



# Effects of Stationary and Moving Textured Backgrounds on the Visuo–Oculo–Manual Tracking in Humans

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Received 28 February 1994; in revised form 5 July 1994

We investigated the effects of stationary and moving textured backgrounds on ocular and manual pursuit of a discrete target that suddenly starts to move at constant speed (ramp motion). When a stationary textured background was superimposed to the target displacement, the gain of the steady-state eye smooth pursuit velocity was significantly reduced, while the latency of pursuit initiation did not vary significantly, as compared to a dark background condition. The initial velocity of the eye smooth pursuit was also lowered. Both the initial acceleration and the steady-state manual tracking angular velocity were slightly, but not significantly, lowered when compared to a dark background condition. Detrimental effects of the stationary textured background were of comparable amplitude ( $\approx 10\%$ ) for ocular and manual pursuit. In a second condition, we compared ocular and manual pursuit when the textured background was either stationary or drifting. Initial and steady-state eye velocities increased when the textured background moved in the same direction as the target. Conversely, when the background moved in the opposite direction, both velocities were decreased. Eye displacement gain remained however close to unity due to an increase in the occurrence of catch-up corrective saccades. The effects of the moving backgrounds on the initial and steady-state forearm velocities were inverse to that reported for smooth pursuit eye movements. Neither manual nor ocular smooth pursuit latencies were affected.

Optokinetic nystagmus Smooth pursuit Visuo–oculo–manual tracking Visual background

## INTRODUCTION

To locate, reach or catch a moving target, we have to integrate various sources of information concerning the displacement of the target relative to ourselves and to the surrounding environment and concerning our own displacements relative to the environment. Most of the information is provided by the visual and the vestibular systems. Moreover, these information often interact in unusual ways, leading to illusions of motion. One well-known example of such illusory motion perception is the sensation of self-motion which can be induced in a static observer by the visual motion of the surrounding (see Dichgans & Brandt, 1978). These illusions can affect the perception of object motion and/or self-motion and the performance of complex motor tasks (Probst, Krafczyk, Brandt & Wist, 1984). Moreover, as each of

these information sources subserve different but overlapping oculo–motor and skeleto–motor systems (see Waespe & Henn, 1987), the simultaneous occurrence of self-motion and object-motion might drive conflicting motor responses, disturbing the control of complex actions.

In particular, an interaction between passive compensatory eye movements resulting from the perception of self-motion and active goal-directed eye movements driven by the perception of object motion can be suspected. For example, during ocular pursuit of a moving target over a structured background, the whole background drifts across the retina. This global motion might induce an optokinetic response of the eyes, opposite to the direction of the moving target. Therefore, a conflict might occur between passive optokinetic responses to the global retinal motion and active pursuit responses to the target motion. However, early observations suggested that this was not the case and claimed that the ocular smooth-pursuit system was able to detect and to track a moving target spot against a background, irrespective of the optokinetic stimulation (Hood, 1975; Guedry, Davenport, Brewton & Turnipseed, 1979; Young, 1971; Kowler, van der Steen, Tamminga & Collewijn, 1984).

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Nevertheless, this conclusion was challenged by experimental data demonstrating that the visual pursuit of a small moving target was more accurate when it occurred over a dark or featureless background than over a textured background (Yee, Daniels, Jones, Baloh & Honrubia, 1983; van den Berg & Collewijn, 1983; Collewijn & Tamminga, 1984; Worfolk & Barnes, 1992). A small but consistent reduction in the steady-state eye velocity was observed when pursuit occurred over a textured background, in both the vertical (20%) and horizontal (10%) directions (Collewijn & Tamminga, 1984). Finally, although no data are available in humans, studies in monkeys suggest that the initiation of the ocular pursuit movements was also degraded in the presence of a stationary textured background, in monkey (Keller & Khan, 1986; Kimmig, Miles & Schwarz, 1992). Some of the discrepancies noted between the aforementioned studies might be due to differences in experimental conditions. In particular, the higher target velocity range which was used in some studies might explain the decrease observed in the smooth pursuit eye velocity. For instance, Niemann, Ilg and Hoffman (1994) demonstrated that there was no significant effect of a stationary background on smooth pursuit eye movement, providing that target velocity did not exceed 10 deg/sec. Above this velocity range, a significant reduction of pursuit velocity was observed. Therefore, the detrimental effect of a stationary background on the oculomotor behavior seems to be dependent on the velocity of the target.

Changes in the smooth pursuit eye velocity were attributed to the occurrence of a reflexive eye movement driven by the optokinetic stimulation resulting from the displacement of the eye over the textured background (e.g. Worfolk & Barnes, 1992). Another method to investigate such interaction between active and passive eye movements consists in drifting the textured background and the target, concurrently. Among others, Yee *et al.* (1983) and Worfolk and Barnes (1992) demonstrated that a textured background decreased (increased) the velocity of smooth-pursuit eye movements when it moved opposite (with) the target. These data provided further support to the hypothesis that the optokinetic response interacts with the smooth-pursuit oculomotor behaviour when a moving background is superimposed to the displacement of the target. By manipulating the background/target relative velocity, the evolution of the interaction between the two oculomotor responses and the range of action of each of these responses may be investigated (Worfolk & Barnes, 1992).

At the perceptual level, results from psychophysical studies help to understand the consequences of such interactions (Young, Dichgans, Murphy & Brandt 1973; Raymond, Shapiro & Rose, 1984; Honrubia, Khalili & Baloh, 1992). Early observations indicated that a moving textured background superimposed over a stationary discrete target may result in induced motion of the target (Duncker, 1929). This illusory motion perception is sufficient to induce an ocular pursuit of the apparent target displacement in both monkeys (Waespe &

Schwarz, 1987) and humans (Collewijn, Conijn, Martins, Tamminga & van Die, 1982). Moreover, when a moving background moves across the retina during ocular smooth pursuit of a discrete target, the perceived velocity of the discrete target is modified (Raymond *et al.*, 1984; Wertheim, 1990; Brenner, 1991). Recently, Honrubia *et al.* (1992) showed that a constant-velocity optokinetic stimulus, which can induce circular vection in a static observer (see Dichgans & Brandt, 1978), or a constant-angular acceleration of the subject's head, both changed the perception of velocity of a small moving visual target. Also, they observed that errors in the perceived velocity of the target was closely related to the characteristics of the vestibulo-ocular reflex. This led them to propose that "the brain judges the motion of objects in relation to the self in a relativistic manner, using internal references that are influenced by sensory stimuli" (p. 745), as the vestibular and the optokinetic stimuli produced by eyes, head or whole-body displacement.

The latter results questioned the earlier belief that motor systems use real, and not perceived, motion of the target to control complex movements (Bridgeman, Kirsh & Sperling, 1981). Farber (1979) and Bacon, Gordon and Schulman (1982) suggested that, in a pointing task, the manual motor system uses the perceived final position of the target, distorted by the presence of an optokinetic stimulation. In the same line, Lepecq, Jouen and Dubon (1993) recently showed that a visually-induced sensation of self-motion influenced the accuracy of reaching movements toward remembered targets, suggesting that self-motion information was used by the subjects to define the position of the target relative to themselves. All these studies considered how position information was used to control reaching movement. However, no experimental data are available about how motion cues which are used to control tracking movement are affected in such conditions.

In the present experiment, we used a visuo-oculo-manual tracking task in order to compare the effects of different background conditions on ocular pursuit and "open-loop" manual tracking. Our first objective was to determine whether manual tracking accuracy of a discrete visual target might be affected when performed against a stationary textured background compared to a dark uniform background. Second, we tried to understand how an optokinetic stimulus (i.e. a moving textured background superimposed over the target) affects visuo-oculo-manual tracking.

## METHODS

### *Subjects*

Four men and one woman (mean age  $25.3 \pm 4$  yr, range 22–30 yr), right-handed, were included in the study. No subject had an history of neurologic or ophthalmologic disease, and they were all emetropes according to the Snellen's visual acuity test. The subjects were all familiar with the experimental environment and three of them had previous experience with similar

oculomotor tasks. However, they were all naive regarding the purpose of the present study. All subjects gave their informed consent before the experiment.

#### *Task and apparatus*

The task was to track, both visually and manually, a target presented on a video graphic display, which moved from the subjects' left to their right, at a constant speed (ramp). Visuo-oculo-manual tracking occurred against different backgrounds.

