Exp Brain Res (1992) 90:599–609

Experimental Brain Research

Oculo-manual coordination control: Ocular and manual tracking of visual targets with delayed visual feedback of the hand motion

J.-L. Vercher and G.M. Gauthier

Laboratoire de Contrôles Sensorimoteurs, Université de Provence–URA CNRS 372, Avenue Escadrille Normandie-Niemen, F-13397 Marseille cedex 13, France

Received September 7, 1991 / Accepted March 16, 1992

Summary. The aim of this study was to examine coordination control in eye and hand tracking of visual targets. We studied eye tracking of a self-moved target, and simultaneous eye and hand tracking of an external visual target moving horizontally on a screen. Predictive features of eye-hand coordination control were studied by introducing a delay (0 to 450 ms) between the Subject's (S's) hand motion and the motion of the hand-driven target on the screen. In self-moved target tracking with artificial delay, the eyes started to move in response to arm movement while the visual target was still motionless, that is before any retinal slip had been produced. The signal likely to trigger smooth pursuit in that condition must be derived from non-visual information. Candidates are efference copy and afferent signals from arm motion. When tracking an external target with the eyes and the hand, in a condition where a delay was introduced in the visual feedback loop of the hand, the Ss anticipated with the arm the movement of the target in order to compensate the delay. After a short tracking period, Ss were able to track with a low lag, or eventually to create a lead between the hand and the target. This was observed if the delay was less than 250–300 ms. For larger delays, the hand lagged the target by 250–300 ms. Ss did not completely compensate the delay and did not, on the average, correct for sudden changes in movement of the target (at the direction reversal of the trajectory). Conversely, in the whole range of studied delays (0–450 ms), the eyes were always in phase with the visual target (except during the first part of the first cycle of the movement, as seen previously). These findings are discussed in relation to a scheme in which both predictive (dynamic nature of the motion) and coordination (eye and hand movement system interactive signals) controls are included.

Key words: Smooth pursuit – Oculo-manual tracking – Coordination control – Self-moved target tracking – Delayed visual feedback – Prediction

Correspondence to: J.L. Vercher

Introduction

In the past few years a large number of studies have shown that smooth pursuit (SP) performance during ocular tracking of a visual target is improved when the target motion is directly controlled by the observer's hand or arm (for simplicity we shall indifferently use arm or hand to refer to arm motion). This was reported both in human beings (Steinbach and Held 1968; Gauthier and Hofferer 1976; Mather and Lackner 1981; Bock 1987; Gauthier et al. 1988) and in trained monkeys (Gauthier and Mussa-Ivaldi 1988; Vercher and Gauthier 1988; Domann et al. 1989). These studies showed a decrease of SP delay, and an increase of SP accuracy and maximum velocity when the observer tracks a target attached to his own hand. This phenomenon has been described as coordination control between two sensori-motor systems simultaneously involved in a motor task (Gauthier et al. 1988), and was hypothetized to be due to an exchange of information between the two sensori-motor systems. It is interesting to note that a similar type of performance improvement (in terms of delay and maximum velocity) has been recently demonstrated in the vergence system by Erkelens et al. (1989) when the hand is used as a target. Coordination between eye and hand movements is greatly dependent on the nature and the congruence of the cues provided to the Subject (S) about the hand motion: indeed, a combination of auditory, tactile, proprioceptive and visual information about the arm position enhances the tracking performance (Levine and Lackner 1979; Mather and Lackner 1980).

Changes of performance of the SP system, between eye-alone tracking of a visual target and tracking one's hand, were essentially quantified in terms of increased maximum velocity, decreased latency at the onset of movement, and widening of the frequency range. All of these parameters characterize a broadening of the limits of the SP system. It is worth noting that if the characteristics of target motion (frequency, amplitude and maximum velocity) are well below the dynamics limits of the SP system, the performance of a human S is quite similar in terms of gain, phase and tracking precision, when tracking an external target moving in a predictable way (sinusoidal motion) or a self-moved target. In particular, a S is able to track with his eyes a sinusoidally moving target with no phase at all, and from time to time with a small lead (Bahill and McDonald 1983a; McHugh and Bahill 1985), due to a predictive mechanism proper to the SP system (Stark et al. 1962; Dallos and Jones 1963; Michael and Melvill-Jones 1966; Sugie 1971; Bahill and McDonald 1983b; Ohashi et al. 1987). In such conditions with low dynamics and predictable target motion, it is difficult to decide if the increase of performance observed during tracking of a self-moved target, especially the decrease of lag, is due to an internal coupling between the arm motor system and the oculomotor system through non-visual signals, or is the effect of a particular form of prediction. Indeed, with a self-moved target, one may assume that the movement of the target is perfectly known by the S. The decrease of latency when tracking the hand-moved target may be compared to the anticipatory smooth eye movement described by Kowler et al. (1984), observed when the S knows both the direction of the target displacement, and the moment of its onset (indicated by a cue). This early slow (low gain) SP eye movement is highly dependent on stimulus conditions (Boman and Hotson 1988).

One way to dissociate internal coupling from prediction is to decorrelate the hand motion and the hand-moved target motion, in such a way that the SP system receives two inputs, one internal, derived from the arm movement itself, the other visual, and thus external. This has been previously done by changing the relationship between the hand motion and the target motion, for instance by introducing a linear or a topological transformation between the hand motion and the target motion (Steinbach 1969; Mather and Lackner 1981), by increasing or decreasing the amplitude of the target motion relative to the hand motion (Mather and Lackner 1981) or even by reversing this relationship (when the hand is moving to the right, the target moves to the left and vice-versa: Neilson and Neilson 1980; Domann et al. 1989).

In order to separately study predictive features related to target movement pattern and self-motion signals, one may decorrelate in terms of time, the hand and the hand-moved target by artificially introducing a delay in the visual feedback loop of the hand. Hand target motion is delayed, relative to hand motion, but hand motion and target motion share the same spatial and dynamical characteristics. The effects of delayed visual feedback on arm tracking performance have been previously described (Smith 1972; Miall et al. 1985). A common observation from these authors is a sudden decrease of performance when a delay larger than 200–250 ms (close to the human response delay) is introduced in the visual loop.

Such a temporal decorrelation between hand motion and visual feedback is encountered in tele-operation of remote robots. These delays can reach several hundred milliseconds, inducing dramatic decreases of performance when the operator tries to make fast corrections on the remote system.

The present study describes how the hand motor system can compensate a delay in the visual feedback if the motion of the target is predictable, and also gives insight into the behavior of the oculomotor system under these conditions. We also looked in detail at the relative contribution of visual information and internal information for SP initiation and control when hand motion and hand-moved target are shifted in time. The data allow a comparison between predictive control of the SP system resulting from predictive target motion and prediction-like coordination control when the target motion is self-induced.

Methods

Subjects

Six Ss, ranging in age between 22 and 50 years were used for this study. They were students or faculty members of the Department and were all familiar with oculo-manual tracking experiments. They gave informed consent to participate to this study. One of the authors (GG) was himself a S.

Experimental setup

Figure 1 shows the experimental setup. The S was seated at 171 cm in front of a projection screen (3 cm on the screen were equivalent to 1° as seen from the S's eye), with his head immobilized by a bite-bar. Eye movements were recorded by means of an infrared corneal reflexion device (IRIS, Skalar). The right arm rested on a metallic plate, with the hand grasping a vertical rod and pointing in the direction of the projection screen. The movement of the arm was recorded with a precision potentiometer, mounted coaxially with the rotation axis of the plate, roughly at elbow level.

