance, when compared with a homogeneous background. The influences of small-field textured backgrounds on steady state pursuit were comparable with those of large-field backgrounds in both stationary and moving conditions.

Key words Smooth pursuit · Steady state pursuit · Pursuit initiation · Textured background · Human

Introduction

Human and nonhuman primates have the ability to focus on moving objects with the fovea, by executing voluntary smooth-pursuit eye movements. In natural environments objects frequently move relative to stationary textured backgrounds. Moreover, these backgrounds can

also be in motion. The background motion may either be induced externally, for example, treetops moving in the wind or flowing water, or induced by self-motion when walking or driving.

However, when moving objects are tracked against a stationary background or one moving in the opposite direction, inhibitory interactions between the optokinetic and smooth-pursuit system may occur. During pursuit the whole background drifts across the retina, and this coherent movement represents an optimal stimulus for the optokinetic system. In fact, these two systems do not seem to work independently, as studies on humans (e.g., Merrill and Stark 1963; Yee et al. 1983; Collewijn and Tamminga 1984; Howard and Marton 1992; Niemann et al. 1994; Masson et al. 1995) and on nonhuman primates (Keller and Khan 1986; Ilg et al. 1993; Mohrmann and Thier 1995) indicate. Eye velocity is reduced when objects are tracked over textured backgrounds, compared with the eye velocity with objects tracked over homogeneous backgrounds. When the target and the background move in the same direction, pursuit is even enhanced (Merrill and Stark 1963; Yee et al. 1983; van den Berg and Collewijn 1986; Masson et al. 1995). Recent neurophysiological data of single neurons in the nucleus of the optic tract (NOT) seem to support the idea of such an interaction (Mustari and Fuchs 1990; Ilg and Hoffmann 1991). Ilg and Hoffmann (1991) reported a reduced response in target-sensitive NOT neurons in monkeys when they pursued a target across a structured background, as compared with the neurons' response when a uniform background was in place. These interactions between the target and the background, and the effects on the steady state pursuit performance have so far only been investigated for large-field backgrounds. We were interested in the influence of stationary or moving small-field textured backgrounds on pursuit in order to determine whether the interactions could be attributed to local rather than to global mechanisms. In fact, we found that the effects on the pursuit performance, using small-field backgrounds or large-field backgrounds were comparable.

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Furthermore, we focused on pursuit initiation. The smooth-pursuit system is not influenced by visual feedback during the initial phase because of the delay in the visual system. The eye acceleration is only dependent on the retinal events preceding the onset of eye movement (e.g., Lisberger and Westbrook 1985; Keller and Khan 1986; Tychsen and Lisberger 1986; Carl and Gellman 1987; but see also Kao and Morrow 1994). The influences of stationary textured backgrounds have so far only been investigated in monkeys and have produced contradictory results (Keller and Khan 1986; Kimmig et al. 1992; Mohrmann and Thier 1995). While Keller and Khan (1986) and Kimmig et al. (1992) demonstrated that the initial eye acceleration is distinctly impeded by a structured background, Mohrmann and Thier (1995) found only a small inhibitory effect. Mohrmann and Thier (1995) mainly attributed these differences to the monkey's experience in the paradigm and to a good target visibility. We tested the influence of stationary structured backgrounds on humans and found effects comparable with those of Mohrmann and Thier (1995) when both experience and good target visibility were provided. Additionally, we examined the influence of moving textured backgrounds on smooth-pursuit initiation. Target and background movement in opposite directions resulted in greater accelerations than when the target and background moved in the same direction. The experiments on initial pursuit were also performed using small-field stationary and moving textured backgrounds. They yielded results very similar to those obtained with large-field backgrounds.

In order to facilitate the comparison of smooth-pursuit performance in our experiments with other studies, we repeated some pursuit initiation and steady-state pursuit experiments with homogeneous, large-field, stationary and moving textured backgrounds. The results obtained concur with the studies cited above for smooth pursuit in humans (e.g., Yee et al. 1983; Tychsen and Lisberger 1986).

Materials and methods

Subjects

The experiment employed three subjects ranging from 29–32 years old with normal or corrected-to-normal vision. Two subjects had prior experience of psychophysical oculomotor experiments.

Eye movement recording

The horizontal eye movements of one eye were measured with an infrared eye-tracker (Ober 2). The sampling rate of the 12-bit analog-to-digital converter was 500 Hz.

Experimental setup

The two monitors used to present the stimuli were positioned at right angles to each other. A semisilvered mirror was positioned at a 45° angle between the monitors in order to optically superim-

pose both stimuli. The presentation of the superimposed stimuli was coplanar. The subject viewed the stimuli from a distance of 57 cm. The subject's head was stabilized using chin and forehead supports. The ambient luminance of the laboratory was <0.01 cd/m².

Stimuli

Two types of stimuli were presented simultaneously, a target stimulus and a background stimulus. Both stimuli were generated by computers (two PCs 486DX with VGA graphic cards) and developed using Nyström, a stimulus generation software implemented in the eye movement recording system (Ober 2). The two stimuli were superimposed optically. Thus, two stimuli, the target and the background stimulus, were viewed by both eyes at the same time. The physical parameters of the two stimuli shown on each monitor were as follows.

On one monitor was a target stimulus comparable with the step-ramp stimulus of Rashbass (1961). Preceding each trial, a stationary target, which had to be fixated, was presented at the center of the screen. After a randomly chosen time between 500 and 1000 ms, the target started to move horizontally to the right or left immediately after it had stepped instantaneously away, right or left of the center. Thus four possible target trajectories could be presented: the ramp moved either in the same direction as the step, (1) to the right or (2) to the left (*foveofugal* stimulus); or in the opposite direction to the step, bringing the target toward the center, (3) to the right or (4) to the left (*foveopetal* stimulus). The direction of the steps and ramps was presented randomly. The step of the target was selected in such a way that the target always needed 200 ms to return to the center during a foveopetal target trajectory irrelevant of the target velocity. In these circumstances foveation saccades on the moving target either do not occur at all or only occur after a delay (Gellman and Carl 1991). Thus the initial pursuit is rarely disturbed by saccades. Two different target velocities were tested (2.5°/s and 10°/s). The target moved for 1000 ms. It had a diameter of 0.2° of visual angle with a luminance of 50 cd/m².