Eye movements were recorded using an infra-red limbus detection apparatus (Gauthier & Volle, 1975). Although binocular vision was permitted, only the horizontal position of the left eye was recorded. Head movements were minimized by a head and a chin rests. This also ensured that the distance between the subjects' head and the visual display remained constant at 113 cm. The subject's right arm was affixed to a near frictionless manipulandum which permits and restricts the rotation of the arm around the elbow joint. Elbow rotation was recorded using a linear potentiometer (1 revolution, 5 k $\Omega$ ) positioned in line with the elbow's axis of rotation. Both the eye movement recording device and the potentiometer signals were low-pass filtered (d.c. - 100 Hz, - 3 dB), collected at a frequency of 250 Hz and digitized using a 12-bit A-D converter. All data were stored for off-line analysis.

#### *Visual stimuli*

Target and random-dot backgrounds were computer generated by a second, synchronized, computer (PC 286/25 MHz) and displayed on a video graphic display (CONRAC 7211, 48 cm, resolution 800  $\times$  600 pixels) having a refresh rate of 50 Hz. Visual field stimulation covered 20 deg of visual angle. Background and target motion were phi-motion for which smooth pursuit is not different from that of real motion (Westheimer, 1954). The target was a bright luminous spot (diameter, 0.1 deg of visual angle with a contrast of 90%, 10 cd/m<sup>2</sup>). Three types of visual background were used. A completely dark background was used as a control situation. The experimental backgrounds were either stationary or moving, and consisted in a random distribution of small luminous dots on the display. These dots were half of the size of the target with a similar contrast (90 %). They were distributed from - 10 to 10 deg of horizontal visual angle and from - 5 to 5 deg of vertical visual angle. The surface of the random dot surface was 589 cm<sup>2</sup>, with a dot density of 0.081 dot/cm<sup>2</sup>.

#### *Procedure*

The experiment took place in a dark room; the target and the random dots were the only source of light. Subjects were allowed 10 min of dark adaptation before each block of trials. Eye position and elbow rotation were calibrated before each block of trials by having the subjects look and point at five different targets located at known positions (- 10, - 5, 0, + 5 and + 10 deg). The calibration procedure was used to convert raw data into

angular values. A linear regression fit was used. In all cases the regression coefficient was always > 0.98.

Except for the calibration routine, subjects were never allowed to see their arm, i.e. the manual tracking was open-loop. An horizontal wood panel prevented vision of the forearm. As the movement produced by the subjects was pure flexion-extension of the elbow, the forearm axis was not strictly aligned with the gaze axis. However, the spatial compatibility between target position and forearm position was controlled. First, the axis of rotation of the manipulandum was located in the fronto-parallel plane, below the eyes. Thus, the horizontal distance between the vertical axis of the subject's head and the axis of rotation of the manipulandum was kept constant at 21 cm. This resulted in a constant of 10.7 deg angular deviation between arm and eye position when both the subject's gaze and forearm were pointing at the centre of the display. This bias remained stable across the experimental conditions. It should be noted that values reported for the forearm flexion-extension, consist in angular position of the manipulandum relative to the target and do not describe the angular position of the joint. Finally, to avoid large variations in initial arm position, the starting position of the manipulandum was insured to be constant, located at - 10 deg (relative to the target) by locking the leftward rotation of the manipulandum at this location. With this procedure, the subjects began manual tracking directly in line with the target starting position.

All subjects began the experiment by performing 50 consecutive trials in the control condition (dark background). The first and last 15 trials were not included in the different data analysis, in order to avoid fatigue effects and to analyse the same number of trials in each background condition (20 trials). Then, they were submitted to three blocks of 50 trials. In each of these blocks, they were randomly presented with 10 trials for each of five experimental background conditions. In the first condition, the random dots (i.e. the textured background) remained stationary throughout the trial. This condition is referred to as the 0 deg/sec background velocity. In the remaining four conditions, the target and background moved simultaneously. The background displacement could be to the subjects' left (negative velocity) or right (positive velocity) and could occur at a velocity of either 6 or 14 deg/sec. It took approx. 15 min to complete each block of trials; a 10-min rest period followed each block.

A trial began by activating a static target and background on the video graphic display. This prompted the subject to both fixate and point to the target; it also initiated data collection. After a constant delay of 2 sec, the target moved for 1.6 sec to the right of the screen at a constant speed of 12.5 deg/sec. As noted above, the target always appeared at the same location (- 10 deg of eccentricity), favouring its detection. Thus, the initial position and the displacement velocity of the discrete target were highly predictable. The subjects were instructed to track the target with their eyes and with their forearm. They were also asked to stop both their

eye and forearm movements as soon as the target disappeared. This occurred when the target reached the +10 deg position. To avoid final position corrections, the video graphic display was totally blanked out at that time. The subjects were also asked to remain stable after target offset for a period of 500 msec. Samples of arm displacement profiles obtained from one subject are illustrated in Fig. 1 for three background conditions. The high spatial predictability of the target motion associated to the fact that background and target appeared/disappeared and moved simultaneously might have reduced the potential effects of background manipulations. However, such experimental procedure allowed us to limit the high variability usually observed in open-loop forearm tracking, and enabled us to compare the effects of background manipulations on the basis of a stable motor performance.

#### Data analysis

Eye and forearm angular velocities were determined by digital differentiation of the eye and of the forearm angular positions over time, respectively. Eye velocity data were low-pass filtered digitally (DC – 40 Hz bandwidth, –3 dB). Hand velocity data were also low-pass filtered (DC – 20 Hz, –3 dB). These data (positions and velocities) were analysed with respect to three different phases of the visuo-oculo-manual tracking: the pursuit initiation, the tracking phase and the final performance.

*1. Pursuit initiation.* The latency and initial velocity of both the ocular and forearm responses were determined from their respective displacements, using a method similar to that described by Carl and Gellman (1987) for eye smooth pursuit movements. Briefly, response initiation was determined by the intersection of two regression lines. The first regression line fits the baseline

signal (pre-movement) whereas the second regression line fits the first segment of the response signal. For eye movement, and according to Carl and Gellman's (1987) method, the baseline was defined as beginning 100 msec before the target onset and ending 80 msec after. From the regression line computed on that 180 msec interval, we determined the value at which eye position differed from the baseline signal by at least 3 SDs from the average position prior response. The second regression line was then computed for a time interval starting with this latter value and covering the next 40 msec. This second regression line was considered to represent the initial displacement of the eye over time. Further, initial eye velocity ( $\dot{e}_i$ ) was given by the slope of this second regression line. Finally, response latency was defined as the time-lag occurring between the onset of the target and the intersection of the two regression lines defined above. The same procedure was applied to the forearm displacement signal, with different temporal values. Briefly, the baseline signal was considered to be the regression line computed from the position data for a time interval beginning 100 msec prior to the target displacement and ending 300 msec after. The starting point of the second regression line was defined as for the eye movement data. However, this second regression line was computed over an interval of 60 msec. The initiation of the manual tracking response and its initial velocity ( $\dot{a}_i$ ) were computed with the method applied to eye movements. Furthermore, the amplitude of the initial peak of acceleration ( $\ddot{a}_i$ ) was determined for each subject following a digital differentiation of the average forearm velocity profiles, in each background condition. Figure 2(A, B) shows typical mean velocity and initial acceleration profiles from one subject, for four of the six background conditions.

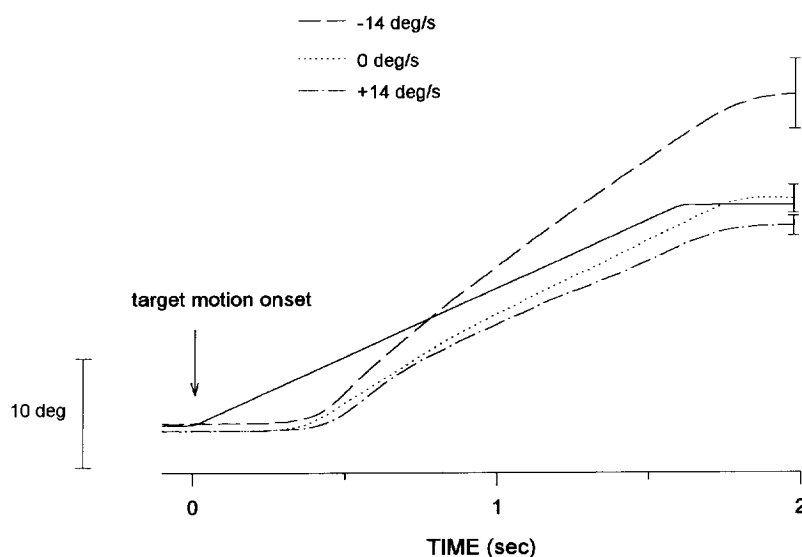


FIGURE 1. Samples of mean manual response to a 12.5 deg/sec rightward moving target, in three textured background conditions, from one subject. Error bars indicate the SD of the final forearm position. When the background moves leftward with a velocity of –14 deg/sec, the final position of the forearm strongly overshoots the final target position. When background is stationary, stop forearm position slightly overshoots the final target position. When the background moves in the same direction as the target with a velocity of +14 deg/sec, stop forearm position undershoots the final target position.