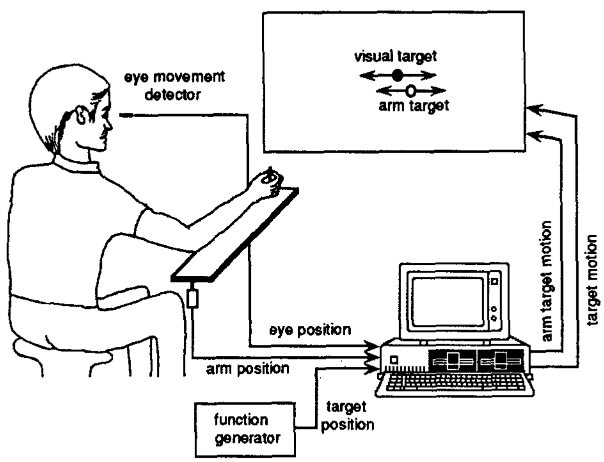

Fig. 1. Experimental setup. The S (S) is seated in front of a projection screen. Eye movements are recorded through an infrared corneal reflexion detector. Movement of the arm is recorded with a precision potentiometer. Both signals are sent to a computer through an analog to digital converter. The S has no direct vision of his hand, but a visual cue of the ongoing movement through a target projected on the screen (HAND TARGET). Another target (VISUAL TARGET) is used to provide an external target to the S. A delay is introduced by computer between the movement of the hand and the movement of the hand-moved target. Hand target motion on the screen is adjusted to provide a one-to-one relationship as seen by the S's eyes between rotation of the handle and hand-target movement

The experiment was controlled by a personal computer provided with a 12-bit A/D-D/A converter board. Signals from a function generator (used to generate target position signal), the eye movement monitor device and the hand position monitoring potentiometer were digitized (500 samples/s) and displayed in real-time on a standard color graphics screen. This allowed the experimenter to monitor the experiment and control the stability of the recorded signals. Individual recording runs were stored on a hard-disk for off-line analysis. Both target position and arm position signals were output at the same rate by the computer and sent to the device controlling the movement of the corresponding targets projected on the screen.

Two spots of light individually driven by mirror-galvanometers (GENERAL SCANNING), were used to provide two targets. For convenience in the ensuing description of the tracking conditions, we shall name the stimulus target the "VISUAL TARGET" (Fig. 1) and that moved by the S the "HAND TARGET". Both targets were physically visual targets, similar in nature but different in shape. The visual target was driven by a function generator and controlled by the computer. Sinusoidal oscillations at 0.2 Hz and 0.5 Hz were used. The amplitude of the target movement was $\pm 5°$, with a maximum velocity for each frequency of 6.28 and 15.7°/s, respectively. We deliberately used highly predictable target motions since the aim of this study was to investigate temporal relationships between arm motion and eye tracking of the visual feedback of the arm. We chose to place the S in a perfectly predictable situation (when tracking an external target), in order to allow the arm motor system to track reasonably well the external target in spite of the delay we were to introduce between arm and arm target motion. High velocity or unpredictable target motion would result in low tracking performance. The effects resulting from the artificially introduced delay between arm and arm target would then be masked out and/or combined with the alteration resulting from the target high dynamics characteristics.

The signal from the potentiometer, proportional to the arm position, was used to move the HAND TARGET. The S had no direct vision of his hand, but only a visual cue of the ongoing movement through the hand-moved target projected on the screen. Before each experiment, a laser beam temporarily mounted on the forearm-resting plate was used to calibrate the displacement of the target controlled by the arm motion. The pointing direction of the arm and the arm rotation amplitude were adjusted so that the arm-driven spot was in line with the arm.

Tracking conditions and instructions

Two tracking conditions were used:

1. *Ocular and manual tracking of a visual target.* The two targets were presented on the screen: the movement of the first one (visual target) was controlled by the function generator, the movement of the second one (arm target) was controlled by the signal from the potentiometer, thus controlled by the movement of the S's hand. The instruction provided to the S was to track the visual target with his eyes and, by moving his arm, try to maintain the hand target in spatial and temporal coincidence with the visual target.

2. *Ocular tracking of a self-moved target.* Only the hand-controlled target was displayed. The instruction was to move the hand sinusoidally and track the hand target with the eyes. Two motion frequencies were tested, 0.2 and 0.5 Hz. To achieve constant frequency and amplitude (set at 10 degrees peak to peak), each run began with a practice period during which the Ss were presented a sinusoidally moving target on the screen, at the appropriate frequency and amplitude. Thus, recording began after 10–15 s of training.

In both conditions, a delay could be introduced in the visual feedback loop between the movement of the arm and the movement of the hand target on the screen. The signal from the potentiometer was digitized, stored, delayed (0 to 450 ms by steps of 50 ms) and output by the computer. The analog signal output by the computer to control the position of the hand target was then a linear function with a one to one relationship to hand movement, but shifted in time.

Experiment 1. Steady-state tracking

In this experiment, the S was allowed 10–15 s to reach stable eye and hand tracking, then a 30 s sequence was recorded and stored on disk. Though aware that a delay would possibly be introduced in the visual loop, the Ss did not know the selected delay before the trial, because the 10 delay values tested in each experiment were applied in random order.

Experiment 2. Transient tracking

In this experiment, eye and hand responses were analysed at the very beginning of tracking of a self-moved target when delayed visual feedback was used. The S was first instructed to maintain the hand target at the center of the screen while fixating it. Then, when a beep was delivered by the computer the S had to move his arm at the frequency practiced 10–15 s before the beginning of the recording run, and track the hand target with the eyes. A delay was randomly introduced in the visual feedback loop. Following the beep, 10 s runs were recorded. All records starting purely with a saccade (only 5%) were rejected from the analysis.

Data analysis

All Ss were tested at least two times. Under the two tracking conditions, all delay values were tested 4 times for each session. This provided at least 8 runs for each delay in each condition and for each S. Eye and hand movements were separately analysed during the initial phase of tracking (first and second cycle) and during steady-state tracking (after 10 to 15 cycles of target motion). Data, recorded as sampled signals, were recalled from the disk for analysis with an interactive program. After removing the saccades (using a method similar to the one described by Ebisawa et al. 1988), gain and phase were computed using a fast-Fourier analysis. Gain was obtained by dividing the module of the response signal (hand or eye velocity) by the module of the target velocity signal. Phase was calculated by subtracting the absolute phase (referred to the signal peak) of the response signal from the phase of the target signal. The mean amount of time-shift between signals (positive values corresponding to a lag, and negative values a lead) was evaluated by cross-correlation. Local time-shift was determined as the time difference between corresponding (zero velocity) points of hand and target signals, yielding one value for each peak and trough of the tracking wave. Phase was finally expressed in ms in order to allow comparison with delays.

Results

Experiment 1

In a first experiment, Ss were instructed to track with their eyes a moving visual target, and to move their arm in order to maintain a second target, controlled by the movement of the arm, in spatial and temporal coincidence with the first one. Ss were allowed to execute the task for 10 to

15 s, before signal acquisition was initiated. Condition 1 (eye and arm tracking) and condition 2 (eye tracking of the arm) were alternately executed. In condition 2, the visual target was presented for training at the beginning of the trial. Table I exhibits average and standard deviation for gain, phase and number of saccades per cycle in each condition and each S.