The second monitor served to present either a homogeneous or a textured (stationary or moving) background. The moving background was a large-field pattern consisting of black and white stripes (spatial frequency 1 cycle/deg) moving horizontally. The velocity of the pattern was adjusted to the tested target velocities (2.5°/s and 10°/s, respectively). The moving background was continuously in motion during an experimental session. The stationary background consisted of the same stripes as the moving background. Both backgrounds were 30° × 20° (large field) or 30° × 0.5° (small field) of visual angle (see Fig. 1). The luminance of the homogeneous and dark parts of the textured background and of the light parts was 1 cd/m² and 4 cd/m², respectively. In both backgrounds conditions, small field and large field, the target moved across the background.

Experimental procedure

All the trials were viewed binocularly. At the beginning of each session the eye-movement recording system was calibrated by instructing the subject to alternately fixate two dots 25° horizontally apart. The subjects had to initially fixate the target until they detected the onset of movement. Subsequently, the subject had to actively follow the target.

When investigating the influence of small-field backgrounds on smooth-pursuit performance, the step of the target was provided with an additional vertical component of 1.5° of visual angle downward. The target trajectory was placed in the middle of the small-field background (see Fig. 1). This experiment was performed with a target and background velocity of 10°/s. All the subjects had to perform at least 50 trials with each background within 3 days, the one exception being the moving background, where 100 trials were required.

Data analysis

Eye velocity was determined by digital differentiation of eye position over time. To reduce the noise of eye velocity, data was digitally low-pass filtered (0–25 Hz bandwidth).

Each trial was displayed on a computer monitor with a position and velocity trace. Saccades were excluded from eye velocity. The beginning and end of the saccades were determined by a keyboard-controlled cursor. The segment of eye velocity between the beginning and end of a saccade was interpolated linearly. The eye acceleration of an initial pursuit and the eye velocity during the steady state in individual trials were calculated within user-defined time intervals. The manually controlled cursor was positioned at the beginning of the pursuit when the eye velocity started to increase. The mean eye acceleration of an initial pursuit was then calculated over an interval of 100 ms, commencing at the onset of pursuit. Steady state pursuit was characterized by its gain, defined as the mean eye velocity calculated over a 300-ms interval 200–400 ms after pursuit onset divided by target velocity. The timing of the steady state interval remained variable in order to examine catch-up saccade free intervals.

In addition, a control analysis was carried out to determine the pursuit acceleration according to the method used by Carl and Gellman (1987). At first a regression line was calculated over a 140-ms interval, beginning 100 ms before the onset of target movement and ending 40 ms later. When the eye velocity of pursuit deviated from this line by 3 SDs, a second regression line was fitted to the next 100 ms of eye velocity starting from this point. Pursuit eye acceleration was given as the slope of this velocity regression line. However, values obtained using this method deviated less than 10% from the values obtained in the original data analysis. Moreover, in some experiments we averaged eye velocity for the same stimulus conditions. Trials were aligned to the onset of target motion and averaged. The mean eye acceleration was also determined according to the method used by Carl and Gellman (1987). Again, the averaged records yielded results comparable with those obtained by the mean of the eye accelerations obtained in the individual trials.

Results

Steady state pursuit

Figure 1 shows the ratio of eye velocity and target velocity (gain) of three subjects pursuing a target over different backgrounds. The data of target movement to the left

and right were pooled. A Kruskal-Wallis ANOVA showed that small-field stationary and moving backgrounds had significant effects on pursuit ($P \leq 0.0001$, all subjects). The small-field, stationary structured background had an inhibitory effect on the steady state pursuit. This is reflected in a reduction in gain of about 6%, compared with the pursuit over a homogeneous background (subject *T.N.* with $P \leq 0.05$, Dunn's test). Moreover, the smooth-pursuit performance depends on the direction of the pattern movement. When the target and pattern move in the same direction (synergistic stimulation), the tracking is comparable with or slightly better than tracking over a homogeneous background (significant improvement in gain for subject *J.L.* with $P \leq 0.05$, Dunn's test). When the target and pattern move in opposite directions (antagonistic stimulation), the tracking is distinctly impaired, when compared with the tracking where a homogeneous background is present (subjects *T.N.* and *V.S.* with $P \leq 0.05$, Dunn's test). Thus, the effect of the moving pattern on pursuit gain is more pronounced in the antagonistic than in the synergistic stimulation.

As a control, we also investigated the influence of large-field stationary and moving backgrounds on the steady state pursuit (Fig. 1). The effects of large-field backgrounds on steady state pursuit were similar to those

Fig. 1 Gain (ratio of eye and target velocity) of steady state pursuit with different backgrounds. Target velocity was $10^\circ/\text{s}$. Individual (*J.L.*, *T.N.*, *V.S.*; gray bars) and accumulated (Σ ; black bars) data of all the subjects are shown. Each bar represents the mean gain in a 300-ms interval of steady state pursuit averaged from at least 40 identical trials. The background conditions are indicated below each bar (*HB* homogeneous, *SB* stationary textured, *MB* moving background). Target movement *with* or *against* the background movement in the *MB* condition is marked under the corresponding bars as *syn* (synergistic stimulation) and *ant* (antagonistic stimulation), respectively. The diagrams shown on the left of the corresponding graphs indicate the spatial extent and relationship between the stationary and moving background and the trajectory of the target. Note that in the case of a small-field background, the target also moved across the background

