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Oculo-manual coordination control: respective role of visual and non-visual information in ocular tracking of self-moved targets

Abstract We evaluated the role of visual and non-visual information in the control of smooth pursuit movements during tracking of a self-moved target. Previous works have shown that self-moved target tracking is characterised by shorter smooth pursuit latency and higher maximal velocity than eye-alone tracking. In fact, when a subject tracks a visual target controlled by his own arm, eye movement and arm movement are closely synchronised. In the present study, we showed that, in a condition where the direction of motion of a self-moved visual target was opposite to that of the arm (same amplitude, same velocity, but opposite direction of movement), the resulting smooth pursuit eye movements occurred with low latency, and continued for about 140 ms in the direction of the arm movement rather than in the direction of the actual visual target movement. After 140 ms, the eye movement direction reversed through a combination of smooth pursuit and saccades. Subsequently, while arm and visual target still moved in opposite directions, smooth pursuit occurred in pace with the visual target motion. Subjects were also submitted to a series of 60 tracking trials, for which the arm-to-target motion relationship was systematically reversed. Under these conditions subjects were able to initiate early smooth pursuit in the actual direction of the visual target. Overall, these results confirm that non-visual information produced by the arm motor system can trigger and control smooth pursuit. They also demonstrate the plasticity of the neuronal network handling eye-arm coordination control.

Key words Smooth pursuit · Oculo-manual tracking Coordination control · Self-moved target tracking Prediction · Visuo-motor alteration · Human

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Introduction

In contrast to what was originally believed (Dodge et al. 1930; Robinson 1968), smooth pursuit (SP) can be elicited by stimuli other than the image of a moving object slipping on the retina. The percept of a visual motion may be sufficient (Yasui and Young 1975; Steinbach 1976). Nonetheless some kind of real (even non-visual) stimulus seems to be necessary, e.g. signals issued from the sensory-motor system of the moving, unseen arm of the observer can trigger and maintain SP, if the subject is asked to imagine and track a target attached to his unseen hand (Jordan 1970; Gauthier and Hofferer 1976).

Simultaneous eye and arm tracking of a visual target shows an improvement of SP (Bock 1987; Gauthier et al. 1988) as compared to eye-alone tracking. When a subject tracks a visual target attached to his self-moved arm, SP is further improved. More specifically, accuracy increases (Steinbach and Held 1968), the number of saccades decreases (Angel and Garland 1972), maximum velocity increases (from 40°/s up to 100°/s; Gauthier et al. 1988), latency decreases from 100–120 ms to zero (Steinbach 1969; Gauthier and Hofferer 1976), and the upper frequency limit of SP is higher both in terms of gain and phase (Vercher et al. 1992).

Gauthier et al. (1988) proposed a model of the coordination control reciprocally exerted between the arm motor system and the oculomotor system, in which non-visual information generated during arm movement contributes to the control of the oculomotor system. In this model the arm efferent copy contributes to the synchrony between arm motion and eye motion, and proprioceptive inflow plays a role in the cross-calibration of both systems. Arm proprioception suppression in human beings (by ischaemic block; Gauthier and Hofferer 1976) as in primates (by section of the dorsal roots; Gauthier and Mussa-Ivaldi 1988) strongly alters the coordination between the arm and the eyes during SP of a self-moved target.

Recently, we have shown (Vercher and Gauthier 1992) that when the arm-moved target motion on the screen is delayed with respect to the subject's actual arm

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motion, the eyes start to move ahead of the visual target. SP is synchronised with the onset of arm movement rather than with the visual target. Moreover, subjects can use non-visual information, generated during the active movement of their own arm, to trigger appropriate SP without visual information about target motion.

The aim of the present work was to further study the role played by visual and non-visual information in the coordination control between the arm motor system and the SP system during eye tracking of a self-moved target. In order to dissociate visual from non-visual signals, the motion of the target was reversed relative to the motion of the arm, i.e. when the subject moved his arm to the right, the target moved to the left, at the same velocity, over the same amplitude. By using a similar paradigm, Domann et al. (1989) showed in monkeys that reversal of the spatial relationship between arm and arm-moved target revealed a dual (visual and non-visual) process in SP initiation. SP latency histograms showed two peaks, one centred around 120 ms, the other around 0 ms. SP always started in a direction coherent with target motion. Since trials with short latency were mixed with trials with longer latencies, the authors proposed that visual and non-visual signals competed in triggering SP of a self-moved target.

As in the Domann et al. (1989) study, the respective roles of visual and non-visual information in oculo-manual coordination have been determined by comparing the performance in different tracking tasks, namely eye-alone tracking of a visual target, and eye tracking of self-moved target, with and without inversion of the arm-to-target motion relationship. In Domann's study, the monkeys were trained with the reversed arm-to-target relationship, whereas in the present work this relationship was randomly either direct or reversed. We also exposed the subjects to a condition in which they were informed of the reversal, to determine by which process they could adapt to the new arm-to-target relationship.