Condition 1. Eye and arm tracking of a visual target. Time recordings such as the ones shown in Fig. 2 provided a first evaluation of the tracking behavior. The eyes and the arm moved sinusoidally, at the same frequency and amplitude as the visual target (0.2 Hz, $\pm 5°$). When no artificial delay was introduced between the movement of the arm and the movement of the arm-controlled target, the behavior was very similar to that observed in previous experiments (Gauthier et al. 1988). When a delay was introduced, Ss were not systematically aware that the arm target was delayed relative to their arm motion. In fact, the lowest (50 ms) delay was never perceived. With 100 ms delay, the Ss reported to feel as if their arm or the arm-attached plate was "elastic". Runs with longer delays were always definitely identified as being "altered". The perception of a delay was concomitant with a major change in the strategy of arm tracking. Quantitative analysis showed that the Ss moved his arm in anticipation of the movement of the target, by an amount of time equivalent to the introduced delay. The use of sinusoidal targets made this possible. When large delays were used, (more than 300 ms), the S was evidently not able to sufficiently anticipate. The resulting tracking was composed of numerous large and fast movements of the arm in an attempt to catch up with the visual target (Fig. 2B). This behavior sometimes generated a kind of oscillation of the arm movement, especially around target direction reversal: the arm accelerated to rejoin the target, then passed it because the target decelerated, then the arm slowed down and so on. The Ss reported that the task was growing more and more difficult as the delay increased, and delays longer than 300 ms were reported as difficult to compensate (as evidenced by the analysis).

Analysis shows that in all runs, including those with long delays, the only change in eye movement morphology was a small, non significant increase in the number of saccades (Table 1). These saccades were not the type of corrective, catch-up saccades observed when the gain of SP was not appropriate (always triggered in the direction of the target motion), but were going back and forth around the position of the target. The amplitude of these saccades could not be correlated to the positional distance between the real arm position and the arm target, resulting from the artificially added delay, nor to the error between the arm target and the visual target.

Figure 3A represents the average gain as a function of the introduced delay for all Ss and all sessions. The gain of eye movement with respect to target movement did not change when a delay was introduced, while the gain of the arm increased, with increasing delay (table 1).

The lag between the eye and the target was very short and remarkably constant over the whole range of delays (Fig. 3B, filled circles). Conversely, as the introduced delay increased, the delay between the arm and the target increased, with the arm leading the target (Fig. 3B, open circles). For the extreme tested delays, the values are as follows: 19.55 ms $\pm$ 29.70 ms for 0 ms delay, 32.50 ms $\pm$ 41.78 ms for 450 ms delay. This is consistent with the observation that the S anticipated the visual target motion with his arm. Adding this delay to the introduced delay provided the overall delay between the arm target and the visual target (Fig. 3B, triangles). The lag between the arm target and the visual target was constant (35.66 $\pm$ 37.91 ms) for delays ranging from 0 to 200 ms. For larger delays, the arm target lagged more and more as the artificial delay increased.

Condition 2. Ocular tracking of a self-moved target. Figure 4A shows an example of ocular tracking of the arm-moved target. When a delay was introduced, the most obvious feature was that the eyes continued to track the arm-moved target with good accuracy. The Ss perceived that a delay was introduced but for higher delay values than in the previous condition. All Ss definitely perceived an alter-

Table 1. Average values for parameters quantifying tracking performance, for all Ss. Gain is calculated as eye velocity over visual target velocity while phase is the time difference (in ms) between the visual target and the eyes. Values are given for the two tracking conditions, with no artificial delay (0 ms) and with the highest tested artificial delay (450 ms)

S's name: sex, age:		GG M,50 y	MV M,45 y	DC M,22 y	DN F,22 y	YZ F,28 y	CB M,36 y
Gain cond 1	0 ms	0,99 ± 0,02	0,98 ± 0,03	0,97 ± 0,06	1,05 ± 0,05	0,97 ± 0,04	1,01 ± 0,04
	450 ms	1,06 ± 0,07	0,89 ± 0,06	1,03 ± 0,09	0,89 ± 0,06	1,03 ± 0,04	1,01 ± 0,11
Gain cond 2	0 ms	0,95 ± 0,01	0,96 ± 0,04	1,09 ± 0,05	0,97 ± 0,06	1,01 ± 0,08	0,95 ± 0,15
	450 ms	0,92 ± 0,04	0,91 ± 0,03	0,92 ± 0,29	0,99 ± 0,16	0,98 ± 0,05	0,90 ± 0,02
Lag cond 1 (ms)	0 ms	31,67 ± 11,55	15,00 ± 26,46	17,50 ± 22,17	18,75 ± 22,87	23,33 ± 16,07	11,67 ± 20,21
	450 ms	16,67 ± 12,58	40,00 ± 7,07	36,67 ± 7,64	23,75 ± 17,00	42,10 ± 6,24	40,00 ± 7,00
Lag cond 2 (ms)	0 ms	24,50 ± 12,12	38,50 ± 10,61	30,50 ± 7,78	31,50 ± 10,21	25,50 ± 9,04	20,50 ± 9,19
	450 ms	−76,00 ± 7,07	35,50 ± 13,54	36,00 ± 11,41	−20,25 ± 54,54	−5,00 ± 43,31	−46,00 ± 42,43
Sacc/cycle cond 1	0 ms	4,25 ± ,77	1,71 ± 0,17	3,53 ± 0,84	2,47 ± 0,98	2,25 ± 0,78	1,88 ± 0,71
	450 ms	5,62 ± 1,61	3,33 ± 1,03	4,33 ± 0,91	4,21 ± 1,02	3,85 ± 0,65	2,98 ± 0,84
Sacc/cycle cond 2	0 ms	3,67 ± 0,66	3,11 ± 1,59	3.95 ± 1,59	1,98 ± 0,84	2,57 ± 1,21	3,35 ± ,050
	450 ms	4,55 ± 0,54	4,58 ± 1,48	6,77 ± 2,02	3,02 ± 1,01	4,12 ± 1,11	3,80 ± 0,67

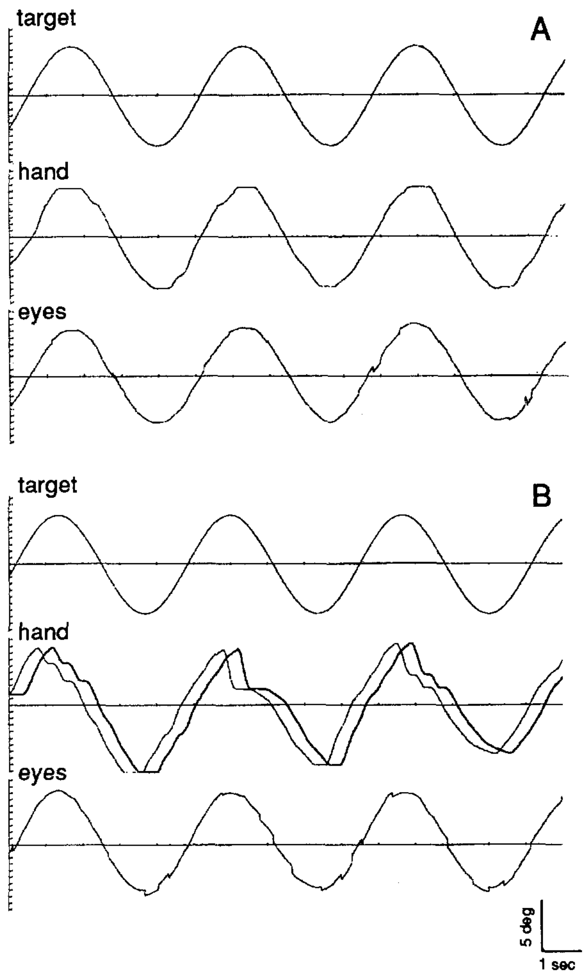

Fig. 2A, B. Typical ocular and manual tracking of a visual target without artificial delay (A) and with a 400 ms artificial delay (B). Traces represent, from top to bottom, position of visual target, hand and eyes as a function of time. In block B, the hand motion is represented by two traces, the thinner trace is the actual hand motion, the thicker one is the hand-moved target motion, that is the hand motion shifted in time by 400 ms. The frequency of the target movement is 0.2 Hz, its amplitude is $\pm 5°$. Total recording time is 15 s. This picture shows that the S is not always successful at anticipating the changes in direction of the target motion for such large delay. The S makes fast arm movement in order to align the delayed hand-moved target with the visual target