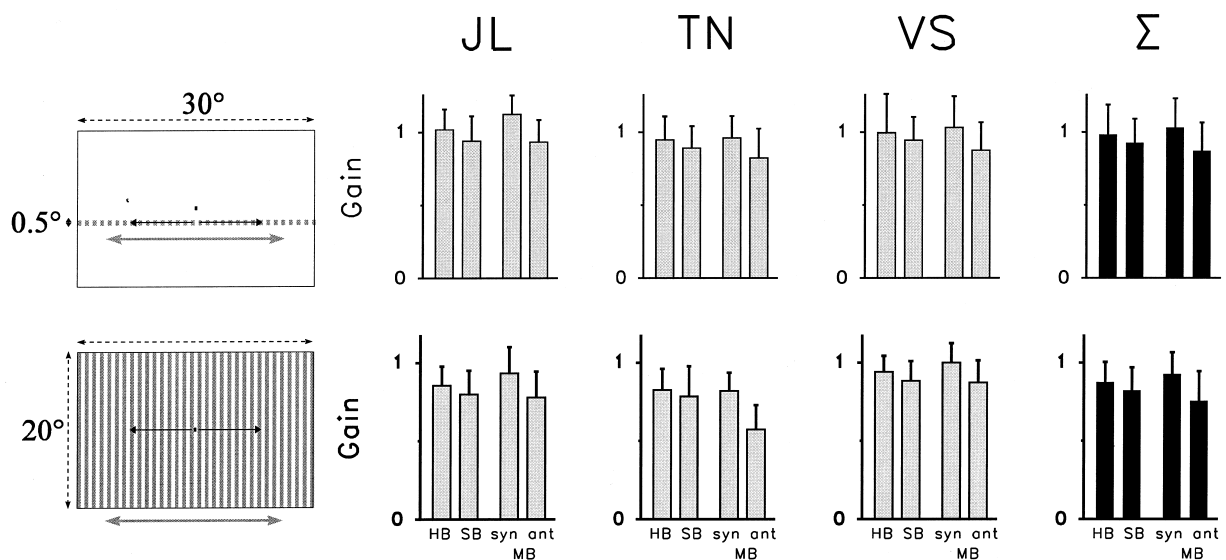


Table 1 Relative values of gain reduction (negative values) or improvement (positive values) of steady-state pursuit with different backgrounds compared with homogeneous background (*HB*)

Background condition	Small-field background (%)	Large-field background (%)
HB → SB	-6.16±1.05	-6.31±1.17
HB → MB syn	+5.09±3.79	+5.94±4.71
HB → MB ant	-11.09±2.04	-14.8±9.41

homogeneous, *SB* stationary textured, *MB* moving background, *syn* synergistic stimulation, *ant* antagonistic stimulation). Mean±SD from three subjects

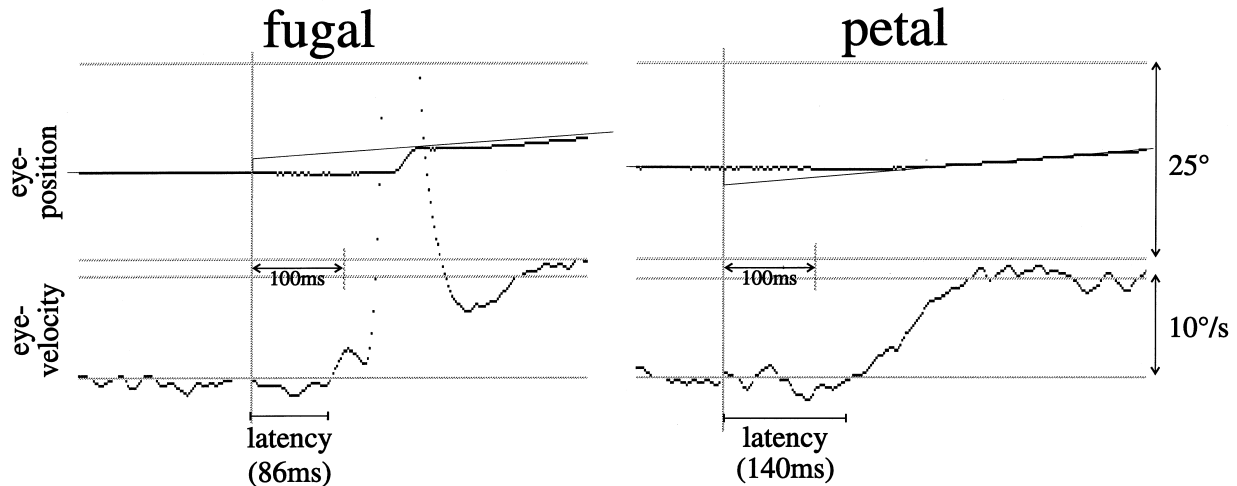


Fig. 2 Representative initial pursuit with a foveofugal (*fugal*) and foveopetal (*petal*) step-ramp target paradigm. The upper trace shows the eye and target position, the lower trace the eye velocity. The target moved to the right with a velocity of 10°/s. The onset of the target movement is marked by a vertical dashed line

of small-field ones (Table 1; Kruskal-Wallis ANOVA, $P \leq 0.0001$, all subjects; *stationary background*: significant reduction in gain with $P \leq 0.05$, subject *V.S.*; *synergistic movement of the background*: significant improvement with $P \leq 0.05$, subject *V.S.*; *antagonistic movement of the background*: significant reduction with $P \leq 0.05$, all subjects; compared with the tracking over a homogeneous background, Dunn's test). The results obtained with large-field backgrounds concur with other studies investigating the influence of stationary structured and optokinetic backgrounds on steady state pursuit in humans (Merrill and Stark 1963; Yee et al. 1983; Collewijn and Tamminga 1984; van den Berg and Collewijn 1986; Howard and Marton 1992; Niemann et al. 1994; Masson et al. 1995).

Initial pursuit

A representative example of initial pursuit in a foveofugal and foveopetal target paradigm is shown in Fig. 2. After a short latency the eye started to move and accelerate up to the velocity of the target. A saccade intruded upon the pursuit initiation with the foveofugal target movement. Saccades occurred frequently during the initial phase with the foveofugal and rarely with the foveopetal target movement. This behavior was also observed

in nonhuman primates (Keller and Khan 1986). Foveopetal stimulation leads to distinctly longer latencies than foveofugal stimulation (approx. 50 ms).

Figure 3 shows the eye acceleration of the initial pursuit with homogeneous and stationary structured backgrounds. Accelerations to the right and left of foveofugal and foveopetal stimulation have been pooled. The following observations were made:

1. The acceleration increases with the faster target velocity.
2. When compared with the foveofugal stimulation, foveopetal stimulation results in distinctly higher accelerations.
3. A stationary structured background only seems to have a slightly inhibitory influence on the initial phase in the foveopetal condition. The effect was significant on subjects *V.S.* and *J.L.* with a target velocity of 10°/s ($P \leq 0.005$, *U*-test). Eye acceleration was reduced by approximately 10%.

The experiments with foveofugal and foveopetal stimulation with a homogeneous background were again performed as a control. The results concur with other studies investigating the initial pursuit in humans (Tychsen and Lisberger 1986; Carl and Gellman 1987; Kao and Morrow 1994).

