

THE smooth pursuit system is traditionally employed using a single small target moving on a homogeneous background. It still is not fully understood, however, how accurate tracking is sustained in the presence of a structured background, which will activate global motion processing in the opposite direction as a consequence of the ongoing eye movement. To further study this interaction, we used brief shifts of a textured background injected at various times during the initiation of smooth pursuit. While shifts opposite to the target direction did not alter smooth pursuit performance, those in the same direction resulted in a marked transient perturbation of the pursuit. These results suggest a simple yet limited mechanism that adjusts the sensitivity of global motion processing. *NeuroReport* 10:2477–2480 © 1999 Lippincott Williams & Wilkins.

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Asymmetry in visual motion processing

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Introduction

Smooth pursuit eye movements (SP) are linked to the occurrence of retinal image slip, and most subjects are unable to generate them voluntarily in the absence of motion cues [1]. Therefore, SP has been used extensively as a convenient probe for local visual motion processing as well as visuomotor transformation. State of the art models of SP focus on the extraction of retinal image slip generated by the moving target [2] (for a review see [3]). However, the contribution of the visual surroundings, which induces global motion processing in the opposite direction during tracking, is not yet fully understood. Recent investigations have shown weak modifications of SP performance in the presence of a textured background [4–10]. Furthermore, it was reported that a stationary textured background was able to modify the initiation of SP, indicating that self-induced optokinetic stimulation due to an eye movement was not the sole mode of interaction [6,7]. The goal of this study was to address the effect of a structured background on the execution of SP by applying brief disturbances to the visual surroundings.

Materials and Methods

Experimental setup: The eye position of 11 healthy naive subjects and one author (US) (age 16–75 years) was measured using the magnetic search coil technique (SKALAR Medical, Delft, The Nether-

lands) [11,12]. We used an i486/50-based real-time computer system to control the experimental paradigm including stimulus presentation and data acquisition. The visual stimuli were back-projected onto a translucent tangent screen (viewing distance 1 m, subtending $\pm 42^\circ$ horizontally and $\pm 32^\circ$ vertically, pixel size 0.2°) using an active-matrix LCD video projector (Sharp). The frame rate of the display system was 70 Hz. Horizontal and vertical positions of the center-aligned right eye were sampled at 1000 Hz with a nominal spatial resolution of 30 s arc.

Experimental paradigm: Each trial started with a computer controlled fixation period (randomized between 500 and 1000 ms, eye position window $\pm 0.5^\circ$) of a small center target ($0.4 \times 0.4^\circ$) surrounded by a textured background (300 randomly distributed vertical line elements, $0.2 \times 0.8^\circ$). After successful fixation a salient target ($0.8 \times 0.8^\circ$) was moved at $11^\circ/s$ to the right or left for 800 ms. During target motion the background was shifted horizontally at $11^\circ/s$ or $22^\circ/s$ in either direction for 200 ms starting at one of five intervals (0, 57, 100, 157 or 200 ms) after target onset. Control trials consisted of target motion on a homogeneous background, target motion across a stationary background, and background shifts only. These resulting 48 conditions were presented randomly interleaved in at least 10 blocks yielding a minimum of 480 trials. In accordance with our regulations for the use of search coils, a session never lasted more than

30 min. This procedure also ensured that the data were not affected by fatigue.

Data analysis: Eye position was first filtered using an adaptive smoothing cubic spline. Then, eye velocity was obtained by a 2-point differentiation [13]. Finally, saccades were detected automatically using combined velocity and acceleration criteria. To quantify the effect of the transient background motion we calculated the cross-correlation between the de-saccaded eye velocity profile of a single trial and one cycle of a sine function (period 300 ms). The modulation of the ongoing SP was expressed as modulation index (MI) which simply represents the value of the maximum of the cross-correlation function. All data processing was performed off-line using a commercial software package (MATLAB 5.3, The MathWorks Inc., Natick, MA).