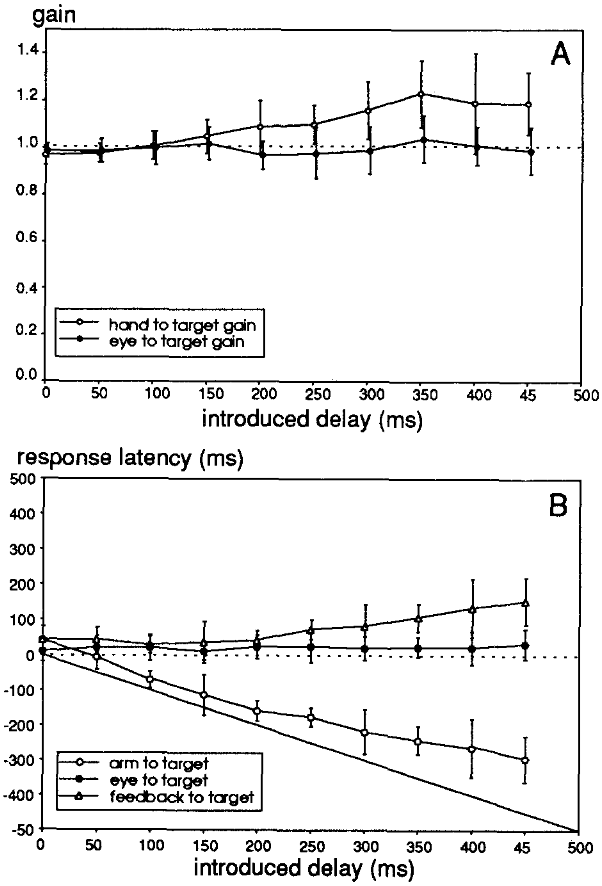

Fig. 3A, B. Tracking gain (A) as a function of artificial delay in ocular and manual tracking of a visual target. Velocity gain between the arm motion and the target motion (open circles) and between the eye motion and the target motion (filled circles) are plotted as a function of the artificial delay between 0 and 450 ms. Values are average and standard deviation for all Ss and 4 trials for each S. The eye/target gain is remarkably constant over the range of delays. Conversely, the hand/target gain increases as a function of the introduced delay. The phase (B) between arm or eyes, and target, is expressed in ms and calculated by cross-correlation applied to signals recorded for 15 s and starting 15 s after the S began to track the target, in order to allow predictive and/or adaptive phenomena to be stationary. Filled circles represent the phase between the eyes and the target; open circles represent the phase between the arm and the target, the triangles represent the phase between the hand-moved target and the visual target. The eyes lag the target by a constant amount (20–30 ms) all over the range of delays, while the arm progressively anticipates the target motion, as characterized by negative values. Between 50 and 250 ms of artificial delay, the arm partially compensates the artificial delay, and a remaining lag of 30–40 ms between the hand-moved target and the visual target is indicated by the filled circles. Between 250 and 450 ms, the arm still anticipates the target, but more poorly, since the lag between the hand-moved target and the visual target increases as a function of the artificial delay

ation when a 200 ms (or larger) delay was used. Besides, while during most of the time, eyes tracked the visual target, with an accurate gain and no phase, as in no delay condition (Fig. 4A) large tracking errors developed around arm movement reversal, and when large delays such as 400 ms were introduced (Fig. 4B).

Figure 5A illustrates the gain curve between the eyes and the arm, as a function of the introduced delay. Even large delays did not affect eye movement gain. The curve refers to SP gain only, since the gain was calculated from velocity signals, after removing the saccades. Concerning the phase between eye movement and arm movement, Fig. 5B shows that the eyes always track the arm moved target with a very low phase (27 ms). Delays as large as 400 or 450 ms did not introduce phase in the eye response.

Gain and phase curves as a function of feedback delay clearly show that on the average, the Ss tracked the arm-moved visual target rather than a perceived position of the arm. However, close examination of time traces reveal interesting behavior, illustrated by Fig. 6. This piece of recording corresponds to an enlarged segment of the run shown in Fig. 4. With large feedback delays (here

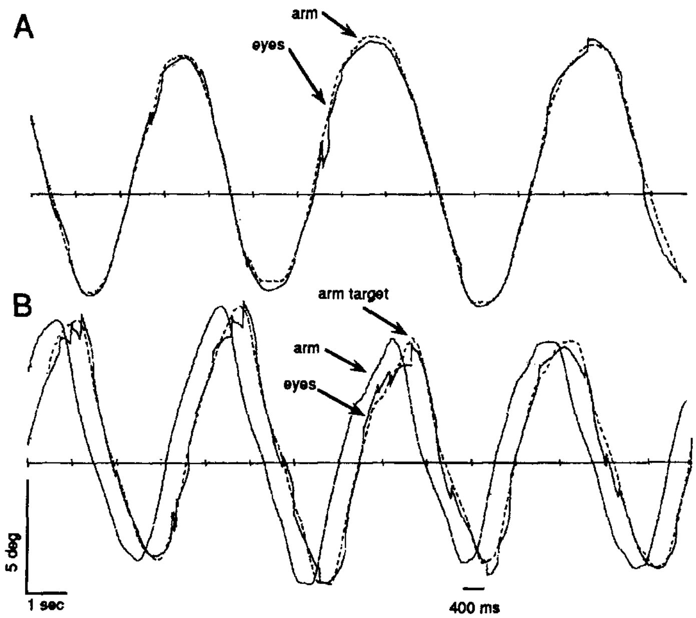

Fig. 4A, B. Typical ocular tracking of the arm-moved target without artificial delay (A) and with a 400 ms delay (B). The S is instructed to move his arm sinusoidally at a frequency of 0.2 or 0.5 Hz, over a $\pm 5°$ range. Traces representing arm and eye motions are essentially superimposed, showing good tracking performance in this condition. In **B**, the dashed line represents the arm-moved target motion, that is the arm motion shifted by 400 ms, while in **A** the dashed line represents the actual arm and target (delay = 0) motions. An enlarged view of traces shown in **B** is provided in Figure 6 to emphasize tracking characteristics when large artificial delays are used