Figure 4 shows the eye accelerations in case of target movements with a large-field moving background. When a moving background is used, four different stimulus configurations can be distinguished: a *foveofugal* movement of the target moving in the same (Fig. 4A) or opposite (Fig. 4B) direction and a *foveopetal* movement mov-

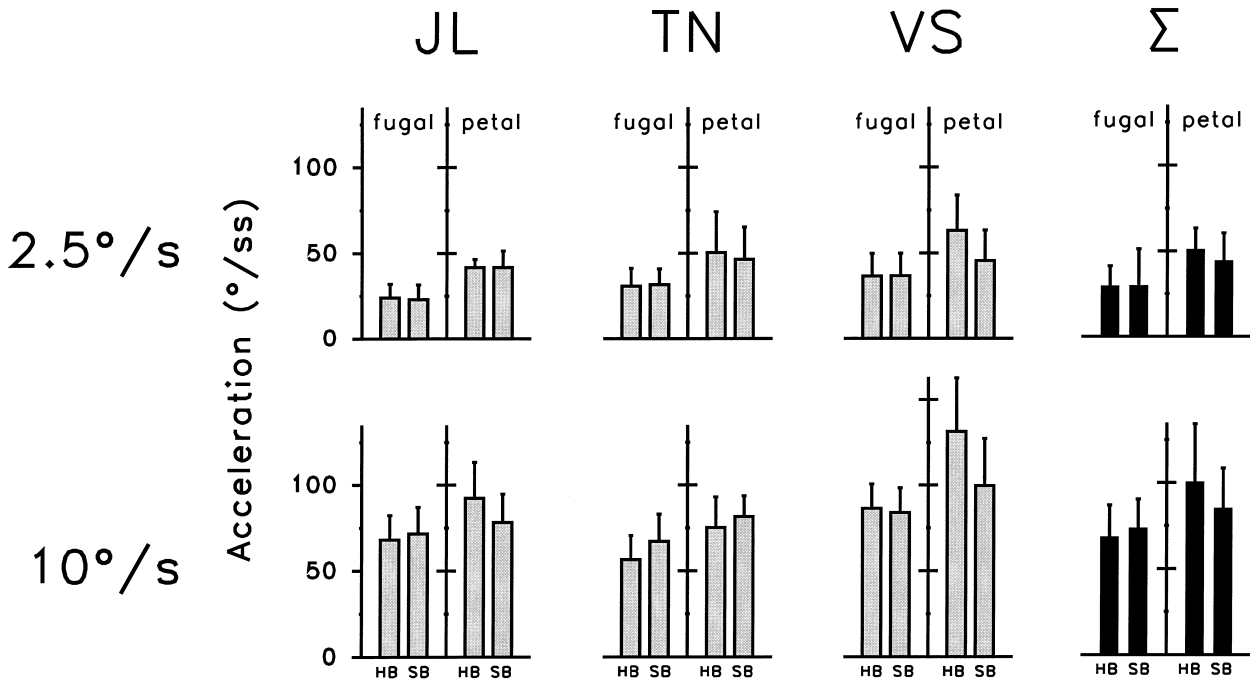
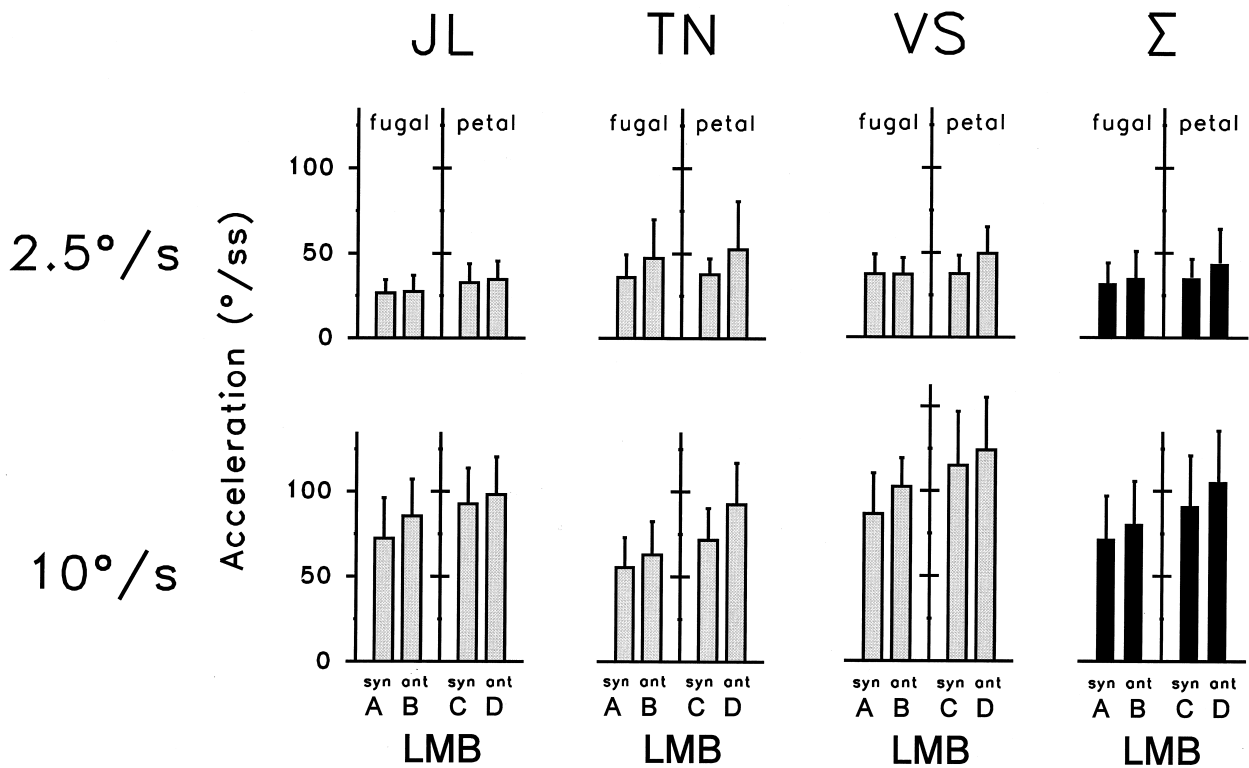


Fig. 3 Eye acceleration of the initial pursuit with different backgrounds, target velocities, and target paradigms. Individual (*JL*, *TN*, *VS*; gray bars) and the accumulated (Σ ; black bars) data of all subjects are shown. Each bar represents the mean eye acceleration in the first 100 ms of pursuit averaged from at least 20 identical trials. Accelerations with foveofugal (*fugal*) and foveopetal (*petal*) are shown *above*, with homogeneous (*HB*) and stationary textured background (*SB*) *below the corresponding bars*. The velocity of the target is shown on the *left* of the corresponding graphs (2.5°/s, 10°/s)

ing in the same (Fig. 4C) or opposite (Fig. 4D) direction of the large-field moving pattern.