Results

First, we looked at the influence of a structured background on the execution of tracking eye movements when compared to those across a homogeneous background. The latency of the initial saccade of SP was consistently and significantly ($p < 0.01$, one-tailed t -test) shorter in the presence of a textured background (247 ± 31 ms) compared with those obtained in control trials with a homogeneous background (267 ± 40 ms, target velocity $11^\circ/\text{s}$, grand average for all 12 subjects). This increase in saccade latency most probably reflected the decrease in initial eye acceleration ($63^\circ/\text{s}^2$ for homogeneous background, $50^\circ/\text{s}^2$ for structured background) induced by the structured background. However, these changes in eye movement parameters were rather small compared to the marked change in visual stimulation induced by the presence of a structured background and were exclusively related to the initiation of SP. To unmask a possible background effect, we used brief movements of the background. If the brief disturbance of the surroundings occurred in the opposite direction of the moving target, the ongoing SP eye movement was not affected and in essence was identical to the response for a stationary background. However, if the background was shifted in the same direction, eye velocity invariably showed a transient perturbation akin a one-cycle sinusoidal wave that started with an acceleration (see Fig. 1). This distinct modulation occurred independent of the onset of target motion and SP, but was clearly time-locked to the onset of the disturbance, as shown in Fig. 1.

Since the main sequence and the latency of the initial saccade were not modified by the disturbance, the perturbation seemed to be merely superimposed

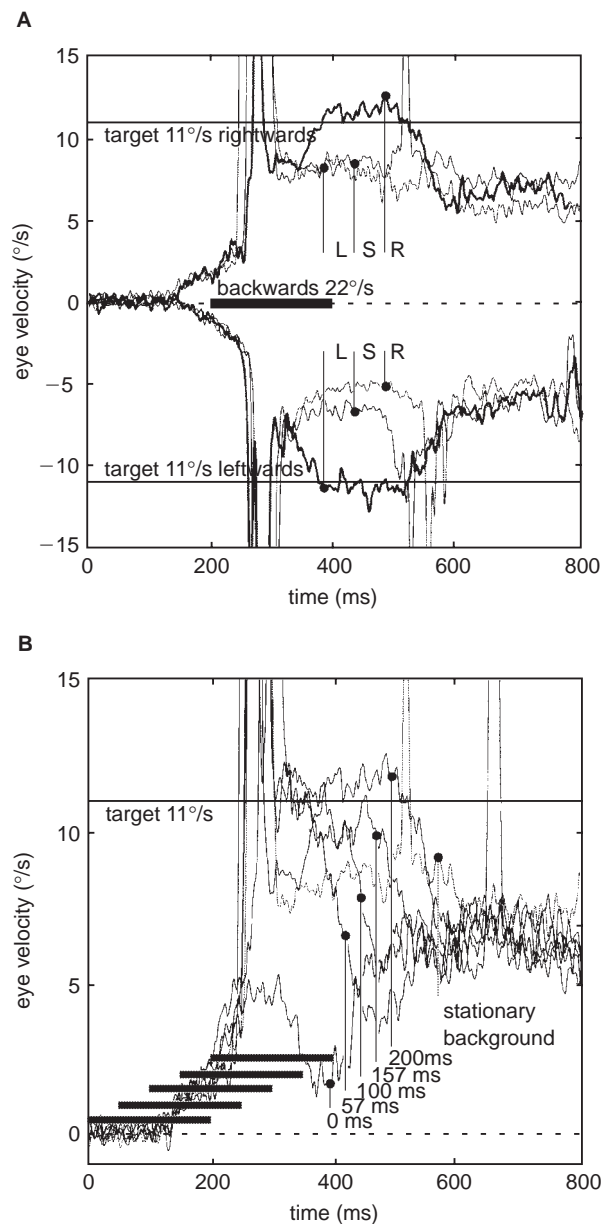


FIG. 1. Median horizontal eye velocity traces (subject N, $n=10$) for different background conditions. Target speed was $11^\circ/\text{s}$. Upward deflection indicates a movement to the right. The duration of the background movement ($22^\circ/\text{s}$) is illustrated by a thick horizontal line. (A) Ocular response to background motion noticeably depends on the direction of the background shift relative to the moving target. The two bold lines represent the conditions where both background shift and target moved in the same direction. (B) Dependence of the modulation in eye velocity on the onset of the background shift as indicated by the labels. Target ($11^\circ/\text{s}$) as well as background ($22^\circ/\text{s}$) moved towards the right.

on an otherwise typical SP response. The presence of the sinusoidal perturbation in the eye velocity is exposed in the cross-correlation function and produces statistically robust changes in the MI depending on the relative retinal image velocity during the disturbance.