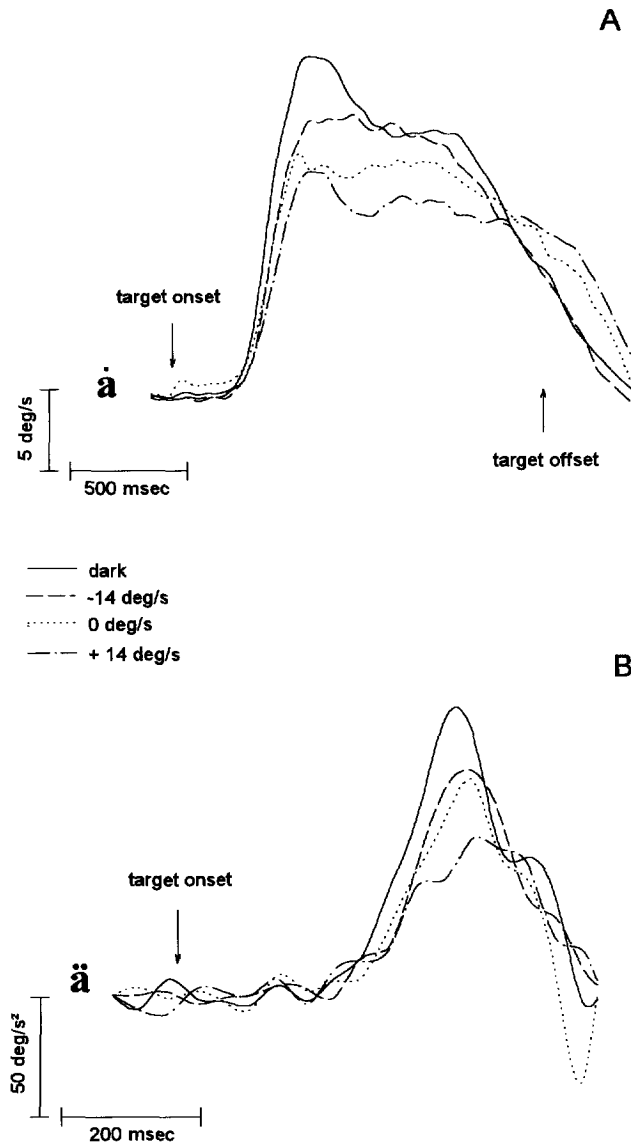


FIGURE 2. Examples of mean velocity (A) and mean initial acceleration (B) profiles from one subject, in four background conditions. At the time indicated by the downward arrow, the target started to move with a constant velocity of 12.5 deg/sec. Each velocity curve is the average of 20 trials. Acceleration profiles are computed by digital differentiation of the average velocity profiles.

2. *Pursuit phase.* The pursuit phase of manual tracking was defined as the time interval between the end of the initial forearm angular acceleration and the beginning of the final deceleration. During this interval, we computed the steady-state angular velocity and the peak angular velocity. Peak velocity was defined manually from forearm velocity recordings. Steady-state velocity of the forearm tracking was estimated as the slope of a regression line fitted through this interval on the forearm displacement recordings. This method enabled us to measure the mean forearm angular velocity and to avoid noise associated with local velocity changes. The effect of the background condition was quantified by computing two different manual suppression indices (MSI). The first index, MSI<sub>m</sub>, compared the data obtained in the conditions in which the background moved to those obtained when a stationary textured background was used.

This index was defined as:

$$\text{MSI}_m = \left( 1 - \frac{\dot{a}_{s1}}{\dot{a}_{s2}} \right) \cdot 100$$

where  $\dot{a}_{s1}$  and  $\dot{a}_{s2}$  are the steady-state forearm angular velocities when the background was moving and stationary, respectively. The second index, MSI<sub>s</sub>, compared the data obtained in the stationary textured background condition to those obtained in the dark background condition. This gave an evaluation of the "masking effect" (Kimmig *et al.*, 1992) of a stationary textured background on the steady-state forearm angular velocity. Similarly, ocular suppression indices (OSI) were computed to compare steady-state velocity of the eye smooth pursuit ( $\dot{e}_s$ , see below) for both the stationary textured vs dark background (OSI<sub>s</sub>) and the moving vs stationary (OSI<sub>m</sub>) textured backgrounds. For both eye and forearm data, a positive suppression index indicates

that eye or forearm angular velocity decreased in presence of either the stationary or the moving background, respectively. Conversely, a negative suppression index indicates an increased velocity. Other such suppression indices have been used to quantify the effects of background on specific kinematics parameters ( $\dot{\epsilon}_1$ ,  $\dot{a}_1$ ,  $\ddot{a}_1$ ), as expressly indicated in the results section.

The steady-state eye velocity was reached several hundred msec after the initiation of the pursuit, that is after the first saccadic eye movement (see Fig. 3). Saccade-free sections of the pursuit eye movements were selected to estimate it. These intervals had to be of at least 200 msec in duration and had to occur after the initial saccadic eye movement. Moreover, at least two such intervals had to occur within a trial to be considered. During the selected intervals, the steady-state eye velocity ( $\dot{\epsilon}_s$ ) was defined as the slope of a regression line computed from the different positions taken by the eye over time. The gain of the smooth pursuit for a particular trial was defined as the mean ratio between  $\dot{\epsilon}_s$  and target velocity. It was computed over each interval, within a trial which met the above mentioned criterion. We did not consider the last 300 msec of the ocular pursuit to compute  $\dot{\epsilon}_s$ , because, as stated by Robinson,

Gordon and Gordon (1986), pursuit begins to slow down several hundreds of msec before target motion stops when subjects know that it will stop at a certain position or time [see Fig. 3(B)]. For each trial, the value of the eye velocity gain was the average of the values measured over all the pursuit phases matching the above mentioned criteria. Such averaging method measures the mean oculomotor behaviour in a given condition and avoids potential overestimation effects related to local, anecdotal changes. Twenty trials were used to yield the mean steady-state eye velocity gain for one given subject, and then averaged across the subjects for each of the six background conditions.

The occurrence of saccadic eye movements during pursuit were determined by a computer algorithm employing an acceleration criterion, and confirmed by visual inspection of the data. The criterion was determined as a function of the signal-to-noise ratio of a large sample of analogue records, for each subject. The analysis of saccades was conducted for each subject for the 20 trials for which we computed  $\dot{\epsilon}_s$ . In all cases, the amplitude of each saccade was determined and both a positive and a negative total saccadic amplitude were computed for each trial (see Howard & Marton, 1992 for

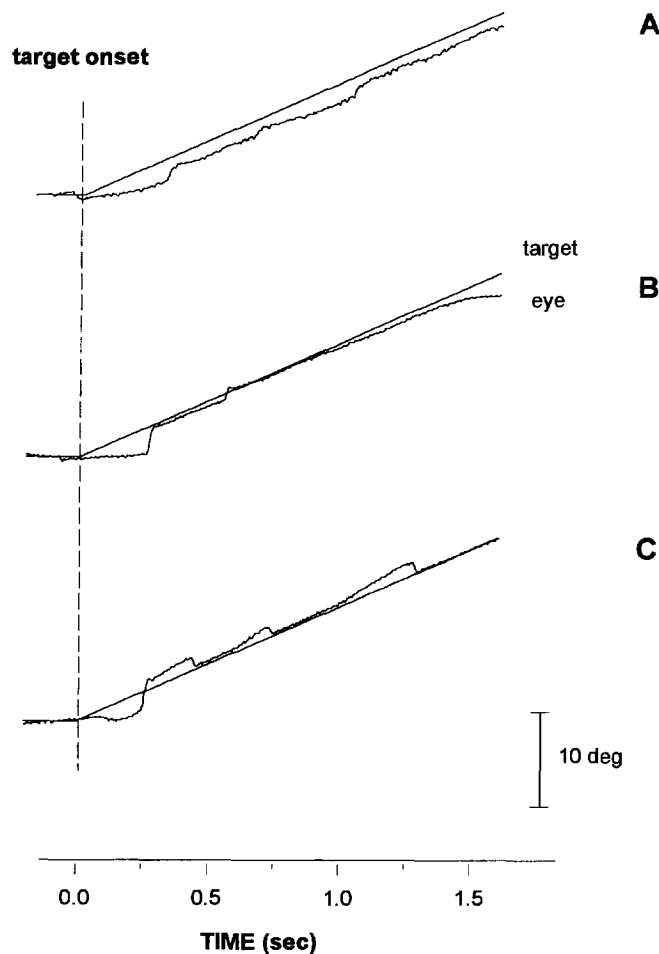


FIGURE 3. Samples eye and target positions in three background conditions. (A) Leftward background motion,  $V_b = -14$  deg/sec. (B) Stationary background. (C) Rightward background motion,  $V_b = +14$  deg/sec. Note the occurrence of catch-up saccades, in the direction of the target displacement (A) or in the opposite direction (C). The vertical broken line indicates target movement onset.

a similar method). In both cases, it consisted in the summation of the amplitudes of saccadic eye movements occurring either in the same direction as the target motion (positive saccade) or in a direction opposite to the target motion (negative saccade). Three examples of ocular movement recordings are illustrated in Fig. 3. The occurrence of "negative" [Fig. 3(C)] or "positive" [Fig. 3(A)] catch-up corrective saccades is related to an increase or a decrease in steady-state eye velocity, depending on the background motion velocity. These data enabled us to confirm those obtained for the steady-state eye velocity because an increase of total positive (i.e. same direction as the target) or negative (i.e., direction opposite to the target) saccadic amplitude indicated that steady-state  $\dot{e}_s$  was decreased or increased, respectively.