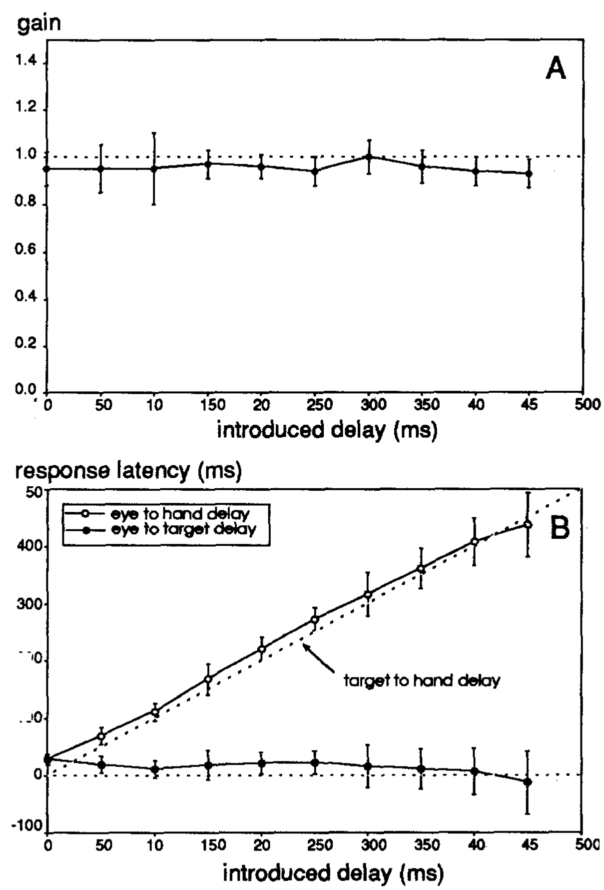

Fig. 5. Tracking gain (**A**) as a function of artificial delay in ocular tracking of the arm-moved target. Conventions are the same as in figure 3, except that only the eye/arm gain is plotted. This gain is remarkably constant (0.96) over the entire range of artificial delays. Values are averages and standard deviations for all Ss. Tracking phase (**B**) as a function of artificial delay in eye tracking of the hand-moved target. Eye-to-hand (open circles) and eye-to-target (filled circles) are plotted as a function of the introduced delay. This phase, expressed in ms, is computed by cross-correlation

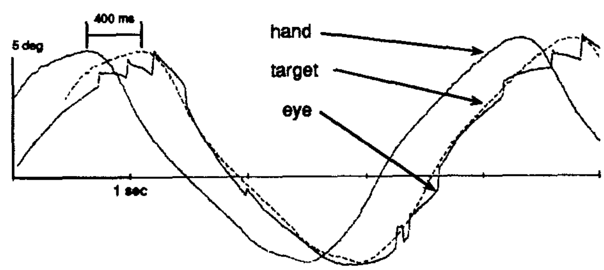

Fig. 6. Ocular tracking of the hand-moved target. This figure shows a detail of the record shown on Fig. 5, in order to emphasize the oculomotor behavior when a large delay (400 ms) is introduced in the visual feedback loop of the hand. The target motion signal is obtained by shifting the hand motion signal by 400 ms. An interesting feature is observed at the reversal of the movement of the hand. This reversal is visually perceived 400 ms latter by the S. During all that time, the hand and the hand-target are moving in opposite directions. A smooth eye movement can be observed in the direction of the hand motion, opposed to the direction of target motion, and thus increasing the retinal error

400 ms), although the eye was evidently tracking the target, when the S reversed the direction of arm motion, segments of SP running in the new direction of the arm were observed (at that time, opposite to the direction of the delayed target). Concomitantly, saccades were generally triggered, taking the eyes back to the ongoing position of the target. This kind of behavior was observed for all Ss, but was not systematic, as evidenced by Fig. 6. Sometimes (generally 30% of the changes in direction) the eyes remained on the visual target, with appropriate gain and phase.

Experiment 2

A second experiment was designed to look at the transient behavior during the early period following the initiation of tracking. To avoid confusion, we will term DELAY the time artificially introduced between the arm motion and the arm-attached target motion, and LATENCY the time between the onset of the visual target motion and the beginning of the concomitant eye movement.

Eye-alone tracking differs markedly from eye-hand tracking. Indeed, when a S is instructed to fixate a visual target, after a latency generally measured as 90–120 ms, the eyes start to move with a segment of SP, followed 100 ms later by a corrective saccade, leading to a reduction of the retinal error. After one or two more saccades, the eyes are on the target, and continue to track it with a correct gain and a very low (if not nil) phase (Fender 1971; Bahill and McDonald 1983a; Buizza and Schmid 1986; Carl and Gellman 1987). The difference in latency reported by these authors is generally interpreted as a dependence of SP latency on the characteristics of the target signal.

As a comparison, our data as in Fig. 7, show the tracking response to the motion of a self-moved visual target. When no delay was introduced in the visual feedback loop, the eyes started to move almost at the same time as the arm. In this condition the response latency was difficult to appreciate, due to the relatively low acceleration of both eye and arm movements. Still, we measured hand-to-eye latencies between -70 ms (eye leading) and $+135$ ms (eye lagging). These data are consistent with previous works from our laboratory (Gauthier and Hofferer 1976; Gauthier et al. 1988; Gauthier and Mussa-Ivaldi 1988) and others (Steinbach and Held 1968; Steinbach 1969; Domann et al. 1989). Immediately after the beginning of eye motion, the gain of the SP system rapidly increased to a value of one (within the first half-period of tracking), which means that the eye velocity was adapted to the velocity of the arm and consequently to the velocity of the target.

When a delay was introduced between the arm motion and the target motion (Fig. 7B shows a typical record for a 150 ms artificially introduced delay), a new feature appeared, consisting in a saccade triggered in the direction opposite to arm target motion. This saccade was systematically observed, in all runs, as soon as a delay (as low as 50 ms) was introduced. Figure 8 illustrates the most common behavior. With or without feedback delay, the eyes started to move almost in synchrony with the arm. When a delay was introduced, the eyes started to move while the visual target was still immobile. This was particularly visible with delays above 50 ms. The Ss perceived and reported that "*at the beginning, the eyes lost the target*" or "*the eyes started to move before the target*" depending on their level of understanding of, and practice in, the experiment. All the Ss perceived the arm target as remaining stationary while the eyes started to move and never interpreted the retinal slip produced by this early slow eye movement as a motion of the target in the opposite direction.

Generally, 200 to 250 ms after the beginning of eye motion, a saccade was triggered towards the target that is in the direction of a reduction of the retinal error, but opposite to the direction of SP and arm movement. If the artificial delay was lower than the saccadic delay, at the end of the saccade the eyes were not on the target because the target had, in the mean time, started to move. The oculomotor system continued to produce SP at low gain, and new saccades were triggered, now in the direction of the pursuit as in Fig. 7B. At the end of the first half cycle of movement, the eyes generally were locked on the visual target and tracked it with appropriate gain and no phase (Fig. 8).