An asymmetry in acceleration, which is dependent on the foveofugal and -petal stimulation, was also observed

Fig. 4 Eye acceleration during initial pursuit with a large-field moving background. Acceleration when the target moved *with* (*A*, *C* synergistic stimulation) or *against* (*B*, *D* antagonistic stimulation) the movement of the large-field background (*LMB*) are shown *below the corresponding bars*. For further details see Fig. 3



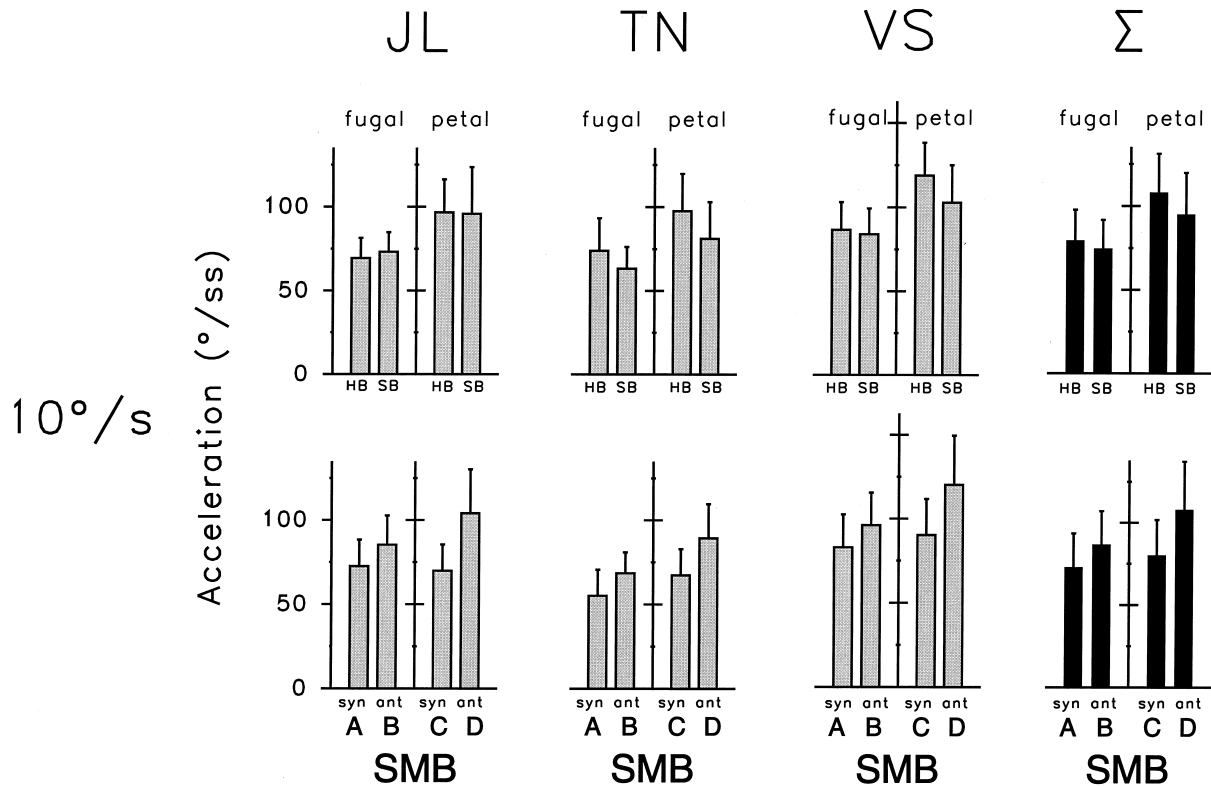


Fig. 5 Eye acceleration during initial pursuit with stationary and moving small-field backgrounds. *Upper row*: homogeneous and stationary textured backgrounds; *lower row*: moving textured background. Individual (*JL, TN, VS*; gray bars) and accumulated (Σ ; black bars) data of all the subjects are shown. (*SMB* small-field moving background) For further details see Figs. 3 and 4

with the large-field moving pattern. However, the initial acceleration was more pronounced when the target and background moved antagonistically (Fig. 4B, D) compared with the synergistic movement direction (Fig. 4A, C; all the data were significant with $P \leq 0.01$, *U*-test, except the foveofugal condition at a target velocity of $2.5^\circ/\text{s}$).

Two reasons might account for this result:

1. Recent investigations concerning the initial pursuit in humans and nonhuman primates have revealed that eye acceleration depends on the retinal image motion preceding the onset of eye movements ("open-loop" mode; e.g., Keller and Khan 1986; Tychsen and Lisberger 1986; Carl and Gellman 1987). Thus, the motion of the background could also be integrated and would be reflected in the acceleration. The acceleration may not only be modulated by the absolute velocity of the target in relation to the retina, but also by relative movements between the target and background.

2. During optokinetic stimulation an optokinetic nystagmus (OKN) should not occur when a target for fixation is simultaneously presented (e.g., Barnes and Crombie 1985). However, in the case of the large-field pattern moving at $10^\circ/\text{s}$, the eyes drifted during the fixation phase with a mean velocity of $2.05 \pm 2.54^\circ/\text{s}$ SD

($n = 213$) compared with $-0.103 \pm 0.67^\circ/\text{s}$ SD ($n = 66$) when a homogeneous background was presented (300-ms interval; see also Murphy et al. 1975). The drift would result in smaller retinal velocities of the target when it moves in the direction of the pattern, and higher retinal velocities when the target moves in the opposite direction. As a consequence, different accelerations might occur because different retinal velocities of a target result in different amounts of acceleration (see Fig. 3; Tychsen and Lisberger 1986).

Control experiment

A control experiment was carried out in order to test which of the two mechanisms described above could be involved. We ensured that the fixation was also stable when a moving background was presented. On the one hand, we reduced the size of the background and, on the other hand, we separated the fixation target from the background (see Materials and methods; Fig. 1). The necessary additional vertical step of the target in this configuration only has a negligible effect on the acceleration (see Tychsen and Lisberger 1986).

Again, we analyzed the eye velocity during the fixation phase with a homogeneous and a moving background. The eyes had a mean velocity of $-0.03 \pm 0.73^\circ/\text{s}$ SD ($n = 140$) with a homogeneous and $0.162 \pm 0.58^\circ/\text{s}$ SD ($n = 142$) with a moving background (300-ms interval). Thus, when the moving background was presented practically, no drift occurred during the fixation phase.