**3. Final performance.** Variations in steady-state forearm velocity should induce changes in the final performance of tracking. The total amplitude of the forearm tracking movement was evaluated as the constant error ( $CE_f$ , signed difference) between the resting position of the forearm when the target disappeared and the final target position (+10 deg). This final position was defined as the angular position reached by the forearm when its angular velocity reached a zero value for the first time following movement initiation. A negative  $CE_f$  indicates that the forearm "undershot" (Fig. 1,  $V_b = +14$  deg/sec) the final position of the target whereas a positive  $CE_f$  indicates that the forearm "overshot" this final position (Fig. 1,  $V_b = -14$  deg/sec). The  $CE_f$  should not be compared to a pointing accuracy index. Changes observed in the  $CE_f$  will rather be considered as a signed consistency with changes in tracking velocity. Similarly an eye displacement gain was computed by the ratio between the displacement of the eye and the displacement of the target, which is a composite resultant of slow and fast eye movements.

All dependent variables were computed independently for each trial and then averaged across conditions for each subject. The mean data obtained for each condition and for each subject were then submitted to independent analyses of variance (ANOVA). When appropriate, *post hoc* comparisons were made using the Neuman-Keuls technique. Figures and Tables illustrate data averaged across subjects for each condition.

## RESULTS

### *Effects of a stationary background on both ocular and manual pursuits*

The observed effects of a stationary background on the ocular smooth pursuit of a discrete target are consistent with previously published data (Collewijn & Tamminga, 1984). First, the latency of the ocular response to the target motion onset was of about 180 msec, and was not different for dark and stationary textured background conditions [ $180 \pm 21$  and  $179 \pm 17$  msec respectively;  $F(1,4) = 0.02$ ; NS]. Secondly, in the presence of a stationary textured background, the time of occurrence of the first corrective

saccadic eye movement was significantly shortened when compared to a dark background condition [ $282 \pm 17$  and  $263 \pm 16$  msec, respectively;  $F(1,4) = 12.74$ ;  $P < 0.05$ ]. This effect might be related to the changes observed in the early phase of the smooth pursuit eye movement. The presence of a stationary textured background significantly decreased the initial eye velocity  $\dot{e}_i$  [average OSIs for  $\dot{e}_i$ ,  $12.7 \pm 10.3\%$ ;  $F(1,4) = 7.62$ ;  $P < 0.05$ ]. The large variability observed for that effect reflects that, although the decrease in  $\dot{e}_i$  with a textured background was observed for all subjects, its magnitude was highly variable. The initial acceleration of the eye was not available using infra-red limbus recording technique (due to a poor signal-to-noise ratio). Therefore, the precise effects of a stationary textured background on ocular pursuit initiation in humans remain to be studied using more accurate eye movements recording techniques.

As was the case for  $\dot{e}_i$ , the gain of the eye steady-state tracking which took place between each saccade was significantly decreased by the presence of a stationary textured background when compared to a dark background [average =  $0.79 \pm 0.05$  and  $0.89 \pm 0.04$ , respectively;  $F(1,4) = 20.35$ ;  $P < 0.05$ ]. Thus, the average OSIs for the steady-state eye velocity was of  $11 \pm 4.6\%$ . To compensate for the lower steady-state velocity of the eye, more corrective saccadic eye movements occurred when the target moved over a stationary textured background. This increase in saccadic eye movements occurrence resulted in an eye displacement gain close to unity, in both conditions.

The results obtained for manual tracking were much different from those reported above, no differences being observed between the two conditions. For instance, the latency of manual tracking was equal to  $336 \pm 21$  and  $346 \pm 26$  msec for the dark and the stationary textured background, respectively [ $F(1,4) = 1.07$ ; NS]. Consequently, the latency between initiation of the ocular and of the manual tracking remained constant at approx. 160 msec. Concerning the kinematics data collected during both the pursuit initiation and the pursuit phase, no significant differences were observed for any of the dependent variables. The data of interest are summarized in Fig. 2 and Table 1. However, the peak angular velocity and steady-state velocity of the manual tracking were slightly reduced ( $\approx 15\%$ ) by the presence of a stationary textured background but this effect was not significant, because two subjects did not demonstrate any change in forearm tracking kinematics. In line with the kinematics data, the  $CE_f$  was not significantly affected by the type of background [ $F(1,4) = 0.38$ ,  $P > 0.05$ ]. However, as can be seen in Table 1, we observed that open-loop tracking of a moving target presented on a dark background resulted in a systematic overshoot (see Table 1). The presence of a stationary textured background resulted in a slight and not significant decrease in the magnitude of this overshoot (see Table 1), which can be related to the slight decrease in the steady-state velocity of manual tracking observed in such condition.

TABLE 1. Summary of response parameters of the manual tracking

Background velocity (deg/sec)	Latency (msec)	$V_{\text{peak}}$ (deg/sec)	$CE_r$ (deg)	$\dot{a}_s$ (deg/sec)	MSIm $\dot{a}_i$ (%)
Dark	336 ± 21	27.5 ± 8	3.6 ± 7.3	16.6 ± 1.8	-6.1 ± 12
-14	348 ± 31	25.4 ± 4.3	2.6 ± 4.1	16.5 ± 2.1	-6.1 ± 12
-6	345 ± 22	24.5 ± 4.3	2.8 ± 4.2	15.0 ± 2.0	7.4 ± 3.6
0	346 ± 26	23.9 ± 4.5	1.8 ± 4.0	13.6 ± 2.0	0
+6	358 ± 28	22.5 ± 4.6	0.3 ± 3.8	12.6 ± 1.6	11.2 ± 5
+14	348 ± 21	21.9 ± 4.3	-0.4 ± 3.6	11.9 ± 1.6	14.6 ± 4.8

Values are averages and SDs across subjects. Abbreviations are explained in the text.

### Effects of moving backgrounds on smooth pursuit eye movements

When the subjects pursued with their eyes the displacement of a discrete target over a moving textured background, modifications of the smooth pursuit were observed. Although the latency of eye pursuit remained unaffected by the background velocity [mean, 180.7 ± 18 msec;  $F(4,16) = 0.12$ ; NS], the initiation of the eye smooth pursuit of the target was modified by the optokinetic background. Specifically,  $\dot{e}_i$  was significantly modulated by the background velocity [ $F(4,16) = 10.95$ ;  $P < 0.05$ ]. Relative to the stationary background condition, *post hoc* comparisons indicated a reduction in  $\dot{e}_i$  when the background moved opposite to the target (mean OSIm for  $\dot{e}_i$ , 16.6 ± 13% and 3.6 ± 11% for background velocities of -14 and -6 deg/sec, respectively) whereas  $\dot{e}_i$  increased when the background moved in the same direction as the target (mean OSIm for  $\dot{e}_i$ , -38.5 ± 32% and -37.8 ± 14%, for background velocities of 6 and 14 deg/sec, respectively). This result is illustrated in Fig. 4(b).