With regard to the initial latency of the eye movement relative to the arm movement, Fig. 9 shows that the average latency changed little over the range of feedback

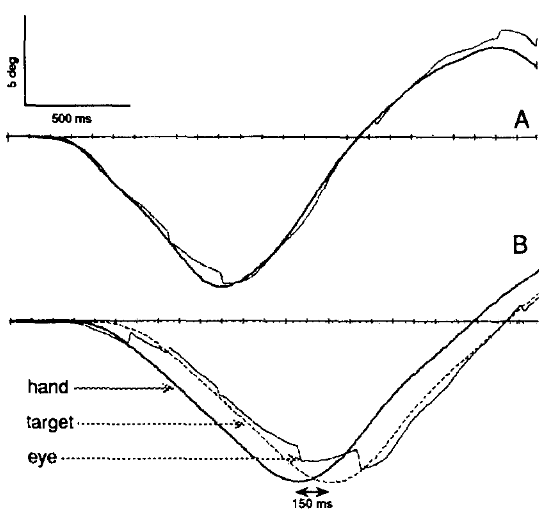

Fig. 7A, B. Early events in eye tracking of a hand-moved target. In the normal condition (**A**), the S is instructed to move his arm at 0.3 Hz, $\pm 5°$, and to track the hand-moved target with his eyes. The thin trace is the eye motion, while the thick trace is the arm motion. Note that the eye movement starts with smooth pursuit with no delay relative to the onset of arm movement, as opposed to the preceeding condition. When a 150 ms delay is artificially introduced in the visual feedback loop (**B**), the eyes always start to move with smooth motion at the arm movement onset, and sometimes even before (as evidenced in the present record). About a cycle of arm movement is necessary for the eyes to precisely rejoin the visual target and to track it in phase. The dotted trace represents the motion of the hand-moved target, this is the arm motion delayed by 150 ms.

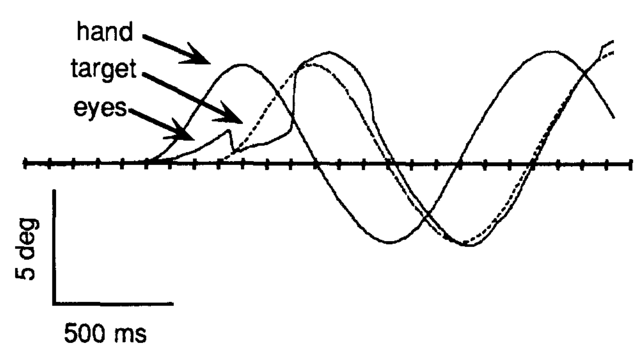

Fig. 8. Beginning of eye tracking of a target moved by the hand, with a 300 ms delay introduced in the visual feedback. Condition and conventions are the same as in Figure 7. Even when a large artificial delay is used (here 300 ms), the eyes always start to move with smooth pursuit in synchrony with the arm. The gain of this non-visual smooth pursuit is low (0.4), and a saccade is always triggered in the direction opposite to the arm motion

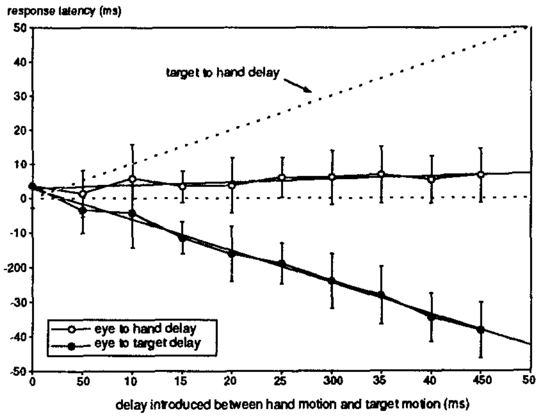

Fig. 9. Ocular tracking latency at the beginning of arm movement. Latency at the onset of arm movement is manually measured from computer displayed recordings. Open circles represent latency between the eyes and the arm, and filled circles represent latency between the eyes and the image of the arm (the introduced delay is substracted from the latency between the eyes and the arm). Values are averages and standard deviations for all Ss. The straight lines along data represent regression lines calculated for these values. This graph shows that the onset of smooth pursuit is synchronized with the onset of arm (but not target) movement. Negative values mean anticipation, the eyes starting to move before the target

delays (35.79 ms ± 62.89 with no feedback delay and 55.27 ms ± 58.97 with 450 ms delay). The overall average latency for all delays was 41.69 ms ± 56.12) which suggests that as soon as the feedback delay was higher than 50 ms, the eyes led the visual target, as illustrated by the filled circles of Fig. 9.

Discussion

In the present study we investigated oculo-manual coordination control by analysing how human Ss overcome delays artificially introduced in the visual feedback of their own hand motion. The goal was to decorrelate the motion of the hand and the motion of a target driven by the hand, in order to provide the SP system with two different cues relative to the motion of the arm: one purely visual, and another internal, non-visual. Our purpose was to determine if the increase of performance of the SP system observed when Ss track their own hand or an image of it (Steinbach and Held 1969; Gauthier and Hofferer 1976; Gauthier et al. 1988) was due to internal coupling between the arm motor system and the oculomotor system, or to a special form of prediction, due to the fact that obviously the S knew a priori the motion of his own arm.

Further understanding of eye-hand coordination with delayed action of the hand on the target has direct implications. Telemanipulation under visual guidance presents a variety of problems, with solutions emerging from basic mechanics, electronics, computer and possibly from physiological sciences. Regarding the latter, recent advances in operator movement monitoring (*data-glove* and other newly designed micromanipulators and 3D movement monitors) and in computer graphic displays (Foley 1987) allow one to envision rapid and major improvements in man-machine interface and communication domains. Delays between operator's action and display of the effect of his action on the remote system and environment are mostly due to transmission time between local and remote system, and local computation time (to calculate and generate the displayed picture). Action preview has been proposed as a way to reduce the decrease of performance (Stark et al. 1987). Such studies are expected to set limits to communication delays in man-machine interaction and help designers adapt new technologies to operator's performance limits.

Few data are available on the effects of artificial delays introduced in the visuo-motor loop, and even fewer on the effects of such delays on ocular SP performance. From our own data, it appears that the arm motor system and the oculomotor system do not behave the same way when the S is exposed to such a condition. In particular, though both motor systems show predictive abilities, the way these predictors operate is different for the two systems. This has been stressed by Bock (1987), who showed different reaction times for arm and eye to unpredictable changes of target velocity, and no correlation between phase and gain variability of the arm motor system and the oculomotor system.

Handling of feedback delays by the hand motor system

The effects of delayed feedback on arm tracking performance was originally described by Smith (1972), who showed a decrease of performance when a S tracked a delayed televised display of his own behavior. For a critical delay of 250 ms, the S had the feeling that his arm was "*made of rubber*". Later, Miall et al. (1985) showed that the introduction of a delay decreased the number of corrections made by the S and increased the amplitude of movement. They also reported a critical delay of 200–250 ms, with both human beings and primates, and concluded that this limitation was due to the visuomotor delay, which is itself close to 200 ms.

We observed such a decrease of performance of the arm motor system for delays higher than 250 ms, both in terms of gain and in terms of phase. In our protocols, we used predictable sinewave motions and instructed Ss to maintain the arm target in coincidence with the external target. When short delays were introduced, the strategy adopted by all the Ss was to anticipate visual target motion with arm motion, in such a way that both targets were constantly in coincidence. This means that the arm preceded the visual target by the amount of time equivalent to the artificial delay. Figure 3B is particularly demonstrative of this behavior. It is also clear from this figure that the Ss could not completely overcome the delay, and the remaining lag was equivalent to the lag measured between the target and the arm without artificial delay (here 40 ms). When the artificial delay was increased to values larger than 200–250 ms, the predictive ability of the visuomotor system decreased, and the arm increasingly lagged the target motion. The behavior of the visuomotor system was then similar to that commonly observed in response to an unpredictable target. This suggests that 200–250 ms is likely to be the upper limit of the delay that can be compensated by the predictor mechanism of the arm motor system.