Fig. 2 shows lack of modulation for any condition yielding a retinal slip opposite to the target direc-

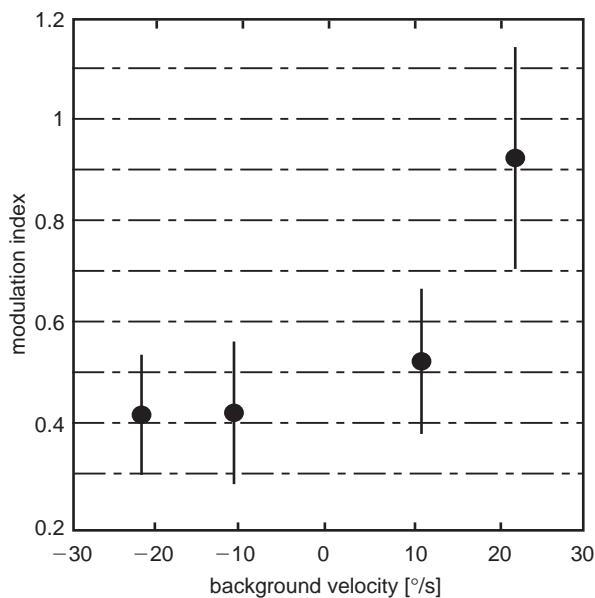


FIG. 2. Modulation index (MI) computed from the cross-correlation function. Values are mean (circles) ± 1 s.d. from all subjects ($n=12$). The abscissa indicates the background velocity. Note that the only value clearly different was the MI obtained for a background velocity of 22°/s in the same direction as the target movement. See text for details of the statistical analysis.

tion, whereas conditions where the background shortly followed the target produced MIs increasing with relative image slip velocity. This observation was supported by an analysis of variance (Kruskal-Wallis) revealing that MI was significantly dependent on the velocity of background velocity. However, a *post-hoc* test revealed that only MI values obtained in the condition of 22°/s background movement in the same direction as the target were significantly different from all other values ($p < 0.001$), which, in turn, were not different among themselves.

Discussion

Our paradigm reveals an interesting asymmetry in the visual processing of global image motion during the execution of smooth pursuit eye movements. Brief injections of full field motion in the direction of a moving target were able to temporarily perturb the appropriately ongoing SP response. The modulation was absent, however, when such a disturbance occurred in the opposite direction, and SP responses were similar to tracking movements on a stationary background. Furthermore, the disturbance did not seem to affect the characteristics of the initial saccade. In addition, saccadic latencies were significantly shorter in all conditions where tracking was executed on a textured background compared to tracking on a homogeneous background. These data

are in agreement with earlier studies [6,7], which reported a reduction in the initial eye acceleration in the presence of a stationary textured background. The reduction in acceleration led to a quicker build-up of the retinal error which resulted in an earlier initial saccade.

In another study, Worfolk and Barnes [14] used sinusoidally moving pursuit targets (0.2 Hz) presented tachistoscopically (pulse duration 20 ms) on a sinusoidally moving structured background (0.66 Hz). They found a background-induced change in SP eye velocity gain, which decreased with increasing inter-pulse intervals (range 20–640 ms). However, these authors did not show a change in SP eye velocity depending on the phase shift between target and background. Lack of asymmetry under these conditions might have been due to the engagement of predictive mechanisms as well as pure visual processing of the moving target [1].