Average values of the gain of the eye steady-state smooth pursuit [the ratio between the eye angular velocity ( $\dot{e}_s$ ) and the target angular velocity] are illustrated in Fig. 4(A). Motion of the background significantly changed the eye velocity gain [ $F(4,16) = 20.49$ ;  $P < 0.05$ ]. These modifications are in line with those reported for  $\dot{e}_i$ . Specifically, *post hoc* comparisons indicated that there was a significant reduction in the gain of steady-state velocity when the background moved opposite to the target as compared to the stationary background. Average of the OSIm computed for  $\dot{e}_s$  were of 11.99 ± 7.33% and 7.45 ± 7.06% for background velocity of -14 and -6 deg/sec, respectively. Alternatively, we observed a significant increase in the gain of steady-state velocity when the target and the background moved in the same direction. Average values of the OSIm were negative and equal to -15.4 ± 6.3% and -28.52 ± 10.9%, for background velocity of +6 and +14 deg/sec, respectively. This resulted in a significant linear relationship between OSIm and velocity of the background [OSIm ( $\dot{e}_s$ ) = 4.89 - 1.52  $V_b$ ,  $r = 0.97$ ,  $P < 0.05$ ].

The presence of significant modifications in the gain of the steady-state velocity of the smooth pursuit eye movement was further confirmed by the analysis of the amplitude and direction of the catch-up, corrective

saccades occurring during the tracking of the target. These results are illustrated in Fig. 4(D). There was a significant effect of background motion on the number of saccades during one trial [ $F(4,16) = 3.67$ ,  $P < 0.05$ ]. A *post hoc* comparison indicated that this number was higher when background was moving than when it was stationary. Moreover, saccadic eye movements with negative amplitude, that is saccadic eye movements opposite to the target direction of motion, were found for a background motion velocity of +14 deg/sec, corresponding to a mean eye velocity gain across subjects of 1.02 ± 0.12 (see Table 2). The total amplitude of negative, "back-up" saccades was significantly higher in this condition than when the background was stationary [ $F(1,4) = 13.04$ ;  $P < 0.05$ ]. This was not the case when the background velocity was of -6 deg/sec, where the average eye velocity gain remained below 1 [ $F(1,4) = 4.86$ ;  $P > 0.05$ ]. Accordingly, there was a significant effect of background motion on the total amplitude of positive, catch-up saccades [ $F(4,16) = 11.76$ ;  $P < 0.05$ ]. When the background velocity increased (from -14 to +14 deg/sec), the total amplitude of these saccadic eye movements decreased (from 69.25 ± 36.26 to 7.01 ± 5.01 deg for 20 trials). These changes in the occurrence and amplitude of catch-up saccades were consistent with the changes observed in steady-state eye velocity gain. These corrective saccades were very efficient, eye displacement gain remaining close to 1.

### Effects of moving backgrounds on manual tracking

Table 1 illustrates the kinematics results of manual tracking for each background condition. First, manual tracking latency was not significantly different across the different conditions [ $F(4,16) = 0.61$ ; NS]. The mean latency of the manual tracking was of about 350 msec. In the same line, movement time remained constant [mean value equal to ≈ 1380 msec;  $F(4,16) = 0.3$ ; NS].

When compared to a stationary textured background, manual tracking performance was modified by both the direction and the velocity of the moving background. The background velocity had a significant effect on the initial forearm angular velocity,  $\dot{a}_i$  [ $F(4,16) = 9.13$ ;  $P < 0.05$ ]. Manual tracking velocity during pursuit initiation was lower (higher) when the background moved in the same (opposite) direction as the target, as compared to the stationary textured background condition.



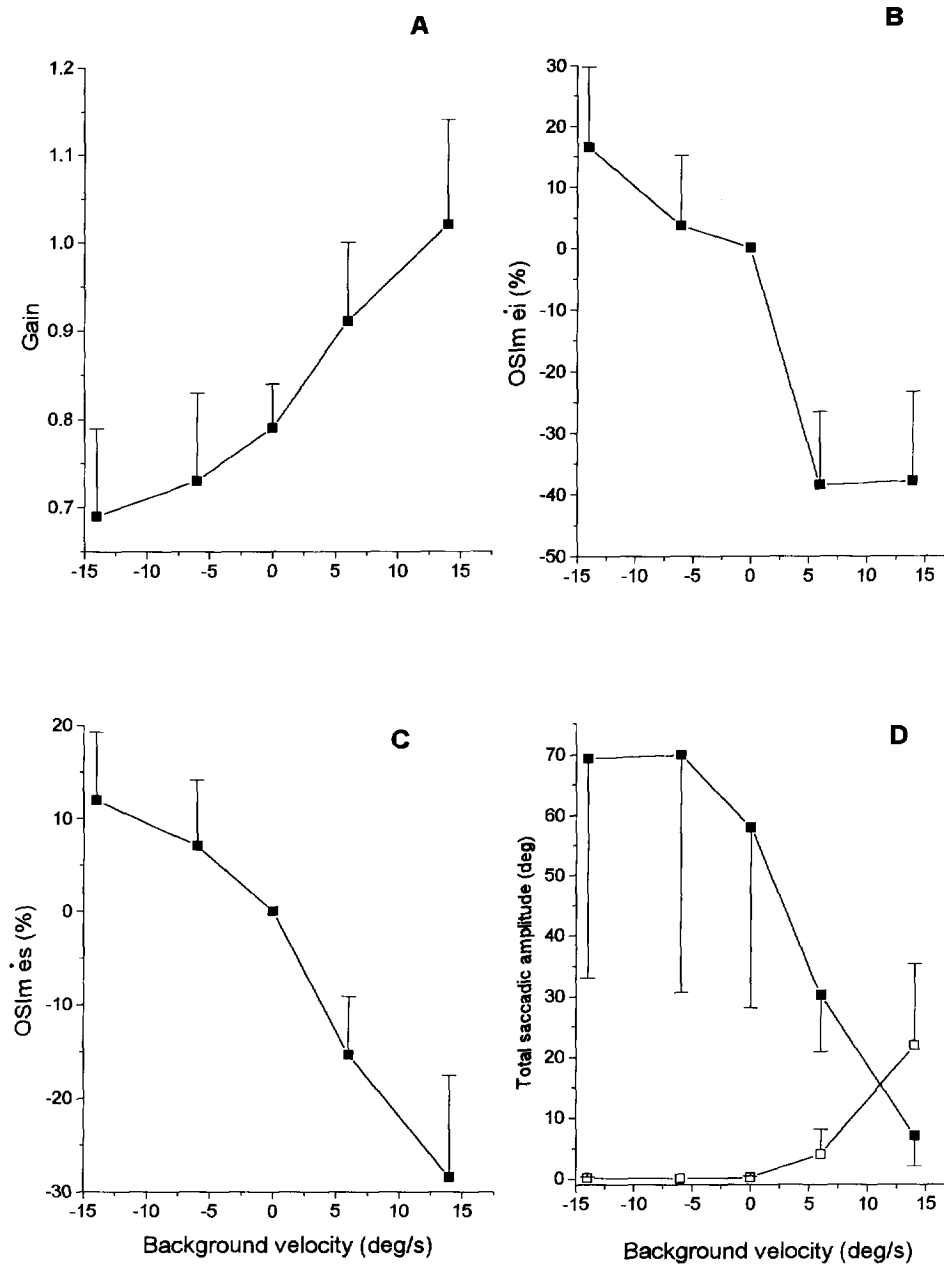


FIGURE 4. (A) Relationships between eye velocity gain during smooth-pursuit (mean and SD) and background velocity. (B, C). Relationships between background velocity and OSIm (mean and SD) for initial eye velocity ( $\dot{e}_i$ ) and steady-state eye velocity ( $\dot{e}_s$ ), respectively. (D) Total amplitude of positive (solid symbols) or negative (open symbols) catch-up corrective saccades occurring during visuo-oculo-manual tracking, as a function of background velocity.

Also, initial acceleration ( $\ddot{a}_i$ ) was affected similarly by the moving background velocity [ $F(4,16) = 3.37$ ;  $P < 0.05$ ], lending confirmation that the initial forearm velocity

was lowered when the background moved with the target and increased when the background moved against it. Of particular interest, we observed that the average  $\ddot{a}_i$

TABLE 2. Summary of response parameters of the ocular pursuit

Background velocity (deg/sec)	Latency (msec)	Gain $\dot{e}_s$	OSIm $\dot{e}_i$ (%)	OSIm $\dot{e}_s$ (%)
-14	182 ± 16	0.69 ± 0.1	16.6 ± 13.2	12 ± 7.3
-6	180 ± 22	0.73 ± 0.1	3.6 ± 11.6	7.1 ± 7
0	179 ± 17	0.79 ± 0.05	0	0
+6	180 ± 22	0.91 ± 0.09	-38.5 ± 32	-15.4 ± 6.3
+14	183 ± 20	1.02 ± 0.12	-37.8 ± 14.5	-28.5 ± 10.9

Values are averages and SDs across subjects. Abbreviations are explained in the text.