Handling of feedback delays by the SP system

The SP system exhibits a delay resulting in a phase lag when tracking a moving target. In some conditions, the SP system is able to overcome this delay. As an example, a sinusoidally moving target is tracked without phase shift, providing that amplitude and frequency (and by consequence velocity) remain within a limited range. This ability can be increased by practice (McHugh and Bahill 1985) and depends on the type of waveform used to drive the target. All periodic waveforms are not predictable (Michael and Melvill-Jones 1966; Bahill et al. 1980; Buizza and Schmid 1986). The predictor operator assumed to be responsible for this particular behavior has been extensively studied by numerous authors (Stark et al. 1962; Dallos and Jones 1963; Kowler and Steinman 1981; Lisberger et al. 1981; Yasui and Young 1984; Buizza and Schmid 1989) and several models have been proposed to describe the phenomenon (Sugie 1971; Bahill and McDonald 1983b; Yasui and Young 1984; Van den Berg 1988).

Prediction in the SP system complicates the interpretation of the reduction of phase lag and of the coupling between the arm and the eyes in a self-moved target tracking task. Indeed, the ability of a S to track a self-moved target with no phase can be interpreted as a special form of prediction related to neural coupling between hand and eye motor systems.

In fact, these two mechanisms can be distinguished through their respective behaviors: the SP system predictor not only reduces the phase between the target and the eyes by compensating for the oculomotor delay, but eventually yields a lead of the eyes with respect to the target (Yasui and Young 1984). Van den Berg (1988) showed that the predictor process must be constantly updated by retinal information from target motion. This implies that the predictor cannot immediately react to changes of target motion. Conversely, in self-arm tracking, as shown in Fig. 6, eye motion can be very quickly influenced by arm motion changes, leading to eye movements opposite in direction to the visual input.

Our data show, in fact, that in eye and hand tracking of a visual target, the eyes always track the visual (external) target, and the SP predictor works throughout the full range of studied delays, on the basis of visual signals: the phase between the external target and the eyes remains low, close to zero. When a large artificial delay is used, eye motion is better correlated in time with real target motion than with arm motion. This observation suggests that SP is mostly under visual control, and does not respond directly to non-visual, arm movement derived signals, except during quick changes of direction of the arm motion. The phase observed between the eyes and the delayed target is then comparable in amplitude to the phase observed between the eyes and an external target during SP (see Fig. 5B).

SP latency in response to self-moved target

One of the striking changes of SP characteristics observed in self-moved target was the decrease of movement latency. This phenomenon has been described by Steinbach (1969), Gauthier and Hofferer (1976), Lackner and Mather (1981), Gauthier et al. (1988) and Domann et al. (1989). Some of these authors also reported a lead of the eyes with respect to the hand when the S tracked a light attached to the hand.

The second experiment described here provides information about the early stages of hand-moved target tracking. In our experiment, with or without delay, the latency of the SP system was much shorter than the 120–130 ms generally reported for eye-alone tracking. Even short latencies described by Gellman et al. (1990) are not less than 70 ms. In eye tracking of the hand, eye and hand movements are almost perfectly synchronized.

When a large delay was used (more than 300 ms), SP started before any movement of the visual target occurred. The smooth eye movement was in the arm direction, and with a low gain, but the velocity was not as low as the one of the anticipatory pursuit described by Kowler et al. (1984). Anticipatory pursuit is a low velocity eye movement, (generally, velocities are less than 1°/s, and are independent of target velocity), occurring eventually before visual target motion, and attributed to expectation of target motion (Boman and Hotson 1988) and not to target motion *per se*. It could be suggested that because the S decided when to move his arm, he knew that the target would move, and he was able to anticipate the motion by the same kind of anticipatory process. We do not believe this interpretation is correct because, in our experiment, SP velocities measured between the beginning of eye movement and the onset of target motion, or before the first saccade, were always higher than half, and often close to the velocity of the arm at the same instant, as can be seen in Figs. 8B and 9. The process leading to the early eye movement observed in eye-hand tracking is undoubtedly not an anticipatory pursuit as described by Kowler et al. (1984).

Non-visual inputs to the SP system

The nature of signals involved in the control of SP is a long debated question. It is well known now that non visual inputs, accompanied or not, by visual signals, are sufficient to trigger slow eye movements. Pure voluntary control has been denied by Gauthier and Hofferer (1976), but Steinman et al. (1969) showed that under some conditions, trained Ss can voluntarily control eye velocity during ongoing pursuit. The percept of motion (Steinbach 1976; Boman and Hotson 1988) or the expectation of a real target displacement (Kowler 1989) may be sufficient to trigger a low velocity pursuit-like movement or to increase the gain of the OKN (Yasui and Young 1984). Signals produced by the motion of the arm, when a S is instructed to track his unseen hand, are also known to be powerful inputs for the SP system (Steinbach 1969; Jordan 1970; Gauthier and Hofferer 1976; Lackner and Evanoff

1977; Levine and Lackner 1979; Mather and Lackner 1981; Gauthier et al. 1988). Two facts from the present work support the idea of a direct, powerful arm control on SP: 1: in the first experiment, with eye and hand tracking of a visual target, when a large delay was used, the tracking condition was eventually such that the motion of the arm and the motion of the arm-target were opposite in direction, for example at the arm movement direction reversal, during a time equal to the introduced delay. SP was produced in the direction of the arm, with an appropriate velocity relative to arm motion. The saccades triggered in the direction of the real visual target showed that the retinal error was detected. It is interesting to note that this behavior did not always appear. A further study is necessary to correlate the pursuit behavior to other environmental factors. 2: In the second experiment in which we concentrated on transient behavior, pursuit movements were triggered with appropriate direction and high gain, while the arm target, still motionless because of the artificially introduced delay, provided a powerful fixation target for the visuo-oculomotor system. Here too, corrections for retinal error were produced only through saccades, driving the gaze back to the fixation point.

Conclusions

The arm motor system definitely shows predictive abilities, comparable but not identical to those described as part of the SP system (Yasui and Young 1984). However, comparative examination of the characteristics of eye-alone tracking and eye-tracking of the hand tends to confirm that the two systems do not share the same predictor.

Signals issued from the arm motor system (efferent copy and/or proprioception) are sufficient to trigger SP eye movements and to control their direction and velocity. Non visual pursuit can be maintained for at least half a second before the target actually starts to move. Even after the visual loop is closed, fixation mechanisms do not suppress the eye movement. The retinal error increases, either because the "strength" of the arm-generated signal is of a level similar to the strength of the visual input, or because the pursuit system does not stabilize the gaze on the stationary visual target.

This tight coupling between the arm and the eyes is quickly compensated, as soon as the visual target moves. During tracking of the artificially delayed hand target, internal signals and visual signals reflecting arm movement are not congruant. The SP system then generally tracks the visual target, and the behavior of this system is very similar to that observed when an external target is used as an input.

Neither our own experiments nor those of other authors clarify the nature of the signals, issued from the arm motor system, which are used to control non-visual SP. Proprioceptive signals are necessary as evidenced by their suppression (Gauthier and Hofferrer 1976, in man; Gauthier and Mussa-Ivaldi 1988, in monkeys) but not sufficient. SP triggered by passive movement has low gain (Gauthier and Hofferer 1976; Lackner and Evanoff 1977). Regarding the role of the arm efferent copy, Gielen et al. (1984) demonstrated that the arm motor system and the oculomotor system do not share the same command signal.