However, an antagonistic movement of the target and background still resulted in significantly higher accelerations than in the case of a synergistic movement

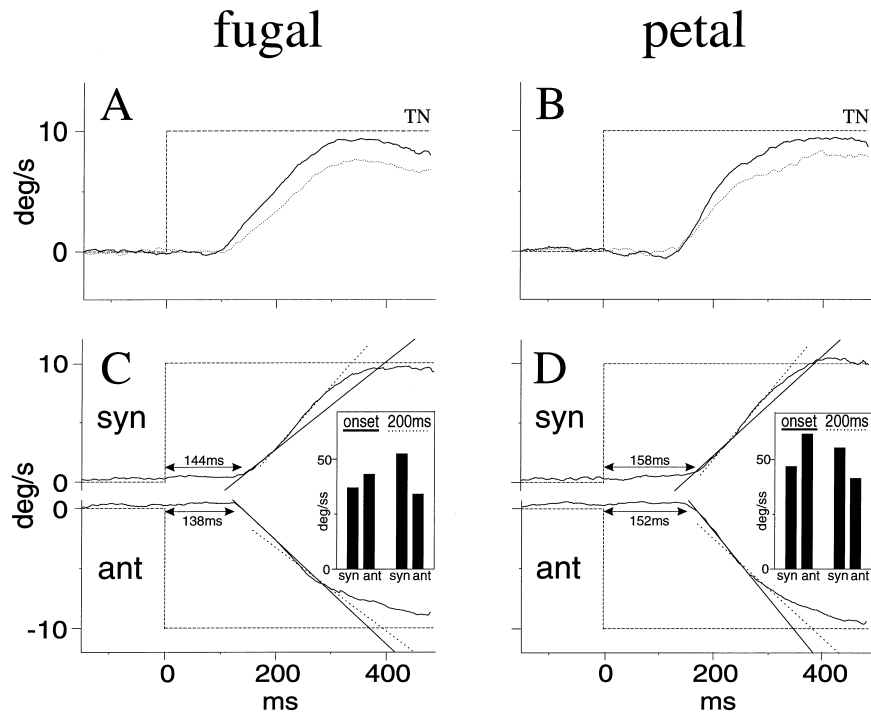


Fig. 6 Averaged initial pursuit velocities with homogeneous and small-field backgrounds and target paradigms. Target velocity was $10^\circ/\text{s}$ and the onset of target movement was at 0 ms (*thin dashed line*). **A, B** The averaged initial pursuit velocity of the subject *T.N.* with a foveofugal (*fugal*) and foveopetal (*petal*) step-ramp target paradigm. The *solid traces* represent the initial pursuit velocity with a homogeneous background (foveofugal $n = 21$, foveopetal $n = 26$), the *dotted traces* with a stationary structured background (foveofugal $n = 26$, foveopetal $n = 19$). **C, D** Averaged initial pursuit velocities and latencies of pursuit onset of all the subjects with a foveofugal (*fugal*) and foveopetal (*petal*) step-ramp target paradigm. The *solid traces* with a negative slope at the *bottom* represent the initial pursuit velocity in the antagonistic condition (*ant*; foveofugal $n = 110$, foveopetal $n = 113$), the *solid traces* with a positive slope at the *top* indicate the initial pursuit velocity in the synergistic condition (*syn*; foveofugal $n = 98$, foveopetal $n = 91$). *Solid regression lines* are plotted through the first 100 ms of pursuit beginning from the pursuit onset; *dotted regression lines* are plotted through 100 ms of pursuit beginning at 200 ms after the onset of target movement. The *bars in the insets* in **C** and **D** compare eye accelerations derived from the slopes of each regression line (*syn* synergistic, *ant* antagonistic stimulation, *onset* regression through 100 ms beginning from onset of pursuit, *200ms* regression through 100 ms beginning at 200 ms after onset of target movement)

($P \leq 0.005$, *U*-test; all subjects and target movement conditions; Fig. 5). Compared with the homogeneous background, a small-field stationary textured background decreased the acceleration slightly ($P \leq 0.005$, *U*-test; subject *T.N.* and *V.S.* in the foveopetal condition).

The influence of small-field stationary and moving structured backgrounds is also exemplified in the trial means in Fig. 6. Figure 6A, B shows the averaged desaccaded eye velocities of one subject as he tracked a moving target over a homogeneous and a small-field, stationary structured background in the foveofugal and foveopetal stimulus condition. The two curves in both conditions start to diverge at the beginning of the pursuit be-

cause of the inhibitory influence of the stationary structured background during the initial and steady state pursuit. Figure 6C, D shows the averaged desaccaded eye velocities of all the subjects when they tracked a moving target over a small-field moving background. The solid regression lines of the first 100 ms of pursuit initiation reveal, in both the foveofugal and foveopetal stimulus condition, that the slope of the line and consequently the degree of acceleration is more pronounced when the target and background move in opposite directions (antagonistic movement). However, approximately 200 ms after the onset of target movement, the velocity of the initial pursuit changes; the corresponding dotted regression lines of the ensuing 100 ms of pursuit show that the acceleration is more pronounced when the target and background move in the same direction (synergistic movement). Eye acceleration derived from the slope of each regression line is also documented in the inserts in Fig. 6C, D. This finding will be discussed in the context of visual feedback onset.

Discussion

The main results documented here indicate that steady state pursuit is affected by small-field stationary and moving textured backgrounds. The initial pursuit is only marginally influenced by stationary and to a greater extent by moving textured backgrounds.

Our observation, namely that a slightly smaller gain is obtained during smooth-pursuit performance over stationary structured backgrounds, is similar to that found by other studies in humans and nonhuman primates (e.g., Collewijn and Tamminga 1984; Keller and Khan 1986; Howard and Marton 1992; Mohrmann and Thier 1995).

Furthermore, our investigation into the influence of a moving large-field pattern obtained results comparable with those found in literature (Merrill and Stark 1963; Yee et al. 1983; van den Berg and Collewijn 1986; Niemann et al. 1994; Masson et al. 1995). Thus, large-field stationary or moving patterns reveal an antagonistic or synergistic interaction between smooth-pursuit and optokinetic systems. However, we were able to show that small-field stationary or moving textured backgrounds covering the trajectory of the target influence the smooth-pursuit performance in a similar fashion. Thus, the local interactions between the target and background seem to be of greater significance than the global interactions.