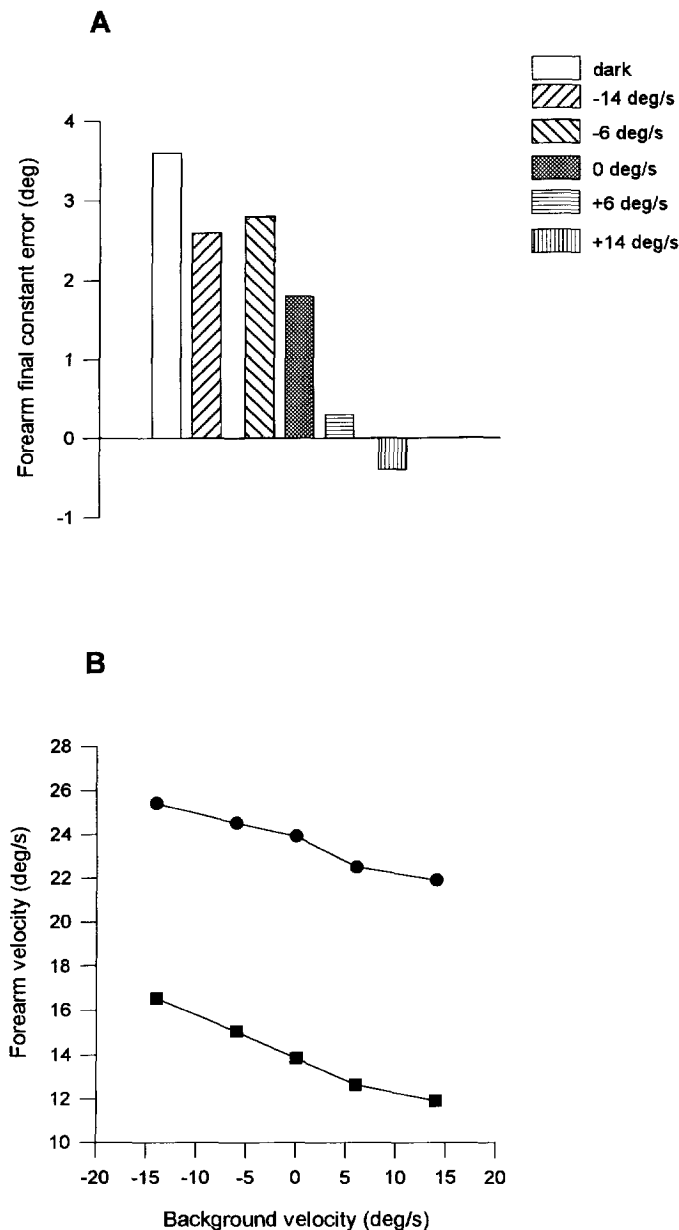


FIGURE 5. (A) Final CE<sub>f</sub> of manual tracking, in the six background conditions. (B) Relationships between background motion velocity and peak velocity (●) and between background motion velocity and steady-state velocity (■) of the manual tracking.

computed across subjects was linearly related to the background velocity ( $\dot{a}_i = -0.78 V_b + 113.2$ ;  $r = 0.98$ ,  $P < 0.05$ ). Samples of mean initial acceleration profiles from one subject are shown in Fig. 2B.

The steady-state velocity of the forearm rotation during its pursuit phase was also affected [ $F(4,16) = 56.9$ ;  $P < 0.05$ ]. More specifically, steady-state velocity was decreased (increased) when the background moved in the same (opposite) direction as the target, when compared to the stationary textured background. MSIm ranged from  $13.9 \pm 5.5\%$  to  $-19.5 \pm 5\%$  for background motion velocities between  $+14$  and  $-14$  deg/sec, respectively. There was a significant linear and inverse relationship between steady-state angular velocity and background velocity, as illustrated in Fig. 5(B) ( $\dot{a}_s = 13.99 - 0.17 V_b$ ;  $r = -0.99$ ,  $P < 0.05$ ).

Moreover, the peak forearm velocity during the pursuit phase was affected by both the direction and velocity of the moving background [ $F(4,16) = 13.48$ ,  $P < 0.05$ ]. *Post hoc* comparisons indicated a higher velocity peak when the target moved opposite to the background and the reverse was found when it moved in the same direction as the background. The relationships between peak forearm velocity and background velocity was best fitted by a linear regression function ( $V_{\text{peak}} = 23.66 - 0.13 V_b$ ;  $r = -0.99$ ,  $P < 0.05$ ). The kinematics data presented above were confirmed by the final performance of the manual tracking movement. As illustrated in Fig. 5(A), the different velocities of the textured background had a significant effect on the final position reached by the forearm [ $F(4,16) = 22.23$ ;  $P < 0.05$ ]. More precisely, subjects “overshot” the final target position when the textured background moved to the

left, whereas “undershoot” was observed when it moved to the right. These results are synthesized by a significant linear relationship between mean  $CE_f$  across subjects and background velocity ( $CE_f = 1.32 - 0.12 V_b$ ,  $r = 0.96$ ,  $P < 0.05$ ).

*Effects of a stationary or of a moving background on oculo-manual co-ordination*

The time delay between eye and arm movements initiation was not significantly affected by the superimposition of either a stationary textured background when compared to dark background [ $F(1,4) = 0.7$ ;  $P > 0.05$ ] or of a moving textured background when compared to a stationary textured background [ $F(4,16) = 0.41$ ;  $P > 0.05$ ]. As indicated in Table 1, this delay varied between 157 and 178 msec.

A first illustration of the differences existing between the effects of a moving background on ocular and manual tracking is provided by the comparison of Figs. 4(A) and 5(B). There is an inverse relationship between steady-state forearm velocity and steady-state eye velocity, as a function of background velocity. A displacement of the background in a direction opposite to the target resulted in a decrease in eye velocity and in an increase in forearm velocity. In the same line, displacement in the same direction of the background and of the target resulted in an increase in eye velocity and a decrease in forearm velocity. This comparison is further summarized in Fig. 6 which illustrates OSIm and MSIm for  $\dot{e}_s$  and for  $\dot{a}_s$ , respectively, as a function of the different background velocities.

We further investigated how changes in the velocity of smooth pursuit eye movements might determine opposite changes in forearm tracking velocity. One

hypothesis is that changes in oculomotor behaviour result in changes in the available information for movement control. In fact, movement control requires information about the actual velocity of a moving target. During smooth pursuit, such information derives from the integration of extraretinal signals encoding eye velocity with respect to the world and retinal signals encoding velocity of the target over the retina (Pola & Wyatt, 1989). Changes in steady-state eye velocity result in variations in the retinal velocity signal. Therefore, we computed the modifications of the retinal velocity of the target due to background-induced changes in smooth pursuit eye movements. The retinal velocity signal [RVS, equivalent to the retinal velocity error signal (see Morris & Lisberger, 1987)] was computed from mean values of the steady-state eye velocity gain (see Table 2) as:

$$RVS = V_t - \dot{e}_s = (1 - g_{es}) \cdot V_t$$

where  $V_t$  is the target velocity (i.e. 12.5 deg/sec) and  $g_{es}$  is the mean gain values of the steady-state ocular output (composite of active and passive smooth pursuit eye movement signals). The results are illustrated in Fig. 7. For a background moving against the target with a velocity of  $-14$  deg/sec, mean RVS was of  $-0.2$  deg/sec, corresponding to the experimental conditions in which saccadic eye movements opposite to the direction of the pursuit were observed [see Fig. 4(D)]. This condition also corresponded to the lowest steady-state forearm velocity. When the retinal velocity signal increased, the steady-state forearm velocity was linearly increased ( $\dot{a}_s = 11.75 + 1.04 RVS$ ;  $n = 5$ ,  $R = 0.96$ ,  $P < 0.05$ ). Thus, changes observed in forearm velocity appear to be related to changes in the retinal velocity of the target.

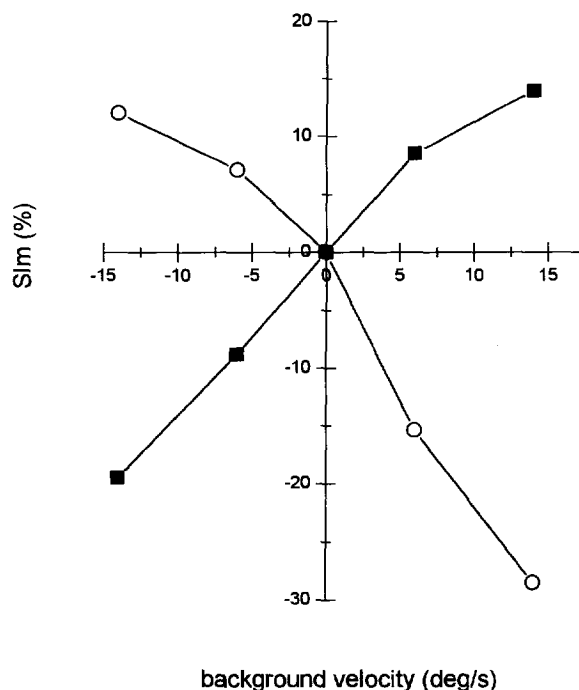


FIGURE 6. Effects of background motion velocity on manual (■) and ocular (○) suppression indexes of steady-state forearm and eye velocities. A negative Sim indicates an elevated tracking velocity; while a positive Sim indicates a decreased tracking velocity.