Results show that non-visual information generated by arm motion are responsible for eye-arm motion synchronisation. When the visual target movement is randomly reversed relative to arm movement, SP is both spatially and temporally coupled to the actual arm movement rather than to the target motion. This observation is opposite to that of Domann et al. (1989), who found that eye movements started in the visually correct direction. After 140 ms, the eye motion direction changes through a combination of SP and saccadic motion. Subsequently, appropriate tracking of the visual target is observed, with the arm moving in one direction and the eyes in the opposite direction. Some of these results have been presented at the 7th European Conference on Eye movements, Durham, UK, September 1993 (Vercher et al. 1994).

Materials and methods

Subjects

Nine subjects ranging from 19 to 31 years of age (six men, three women) participated in the present study. They were undergradu-ate students or staff members from the Neuroscience Department of the University of Provence. They were instructed and trained with the apparatus in a preliminary session, during which they all gave their informed consent for their participation to the study. They were all exempt of known visual, oculomotor or neurological disorders and used their preferred arm during the experiment (one subject was left-handed, the others were right-handed).

Experimental set-up

A thorough description of the experimental set-up has been published elsewhere (Vercher and Gauthier 1992; Vercher et al. 1993). The subject was seated in front of a projection screen. His/her head was immobilised by a dental print bite-bar. The tested arm rested on a horizontal hemi-cylindrical mobile gutter, with the elbow aligned with the rotating axis of the gutter, and with the hand oriented towards the screen. Horizontal eye movements were recorded by means of an infrared corneal reflection device (IRIS; Skalar). The arm motion was recorded by means of a precision potentiometer aligned with the rotating axis of the manipulandum. The experiments were performed in darkness. Two white visual targets (3 mm in diameter each, 0.1° as seen from subject's head) could be projected on the screen (uniform background). Their respective motions were controlled through galvanometer-mounted mirrors (General scanning). The motion of the first target (called here the *external target*) was derived from a waveform generator whose output was a cosine signal triggered by the computer. The movement of this target had a frequency of 0.3–0.4 Hz, over an amplitude of 10° peak-to-peak, as seen from the subject's eyes. The target motion was chosen to simulate a typical arm movement (see Fig. 1A). A second target (named the *self-moved target*) was controlled by a signal issued from the potentiometer. The vision of the arm was occluded with a black curtain to definitively prevent direct vision of the arm motion.

The signal from the potentiometer (monitoring arm position) was amplified and filtered (low-pass filter, 200 Hz at –3 dB). Target position, eye position and arm position signals were digitised at 500 samples/s, and displayed in real-time on a graphic screen. Sections of 5 s were recorded on a disk for off-line analysis.
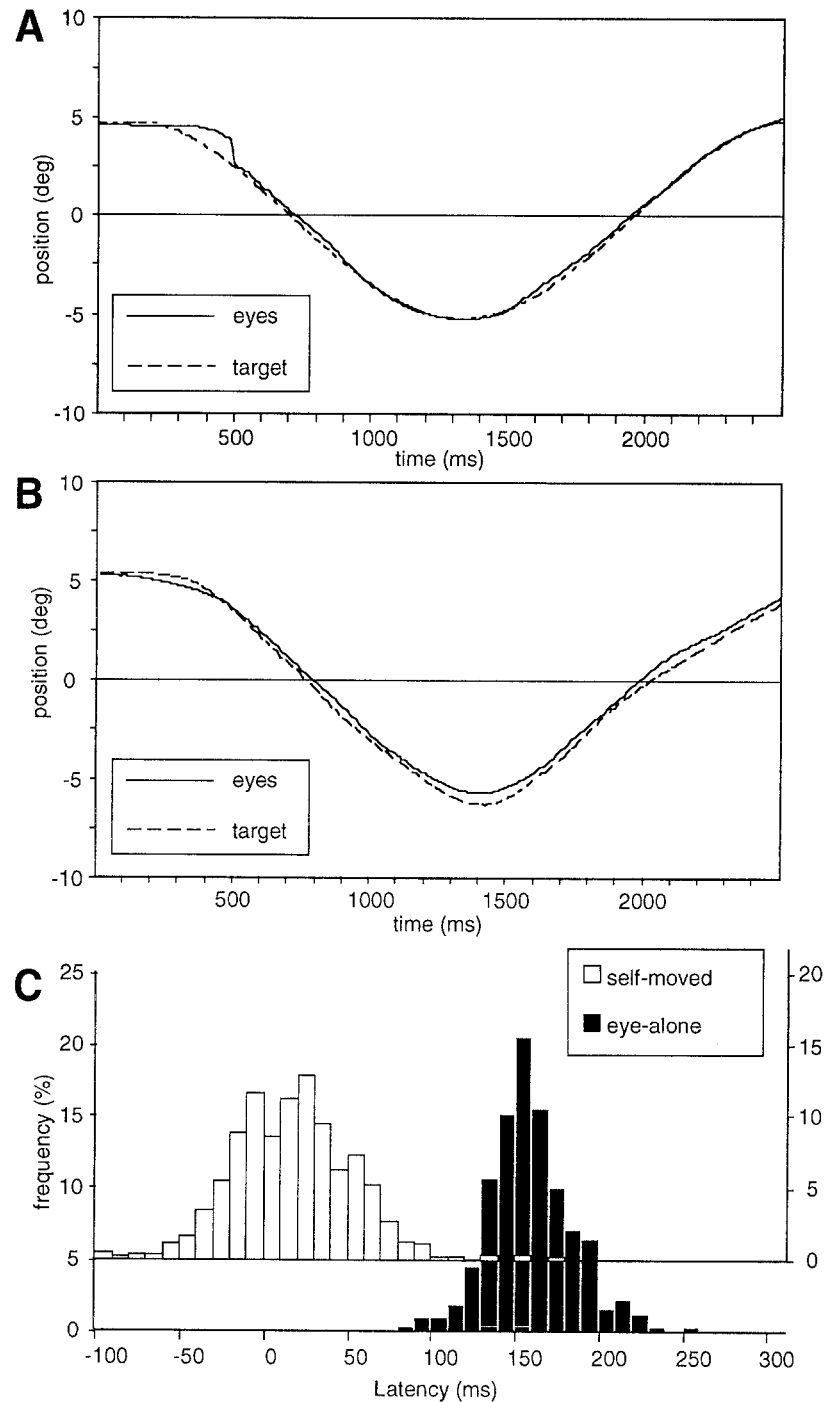
Tracking tasks