Conversely, it is clear that proprioceptive and efferent copy signals participate in manuo-ocular coordination, but in a different way. Efferent copy is certainly involved in the triggering of non-visual SP and in synchronization of motor activities (reflected by the short latency). Proprioceptive information might be involved in control processes and in maintenance of SP of self-moved targets in the absence of visual information.

Acknowledgements. This work was supported by grants from the European Community Commission, project BRAIN # 88100040, and from CNRS URA 372. The authors are grateful to Prof. B.L. Zuber, from the University of Illinois at Chicago, for reviewing the manuscript and for constant advice and help during the experiments.

References

Bahill AT, Iandolo MJ, Troost BT (1980) Smooth pursuit eye movements in response to unpredictable target waveforms. Vision Res 20: 923–931

Bahill AT, McDonald JD (1983a) Smooth pursuit eye movements in response to predictable target motions. Vision Res 23: 1573–1583

Bahill AT, McDonald JD (1983b) Model emulates human smooth pursuit system producing zero-latency target tracking. Biol Cybern 48: 213–222

Bock O (1987) Coordination of arm and eye movements in tracking of sinusoidally moving targets. Behav Brain Res 24: 93–100

Boman DK, Hotson JR (1988) Stimulus conditions that enhance anticipatory slow eye movements. Vision Res 28: 1157–1165

Buizza A, Schmid R (1986) Velocity characteristics of smooth pursuit eye movements to different patterns of target motion. Exp Brain Res 63: 395–401

Buizza A, Schmid R (1989) Influence of smooth pursuit dynamics on eye tracking: a mathematical approach. Med Biol Eng Comput 27: 617–622

Carl JR, Gellman RS (1987) Human smooth pursuit: stimulus-dependent responses. J Neurophysiol 57: 1446–1463

Dallos PJ, Jones RW (1963) Learning behavior of the eye fixation control system. IEEE Trans Autom Contr 8: 218–227

Domann R, Bock O, Eckmiller R (1989) Interaction of visual and non-visual signals in the initiation of smooth pursuit eye movements in primates Behav Brain Res 32: 95–99

Ebisawa Y, Minamitani H, Mori Y, Takase M (1988) New methods for removing saccades in analysis of smooth pursuit eye movement. Biol Cybern 60: 111–119

Erkelens CJ, Van Der Steen J, Steinman RM, Collewijn H (1989) Ocular vergence under natural conditions. I. Continuous changes of target distance along the median plane. Proc R Soc Lond, B 236: 417–440

Fender DH (1971) Time delays in the Human eye-tracking system P Bach-y-Rita, CC Collins, JE Hyde, Academic press

Foley JD (1987) Interfaces for advanced computing. Scientific American, 122: 83–90

Gauthier GM, Hofferer JM (1976) Eye tracking of self-moved targets in the absence of vision. Exp Brain Res 26: 121–139

Gauthier GM, Mussa Ivaldi F (1988) Oculo-manual tracking of visual targets in monkeys: role of the arm afferent information in the control of arm and eye movements. Exp Brain Res 73: 138–154

Gauthier GM, Vercher JL, Mussa Ivaldi F, Marchetti E (1988)

Oculo-manual tracking of visual targets: control learning, coordination control and coordination model. Exp Brain Res 73: 127–137

Gellman RS, Carl JR, Miles FA (1990) Short latency ocular-following responses in man. Visual Neuroscience, 5: 107–122

Gielen CCAM, Van den Heuvel PJM, van Gisbergen, JAM (1984) Coordination of fast eye and arm movements in a tracking task. Exp Brain Res 56: 154–161

Jordan S (1970) Ocular pursuit movement as a function of visual and proprioceptive stimulation. Vision Res 10: 775–78

Kowler E (1989) Cognitive expectations, not habit, control anticipatory smooth oculomotor pursuit. Vision Res 29: 1049–1057

Kowler E, Martins AJ, Pavel M (1984) The effect of expectations on slow oculomotor control-IV Anticipatory smooth eye movements depend on prior target motions. Vision Res 24: 197–210

Kowler E, Steinman RM (1981) The effect of expectations on slow oculomotor control-III Guessing unpredictable target displacements. Vision Res 21: 191–203

Lackner JR, Evanoff JN (1977) Smooth pursuit eye movement elicited by somatosensory stimulation. Neurosci Let 4: 43–48

Lackner JR, Mather, JA (1981) Eye-Hand tracking using afterimages. Evidence that sense of effort is dependent on spatial constancy mechanisms. Exp Brain Res 44: 138–142

Levine MS, Lackner JR (1979) Some sensory and motor factors influencing the control and appreciation of eye and limb position. Exp Brain Res 36: 275–283

Lisberger SG, Evinger LC, Johanson GW, Fuchs AF (1981) Relationship between eye acceleration and retinal image velocity during foveal smooth pursuit in Man and Monkey. J Neurophysiol 46: 229–249

Mather JA, Lackner JR (1980) Multiples sensory and motor cues enhances the accuracy of pursuit eye movements. Aviat Space Env Med 51: 856–859

Mather JA, Lackner JR (1981) The influence of efferent, proprioceptive, and timing factors on the accuracy of eye-hand tracking. Exp Brain Res 43: 406–412

McHugh DE, Bahill AT (1985) Learning to track predictable target waveforms without a time delay. Invest Ophthalmol Visual Sci 26: 932–937

Miall RC, Weir DJ, Stein JF (1985) Visuomotor tracking with delayed visual feedback. Neuroscience 16: 511–522

Michael JA, Melvill-Jones G (1966) Dependence of visual tracking capability upon stimulus predictability. Vision Res 6: 707–716

Neilson PD, Neilson MD (1980) Influence of control-display compatibility on tracking behaviour. Quart J Exp Psychol 32: 125–135

Ohashi N, Watanabe Y, Mizukoshi K (1987) Prediction in smooth pursuit. Acta Oto-Laryngologica 103: 131–136

Smith WM (1972) Feedback: Real-time delayed vision of one's own tracking behavior. Science 176: 939–940

Stark L, Kim, WS, Tendick F, Hannaford B, Ellis S, Denome M, Duffy M, Hayes T, Jordan T, Lawton M, Mills T, Peterson R, Sanders K, Tyler M, Van Dyke S (1987) Telerobotics: display, control, and communication problems. IEEE J of Robotics and Automation 3: 67–75

Stark L, Vossius G, Young LR (1962) Predictive control of eye tracking movements. IRE Trans on Human Factors in Electronics 3: 52–57

Steinbach MJ (1969) Eye tracking of self-moved targets: the role of efference. J Exp Psychol 82: 366–376

Steinbach MJ (1976) Pursuing the perceptual rather than the retinal stimulus. Vision Res 16: 1371–1376

Steinbach MJ, Held R (1968) Eye tracking of observer-generated target movements. Science 161: 187–188

Steinman RM, Skavenski AA, Sansbury RV (1969) Voluntary control of smooth pursuit velocity. Vision Res 9: 1167–1175

Sugie N (1971) A model of predictive control in visual target tracking. IEEE Transactions on Systems. Man and cybern 1: 2–7

Van Den Berg AV (1988) Human smooth pursuit during transient perturbations of predictable and unpredictable target movement. Exp Brain Res 72: 95–108

Vercher JL, Gauthier GM (1988) Cerebellar involvement in the coordination control of the oculomanual tracking system: effects of cerebellar dentate nucleus lesion. Exp Brain Res 73: 155–166

Yasui S, Young LR (1984) On the predictive control of foveal eye tracking and slow phases of optokinetic and vestibular nystagmus. J Physiol 347: 17–33