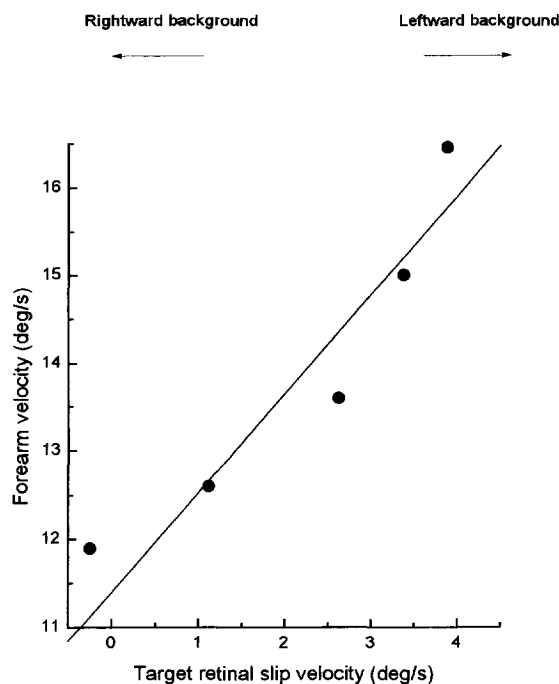


FIGURE 7. Relationships between steady-state forearm angular velocity and target retinal velocity. When the background moves rightward (i.e. in the same direction as the target) with a velocity of +14 deg/sec, the average target retinal velocity is of  $-0.2$  deg/sec, corresponding to the lowest manual tracking velocity. In this condition, catch-up negative saccades [see Fig. 4(D)] are observed.

## DISCUSSION

The goal of the present study was to determine whether visuo-oculo-manual tracking accuracy of a discrete target would be affected by the presence of textured backgrounds, either stationary or moving. Because the presence of a stationary or a moving textured background actually changed the oculomotor behaviour, we will first consider the characteristics of smooth pursuit eye movements before discussing how changes observed in eye movements and forearm movements might be related.

### *Pursuit eye movements in the presence of a stationary or a moving background*

The present study confirms that oculomotor behaviour is changed when a target displacement occurs over a textured background, either stationary or moving. First, smooth pursuit eye velocity during visuo-oculo-manual tracking was slightly but significantly lowered by the presence of a stationary textured background. This background effect, also called "masking effect" (Kimmig *et al.*, 1992), reduced both initial and steady-state velocities by approx. 10% and 13% respectively, which is consistent with previously published data in monkey (Keller & Khan, 1986; Kimmig *et al.*, 1992) and in humans (Collewijn & Tamminga, 1984). Nonetheless, the eye displacement gain (the ratio between eye and target displacement), which is the result of both slow and fast eye movements remained close to unity and this regardless of the presence or absence of a textured background (Collewijn & Tamminga, 1984; Worfolk & Barnes, 1992).

It is obvious that pursuing a moving target over a stationary textured background causes the background image to slip across the retina, in the direction opposite to that of the target. In general, such background image motion drives optokinetic, passive smooth pursuit eye movements. The present experimental data suggest that this optokinetic response is not completely switched off during ocular pursuit of a visual target and caused an interaction between active and passive eye movements (Howard & Marton, 1992; Worfolk & Barnes, 1992). In order to investigate this interaction the background and the target were set into motion simultaneously. As illustrated in Fig. 4, a background moving against the target resulted in both a lower initial and steady-state velocity of the eyes whereas increased initial and steady-state velocities were observed when the background moved in the same direction as the target. However, although the smooth pursuit eye velocity was changed as a function of background velocity and direction, a modulation in the occurrence, amplitude and direction of saccadic eye movements (back-up saccades when the background and target moved in the same direction or catch-up saccades when the background and target moved in opposite directions) resulted in an eye displacement gain remaining close to unity.

Finally, the size of the background-induced modulations was larger for initial eye velocity than for steady-state velocity (see Table 2). Thus, the initial, open-loop phase of the ocular smooth pursuit was strongly affected by background motion. However, with the present eye movement recording technique, we could not analyse the initial acceleration of smooth pursuit eye movements in these background conditions. We can

expect from studies conducted in monkeys by Keller and Khan (1986) and Kimmig *et al.* (1992) that a stationary textured background changes the initial response of the ocular pursuit in humans. Nevertheless, the precise effects of a moving background on the initial, open-loop velocity raise of the smooth pursuit eye movement remain to be investigated with appropriate recording techniques. Such experimental studies would provide valuable information about the interaction between active and passive slow eye movements.

The latency of the smooth pursuit eye movement was not affected (about 180 msec) by the type of background. This average latency was somewhat longer than that reported in previous studies using a pure ocular tracking task [between 100 and 135 msec (Carl & Gellman, 1987; Tychsen & Lisberger, 1986)] or visuo-oculo-manual tracking [about 150 msec (Domann, Bock & Eckmiller, 1989)]. The longer latency observed in the present study might be related to the procedure we used for detecting movement onset (based on eye position rather than eye velocity). Moreover, we used a ramp target-displacement paradigm, and not a "step-ramp" stimulus which usually results in short latencies of smooth-pursuit initiation (Rashbass, 1961). Finally subjects were not aware of which background condition would occur, and such unpredictability might delay ocular responses (Kowler & Steinman, 1979). However, this difference is not crucial, considering that in the present experiment, latency of smooth pursuit was rather constant across the different background conditions. This indicates that the salience or detectability of the target was not strongly modified by the presence of a background, either stationary or moving.

In short, the present data indicate that both velocity and direction of motion of a textured background change the oculomotor behaviour, and suggest that these effects cannot be explained by cognitive or attentional processes. However, two aspects of our experimental conditions should be considered before extending the observed effects to the general case. First, the apparent angle of the optokinetic stimulation was restricted to 20 deg in central vision. Although the central visual field is a powerful determinant of optokinetic responses in humans (van Die & Collewijn, 1982), the gain of the optokinetic reflex is determined by the velocity of the stimulation but also by its apparent angular extent (Henn, Cohen & Young, 1980). In this context, our results on smooth pursuit eye movements are consistent with previous studies using larger optokinetic stimulation (Yee *et al.*, 1983; Collewijn & Tamminga, 1984). Still, the effect of the apparent angle of the optokinetic stimulation during visuo-oculo-manual tracking remains to be evaluated. This point might be crucial to our understanding of the interaction between self-motion perception, object-motion perception and goal-directed behaviour. Secondly, the contrast level of the target and the background dots were equal in the present experiment. Whether different contrasts, or different colours of the target and the background dots might change the results by enhancing the salience of the target

remains to be investigated. This point is particularly important in order to understand in which conditions subjects are able to select and track a discrete moving object and whether they are able to "ignore" the visual motion of the surrounding.

#### *Effects of background and target velocities on oculomotor behaviour*

The existence and the signification of the background effects on smooth pursuit eye movements remains controversial. Originally, it was thought that the presence of a stationary, textured background had no effect on tracking ocular movements of a target moving against it. For instance, Kowler *et al.* (1984) found only a negligible effect of a stationary, structured background on steady-state human pursuit. They explained the decrease in gain values of steady-state eye velocity (about -10% and -20% in the horizontal and vertical directions respectively) reported by Collewijn and Tamminga (1984) as representing a failure of the subjects to apply sufficient effort or attention to select the target over the background as the stimulus to attend. However, this interpretation was challenged by Keller and Khan (1986) and Kimmig *et al.* (1992), from studies conducted in monkeys. In the present study, such cognitive interpretations can be rejected because the latency of the ocular smooth pursuit was not significantly modified by the presence of a textured background compared to a dark one, while smooth pursuit velocity was modified. A lack of attention should have resulted in a longer latency in the presence of a textured background. Explanations based on the difficulty to attend to the target over a textured background can thus be rejected. A more plausible explanation of the discrepancies between the results of these different studies lies in the velocity at which the target crossed the visual display. Kowler *et al.*'s (1984) used targets moving at 1.2 deg/sec whereas experiments in which a significant effect of a stationary textured background was observed used targets moving at 10 deg/s or more, as in the present study (e.g. Niemann *et al.*, 1994). Therefore, the changes observed in the oculomotor behaviour when the background is stationary becomes more and more apparent when the gain of the active slow eye movement system decreases (Worfolk & Barnes, 1992).