Recently, Schwartz and Lisberger [15] measured changes in monkey SP eye velocity following brief perturbations (duration 100 ms) of ongoing target motion. They found an increase in sensitivity of the response to the disturbance as a function of the interval between the onset of target motion and the onset of perturbation (range 100–600 ms). These results reflect the strength of interaction between local motion processing and motor output.

A possible neuronal substrate for the processing of relative image motion has been described: neurons in the ventral part of area MST in the monkey seem to respond exclusively to relative image motion, and it was suggested by the authors that these neurons are essential for the decoding of object motion in external space [16]. Furthermore, it was shown recently that neurons in the lateral part of area MST also modulated their response dependent on relative image motion [17].

Our data, on the other hand, show a statistically robust, time-independent and asymmetrical modulation of ongoing SP eye movements by a brief perturbation of the textured background. We hypothesize that these results unmask a yet unknown mechanism that ensures appropriate visuo-visual interaction between local and global motion processing in order to maintain an accurate internal signal reflecting the target motion in extrapersonal space. Such an internal representation has been suggested by others to take place in primate area MST-l [18,19]. This directional mechanism depending on the internal representation of target movement in space would be able to solve two problems: first, the self-induced retinal image motion during eye movements would not be processed and therefore would not be able to affect the ongoing eye movement. Second, since the processing of information neces-

sary to execute the eye movement is in the direction of the target movement, this processing would still be possible.

Conclusions

A brief shift of the textured background during the initiation of the smooth pursuit system by a small moving target strongly modifies the eye movement response if both background and target move in the same direction but has no effect if they move opposite to each other. These results indicate a simple yet powerful mechanism of the visual system in handling the interaction between local and global motion processing. They imply that local processing not only computes the eye movements necessary to track the target, but at the same time, tunes the sensitivity of the global motion detectors in anticipation of their activation due to the subsequent retinal slip during tracking. As revealed by the anomalous condition where the background unex-

pectedly moves in the same direction as the tracking, this gating seems to be strictly selective for the opposite direction.

References

1. Carpenter RHS. *Movements of the Eyes*. London: Pion Ltd, 1988.
2. Robinson DA, Gordon JL and Gordon SE. *Biol Cybern* **55**, 43–57 (1986).
3. Lisberger SG, Morris EJ and Tychsen L. *Annu Rev Neurosci* **10**, 97–129 (1987).
4. Barnes GR and Crombie JW. *Exp Brain Res* **59**, 548–558 (1985).
5. Collewijn H and Tamminga EP. *J Physiol Lond* **351**, 217–250 (1984).
6. Keller EL and Kahn NS. *Vision Res* **26**, 943–955 (1986).
7. Kimmig HG, Miles FA and Schwarz U. *J Neurophysiol* **68**, 2147–2164 (1992).
8. Mustari MJ, Fuchs AF and Wallman J. *J Neurophysiol* **60**, 664–686 (1988).
9. van der Steen J, Tamminga EP and Collewijn H. *Vision Res* **23**, 1655–1661 (1983).
10. Yee RE, Daniels SA, Jones OW *et al.* *Invest Ophthalmol Visual Sci* **24**, 1115–1122 (1983).
11. Collewijn H, van der Mark F and Jansen TC. *Vision Res* **15**, 447–450 (1975).
12. Robinson DA. *IEEE Trans Biomed. Electron* **BME-10**, 137–145 (1963).
13. Schwarz U and Miles FA. *J Neurophysiol* **66**, 851–864 (1991).
14. Worfolk W and Barnes GR. *Exp Brain Res* **90**, 589–598 (1992).
15. Schwartz JD and Lisberger SG. *Visual Neurosci* **11**, 411–424 (1994).
16. Tanaka K, Sugita J, Moriya M and Saito H. *J Neurophysiol* **69**, 128–142 (1993).
17. Eifuku S and Wurtz RH. *J Neurophysiol* **80**, 282–296 (1998).
18. Newsome WT, Wurtz RH and Komatsu H. *J Neurophysiol* **60**, 604–620 (1988).
19. Thier P and Erickson RG. *Eur J Neurosci* **4**, 539–553 (1992).

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