Recent neurophysiological data of single neurons in the NOT of monkeys appear to support the idea of such an interaction (Mustari and Fuchs 1990; Ilg and Hoffmann 1991). During pursuit across a structured background, two types of neurons were described in NOT, one coding target slip and one coding background slip. Target-sensitive neurons in NOT showed reduced responses to the target during a smooth-pursuit over a textured background, compared with the responses during a pursuit across a uniform background. Cortical areas such as the middle temporal area (MT) and the medial superior temporal area (MST), projecting to NOT and pontine nuclei, might represent a site where the target and background interactions during steady state pursuit occur. For example, MST cells in monkeys discharge in relation to smooth-pursuit eye movements as well as to image motion during fixation (Newsome et al. 1988): MT and MST are parts of the parieto-occipito-pontocerebellar circuit for smooth pursuit in alert monkeys (e.g., Komatsu and Wurtz 1988). Moreover, MT cells in awake monkeys show reduced responses when, in addition to the preferred direction, a nonpreferred direction is presented (e.g., Snowden et al. 1991).

The initial acceleration phase of smooth pursuit was observed to be dependent on the target velocity and on the foveofugal or foveopetal target trajectory. These results are comparable with those obtained by Tychsen and Lisberger (1986) and Carl and Gellman (1987). The influence of a stationary structured background on the initial acceleration of pursuit was only tested on nonhuman primates. Contradictory results were found by Keller and Khan (1986), Kimmig et al. (1992), and Mohrmann and Thier (1995). While Keller and Khan (1986) and Kimmig et al. (1992) found distinct reductions of up to 50% in the acceleration with a textured background, Mohrmann and Thier (1995) only found marginal reductions (only about 7% smaller accelerations). According to Mohrmann and Thier (1995), the differences in the size of the reduction are mainly due to the monkey's experience in the paradigm and the spatial frequency of the target and background. Large reductions in acceleration were only observed when the monkey was inexperienced and when the target and background had similar spatial frequencies. When good target visibility is provided, a textured background might have little effect on the accel-

eration. Our results appear to support the observations made by Mohrmann and Thier (1995), as we also observed only a slight reduction of about 10% in eye acceleration with stationary textured backgrounds. All of the tested subjects were familiar with the stimulus configuration, and two of them even had prior experience of oculomotor experiments. Moreover, target visibility was good because of a high contrast between the target and background ($K = 0.85$). Masson et al. (1995) investigated the initial eye *velocity* of pursuit when tracking a target over a stationary textured background. They reported a decrease in the initial eye velocity of up to 12% compared with the initial eye velocity when tracking a target over a dark background. This correlates quite well with the reduction in eye *acceleration* in humans we measured and those found by Mohrmann and Thier (1995) in monkeys.

However, the initial eye acceleration also depends on a moving background. If the target and background move in opposite directions, this results in higher accelerations than if they move synergistically. Thus, to accelerate the eye up to the target velocity, the smooth-pursuit system does not only analyze the motion of the target, but also the motion of the background. Apart from the retinal velocities of the target, movements of the background are important for the initial pursuit. Our results apparently contradict the results of Masson et al. (1995) who found an *increased* initial pursuit when the target and background moved in the same direction (synergistic movement). However, Masson et al. (1995) measured initial eye *velocities* while we were interested in the initial eye *acceleration*. Their evaluation (based on eye position rather than eye velocity) perhaps accounts for why they discovered latencies of ocular pursuit that are well above those obtained in other studies (approx. 180 ms latency compared with 100–135 ms recorded by Tychsen and Lisberger, 1986, and Carl and Gellman, 1987). In contrast, our latencies of ocular pursuit agree with those documented by Tychsen and Lisberger (1986) and Carl and Gellman (1987); (see our Figs. 2, 6). The first 100 ms of pursuit reveal that pursuit acceleration is greater with an antagonistic target and background movement. However, approximately 200 ms after the onset of target movement, the course of eye velocity changes: the acceleration increases when the target and background move in the same direction and decreases when the target and background move in opposite directions (Fig. 6, dotted regression lines compared with solid regression lines). Moreover, the acceleration during this temporal interval can even be reversed by antagonistic and synergistic stimulation, compared with the acceleration when measuring the first 100 ms of pursuit (see also inserts in Fig. 6C, D). The results of Masson et al. (1995) correspond to our result for the later temporal interval. They started their analysis approximately 180 ms after the onset of target movement. We suppose that the early temporal interval of the initial acceleration reflects the open-loop behavior of initial pursuit over moving backgrounds. In contrast, Masson et al. (1995) measured the

initial pursuit when the first corrective feedback of the visual system comes on (see also Tychsen and Lisberger 1986).

Our control experiments with the small-field stationary and moving backgrounds reveal that the initial pursuit is also influenced by local rather than global interactions between the target and background. The experiments on initial pursuit with large-field moving backgrounds could also be interpreted with different retinal target velocities due to the drift of the eye. But, as the control experiment showed, the integration of background motion rather than different retinal target velocities is important for controlling initial pursuit.

Ferrera and Lisberger (1995) investigated the initial pursuit in monkeys with a moving target when a second small moving target was simultaneously presented as a distractor. They interpreted the results in terms of target selection. As we also used a second moving stimulus (background stimulus) together with the moving target in our experiments, our results may also be interpreted in the context of target selection rather than background interaction. We disagree with such an interpretation for the following reasons. First of all, the monkeys in the experiments carried out by Ferrera and Lisberger (1995) always had to choose a "goal target" from two moving targets just before the onset of target movement. In contrast, our subjects always knew in advance which stimulus they had to pursue and which stimulus would serve as a background. Thus, target selection could readily be made beforehand throughout the experiments. Secondly, the results of Ferrera and Lisberger (1995) are quite different to ours. Whereas Ferrera and Lisberger (1995) found distinct differences between the pursuit latencies dependent on the movement of the distractor (approx. 70 ms), the pursuit latencies in our experiments, although not quantitatively investigated, showed no distinct differences in the antagonistic and synergistic stimulus condition (see Fig. 6C, D). Moreover, contrary to our experiments, Ferrera and Lisberger (1995) found no significant effect on the acceleration profile. Altogether, this suggests that our results on initial pursuit during simultaneous presentation of moving backgrounds can be accounted for by background interaction rather than by target selection.