Thus, the velocity of the target to be pursued has been considered as a major factor in the occurrence and magnitude of these effects (Worfolk & Barnes, 1992). Nevertheless, when the eye pursues a target moving faster, the opposite apparent motion of the background on the retina also becomes faster. Hence, we might expect that optokinetic intrusions were induced by the background apparent motion. Furthermore, in the case of an actually moving background, these optokinetic intrusions should also depend on the background actual motion. The present results show that the velocity gain of slow eye movements is inversely related to the background velocity [Figs 4(A) and 6]. This clarifies discrepancies between previously published data. For instance, Ter Braak (1957) and Hood (1975) first noticed

an enhanced velocity gain of the ocular smooth pursuit of a discrete target, when the target and background moved in opposite directions. In contrast, Stark (1971) claimed that smooth pursuit eye movements were accelerated when target and background move in the same direction but were lowered when target and background move opposite each other. Yee *et al.* confirmed this last result, suggesting a facilitator or inhibitory interaction between voluntary eye pursuit related to target motion and reflexive following eye movements related to background motion when backgrounds moved with or against the target direction, respectively (Yee *et al.*, 1983). Our data support those reported above by Stark (1971) and Yee *et al.* (1983). They show that the facilitator or inhibitory effect associated with background motion are modulated by the relative velocity existing between the target and the background.

#### *Consequences of the optokinetic stimulation on manual control*

The oculomotor system can override the effect of optokinetic intrusions by monitoring retinal position error of the target. More frequent saccades may help keeping the eye displacement gain close to unity (Collewijn & Tamminga, 1984; Worfolk & Barnes, 1992). However, significant modifications of the steady-state eye velocity remain. In the present study, we were interested in the consequences of such modifications on manual tracking. We showed that steady-state forearm velocity was increased or decreased when the background moved against or with the target, respectively. Both initiation and final performance of the forearm tracking were changed in a similar way (see Fig. 5 and Table 1). Moreover, all these kinematics changes were linearly related to the background velocity. A particular point in the present experiment is that background motion velocity and direction have opposite effects on oculomotor behaviour and forearm tracking movement. When the background moves opposite to the target, smooth pursuit eye velocity is decreased and forearm tracking velocity is increased. The opposite effect occurs when the background moves in the same direction as the target. Two questions are directly related to this result. First, does the manual motor system use perceived velocity of the target in such conditions? Secondly, how changes in both perceived target velocity and forearm tracking velocity are related to changes in oculomotor behaviour?

#### *Does the manual motor system use perceived velocity?*

Bridgeman, Lewis, Heit and Nagle (1979) and Bridgeman *et al.* (1981) have answered the preceding question in a negative way and claimed that the motor system is immune to manipulations of visual stimuli that modify the perceived location of objects. Their results led to the proposition that perception and visually guided behaviour use distinct visual representations of target position and/or motion. On the contrary, our results and that of psychophysical studies about perceptual consequences of optokinetic backgrounds suggest

that manual tracking modifications are related to perceptual consequences of a moving background. In the present experiment, the target was spontaneously perceived by the subjects as moving faster when the background moved against the target, but slower when the background moved with the target. Moreover, Raymond *et al.* (1984) demonstrated that subjects over- or under-estimated the velocity of an actively pursued object when a textured background moved against or with that object. A uniform or a stationary textured background never lead to such misperception of target motion. Recently, Honrubia *et al.* (1992) reproduced these results and showed that changes in perceived velocity were linearly related to background velocity in the range used in the present study. The magnitude of the modifications of the perceived velocity reported in the above psychophysical experiments lied between 5% and 15% (Raymond *et al.*, 1984; Honrubia *et al.*, 1992). A similar dependency (and magnitude) of the changes in forearm velocity on both background motion velocity and direction was observed in the present study. Therefore, our data are consistent with the hypothesis that the manual motor system is programmed and controlled on the basis of the perceived velocity of the pursued object.

In a consistent way, Farber (1979) and Bacon *et al.* (1982) showed that perceived location (as manipulated by a superimposed optokinetic stimulation) of a target might be used instead of its actual location as an input for reaching movements. Similar evidence were recently published by Grüsser, Guldin, Harris, Lefebvre and Pause (1992). However, the aforementioned studies were mainly concerned with position input to the manual reaching motor control. Thus, no data were available on velocity input to the manual tracking motor control in similar conditions. The present study extends these results by showing that an optokinetic stimulation can alter motion perception and tracking behaviour in a similar way. Thus, it appears that the perceptual apparatus and the manual motor system use similar information about target velocity. The question is then to describe the nature of this information, and its relationships to the oculomotor behaviour.

#### *Relationships between forearm velocity, perceived velocity and target retinal motion*

In Raymond *et al.*'s study (1984), when the subjects were asked to stare at a fixation point, misperceptions of the object motion due to a moving background did not occur. Hence a misperception of target motion seemed to be dependent on eye movements in such conditions. We show in the present study that changes in manual tracking accuracy are related to the changes observed in oculomotor behaviour. Consistent with this assumption is the linear relationship found between the steady-state manual tracking velocity and the target retinal velocity (Fig. 7), suggesting that changes in forearm velocity might be related to changes in target retinal velocity, which are themselves generated by the decrease or the increase of the actual eye velocity. This suggestion is supported by the fact that the average steady-state

forearm velocity and the average retinal velocity signal are linearly related (with a proportionality factor close to 1). When the retinal velocity signal is increased by a value of 4 deg/sec, we observed a change of about 4.5 deg/sec in the forearm movement velocity. Thus, changes in retinal slip velocity and forearm velocity seem to be closely related. This relationship suggests that the manual motor drive is closely dependent on the retinal velocity signal. However, our results have to be extended with precaution. In particular Brenner and Smeets (1994) recently observed, when background motion was superimposed to target motion, that both the perceived velocity of the target and the velocity of hitting movement made towards the target were modified. However, neither the final judged position of the target nor the direction of the hitting movement were affected. Their results argue for the existence of different processing modes for motion and position information at both the perceptual and the motor level.

To accurately pursue a moving target, the limb movement control system needs information about target position and/or target velocity relative to the self. In open-loop conditions, as in the present experiment, no retinal feedback about the limb-target position error is available. The limb movement control system must therefore use an estimation of the actual target velocity, which is a combination of a retinal signal and of an extraretinal signal about the velocity of the eye in the orbit (von Helmholtz, 1867; Pola & Wyatt, 1989; Wertheim, 1990). We have observed that the retinal velocity signal changed as a function of the actual eye output velocity, which was, in the present study, a combination of active and passive eye-velocity commands (see also Yee *et al.*, 1983). Raymond *et al.* (1984) suggested that misperceptions of target velocity in similar experimental conditions may be explained by the lack of efference copy from the passive eye-velocity command to the perceptual apparatus (Dichgans & Brandt, 1978). Thus, the extraretinal signal should inform the perceptual apparatus about the voluntary eye-velocity command without considering the additional reflexive eye-velocity command. Hence, we suggest that the perceptual apparatus integrates an efference copy from the active eye-velocity command and a modulated, background-velocity dependent, target retinal velocity signal. Such integration leads to a misperception of the actual target velocity, and consequently to changes in motor behaviour.

We consequently suggest that neither the perceptual apparatus nor the limb movement control system are able to use the actual velocity of the eye in the orbit to compute the actual target velocity. Our data are coherent with the hypothesis that the limb movement control system uses perceptual information about target motion, based on outflow from the active smooth-pursuit generator and the retinal target velocity. In line with this, Newsome, Wurtz and Komatsu (1988) have brought experimental evidence suggesting that such constructed velocity might be elaborated in the cortical areas MT and MST, this latter projecting directly to the parietal

lobe, which appears to be crucial for the perception of the changing relations between the body and objects in surrounding space as well as for the control of goal-directed movements (see Jeannerod, 1988).

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*Acknowledgements*—This study was supported by the Centre National de la Recherche Scientifique and by grants from Naturalia & Biologia and Ministère de la Recherche et de l'Espace (GM) and from the Conseil de la Recherche en Sciences Naturelles et Génie of Canada (LP). We thank D. Benza for software development, G. M. Gauthier and J. L. Vercher for providing us the apparatus for eye-movement recording and for their helpful suggestions to improve the earlier versions of the manuscript.