Electrophysiological recordings of MT neurons in anesthetized monkeys revealed modulatory influences of textured backgrounds outside the classical receptive field (CRF) on the response of these neurons (Allman et al. 1985). The CRF of direction-selective neurons were stimulated in the preferred direction. Additionally, a moving background outside the CRF in the preferred direction of this neuron was capable of inhibiting the response completely, while a background movement in the opposite direction could enhance the neuronal response rate. Similar observations were made by Tanaka et al. (1986) in neurons in MT and MST. As MT and MST are part of the parieto-occipito-pontocerebellar circuit for smooth pursuit in monkeys (e.g., Lisberger et al. 1987; Komatsu and Wurtz 1988; Newsome et al. 1988; Keller

and Heinen 1991), these findings might represent a neuronal substrate of our observed behavior of eye acceleration with moving backgrounds. As the electrophysiological experiments of Allman et al. (1985) were done with anesthetized monkeys, the animals' eyes were immobile. The motion information responsible for the eye acceleration is collected and analyzed approximately 100 ms before the onset of eye movement during the fixation phase, in which the eyes are also immobile (Carl and Gellman 1987). During this period, the antagonistic movement of the target and background could enhance the neuronal response rate, resulting in higher eye accelerations. Synergistic stimulation would result in the reverse effect.

The initial acceleration bias depending on the foveofugal and foveopetal paradigm may be caused by the neuronal behavior of NOT neurons being involved in pursuit. NOT neurons in anesthetized and awake monkeys show an increase in response during ipsiversive object motion (Hoffmann and Distler 1989; Mustari and Fuchs 1990; Ilg and Hoffmann 1991). Ipsiversive movements toward the fovea in the contralateral visual field or across the nasal retina evoke stronger responses than movements away from the fovea in the ipsilateral visual field or across the temporal retina. As the results of Mustari and Fuchs (1990) and Ilg and Hoffmann (1991) indicate a functional connection between the smooth-pursuit and optokinetic system, the asymmetry in eye acceleration due to foveofugal or foveopetal stimulation might reflect features of receptive fields of neurons in NOT.

Stationary textured backgrounds only have marginal effects, while moving backgrounds have noticeable effects on steady state and initial pursuit. In natural circumstances the object and background usually occur at different depths. In psychophysical experiments investigating the smooth-pursuit gain with moving objects at a depth other than the textured background, no or only a negligible influence of the background on the smooth-pursuit performance has been found (Howard and Marton 1992). Thus, in naturally occurring situations a stationary or moving background probably has only a negligible influence on the smooth-pursuit system.

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References

- Allmann J, Miezin F, McGuiness E (1985) Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons. *Annu Rev Neurosci* 8:407-430
- Barnes GR, Crombie JW (1985) The interaction of conflicting retinal motion stimuli in oculomotor control. *Exp Brain Res* 59: 548-558
- Berg AV van den, Collewijn H (1986) Human smooth pursuit: effects of stimulus extent and spatial and temporal constraints of the pursuit trajectory. *Vision Res* 26:1209-1222

- Carl JR, Gellmann RS (1987) Human smooth pursuit: stimulus-dependent responses. *J Neurophysiol* 57:1446–1463
- Collewijn H, Tamminga EP (1984) Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *J Physiol (Lond)* 351:217–250
- Ferrera VP, Lisberger SG (1995) Attention and target selection for smooth pursuit eye movements. *J Neurosci* 15:7472–7484
- Gellman RS, Carl JR (1991) Motion processing for saccadic eye movements in humans. *Exp Brain Res* 84:660–667
- Hoffmann K-P, Distler C (1989) Quantitative analysis of visual receptive fields of neurons in nucleus of the optic tract and dorsal terminal nucleus of the accessory optic tract in macaque monkey. *J Neurophysiol* 62:416–428
- Howard IP, Marton C (1992) Visual pursuit over textured backgrounds in different depth planes. *Exp Brain Res* 90:625–629
- Ilg UJ, Hoffmann K-P (1991) Responses on monkey nucleus of the optic tract neurons during pursuit and fixation. *Neurosci Res* 12:101–110
- Ilg UJ, Bremmer F, Hoffmann K-P (1993) Optokinetic and pursuit system: a case report. *Behav Brain Res* 57:21–29
- Kao GW, Morrow MJ (1994) The relationship of anticipatory smooth eye movement to smooth pursuit initiation. *Vision Res* 34:3027–3036
- Keller EL, Heinen SJ (1991) Generation of smooth-pursuit eye movements: neural mechanisms and pathways. *Neurosci Res* 11:79–107
- Keller EL, Khan NS (1986) Smooth-pursuit initiation in the presence of a textured background in monkey. *Vision Res* 26:943–955
- Kimmig HG, Miles FA, Schwarz U (1992) Effects of stationary textured backgrounds on the initiation of pursuit eye movements in monkeys. *J Neurophysiol* 68:2147–2164
- Komatsu H, Wurtz RH (1988) Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *J Neurophysiol* 60:621–644
- Lisberger SG, Westbrook LE (1985) Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *J Neurosci* 5:1662–1673
- Lisberger SG, Morris EJ, Tychsen L (1987) Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annu Rev Neurosci* 10:97–129
- Masson G, Proteau L, Mestre DR (1995) Effects of stationary and moving textured backgrounds on the visuo-oculo-manual tracking in humans. *Vision Res* 35:837–852
- Merrill EG, Stark L (1963) Smooth phase of optokinetic nystagmus in man. *Q Prog Rep Res Lab Electr MIT* 71:286–291
- Mohrmann H, Thier P (1995) The influence of structured visual backgrounds on smooth-pursuit initiation, steady-state pursuit and smooth-pursuit termination. *Biol Cybern* 73:83–93
- Murphy BJ, Kowler E, Steinmann RM (1975) Slow oculomotor control in the presence of moving backgrounds. *Vision Res* 15:1263–1268
- Mustari MJ, Fuchs AF (1990) Discharge patterns of neurons in the pretectal nucleus of the optic tract (NOT) in the behaving primate. *J Neurophysiol* 64:77–90
- Newsome WT, Wurtz RH, Komatsu H (1988) Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. *J Neurophysiol* 60:604–620
- Niemann T, Ilg UJ, Hoffmann K-P (1994) Eye movements elicited by transparent stimuli. *Exp Brain Res* 98:314–322
- Rashbass C (1961) The relationship between saccadic and smooth tracking eye movements. *J Physiol (Lond)* 159:326–338
- Snowden RJ, Treue S, Erickson RG, Andersen RA (1991) The response of area MT and VI neurons to transparent motion. *J Neurosci* 11:2768–2785
- Tanaka K, Hikosaka K, Saito H, Yukie M, Fukada Y, Iwai E (1986) Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *J Neurosci* 6:134–144
- Tychsen L, Lisberger SG (1986) Visual motion processing for the initiation of smooth-pursuit eye movements in humans. *J Neurophysiol* 56:953–968
- Yee RD, Daniels SA, Jones OW, Baloh RW, Honrubia V (1983) Effects of optokinetic background on pursuit eye movements. *Invest Ophthalmol Vis Sci* 24:1115–1122