Two tracking tasks were used:
1. *Eye-alone tracking of an external target.* The subjects fixated a visual target presented on one side of the screen. This target started to move towards the other side of the screen. Only one starting direction (from right to left) was used. The subjects were instructed to track the visual target with their eyes, as accurately as possible.
2. *Ocular tracking of a self-moved target.* The instruction was to sinusoidally move the arm at a learned frequency (0.3–0.4 Hz) and amplitude (10° peak-to-peak) and to track the arm-moved target with the eyes, starting to move the arm any time after a "go" signal (1-kHz, 100-ms beep, generated by the computer).

Experimental procedures

In the ocular tracking of a self-moved target task, the arm-to-target motion relationship could be either direct or reversed. This alteration of the arm-target relationship was either systematically or randomly applied in different sessions. At the beginning of each trial, the subjects positioned the self-moved target at the centre of the screen and visually fixated it. When recording started, the relationship between arm motion and target motion could be reversed. It follows that the subjects could not determine whether the relationship was reversed or not unless they moved their arm. Trials where the subjects inadvertently moved (even slightly) their arm between the beginning of the recording and the volitional arm movement were rejected from the analysis. Three experiments were successively performed, with the same subjects:

Fig. 1 A Eye-alone tracking.
Subjects were instructed to first
fixate then track the target
when it started to move. The
solid line represents eye motion
and *dashed line* target motion.
B Self-moved target tracking.
Subjects were instructed to
start moving the arm and to fol-
low with the eyes the self-
moved target. Smooth pursuit
started almost at the same time
as the arm, sometimes before,
as here, but always in the direc-
tion of the arm motion. **C** La-
tency histograms, in the eye-
alone tracking condition (*black
blocks*) and in the self-moved
target tracking condition (*white
blocks*). The ordinates plot rela-
tive frequencies (percentage of
total trials, for all subjects and
all sessions) and the abscissas
the eye-to-arm or eye-to-target
latency (by bins of 10 ms). See
text for mean values

1. In the first experiment, subjects were tested under each of the two tracking tasks for a series of 50 trials. Eye-alone tracking was compared with self-moved target tracking without alteration of the relationship between the arm motion and the target motion.

2. In the second experiment, only self-moved target tracking was recorded, and the spatial relationship between the arm motion and the target motion was reversed for randomly chosen trials (on average one trial was reversed for every three non-reversed trials). Each session consisted of 80 trials of self-moved target tracking, comprising around 20 trials with a reversed arm-to-target motion relationship.

3. In the third experiment, the relationship between arm motion and target motion was systematically reversed, and the subjects were always informed and aware of this alteration. The experiment started with ten trials in the normal arm-to-target motion relation-

ship condition. These trials were used as controls for the ensuing 60 trials, where the subjects were informed that the target motion relationship would be systematically reversed. Ten more trials were executed without inversion, but the subjects were not informed when the inversion had been suppressed.

Data analysis

Off-line signal analysis started with digital low-pass filtering (cut-off frequency of 30 Hz). We focused our analysis on the period covering the first 500 ms of tracking, although the subject performed the task for a longer period of time. During such a short period one may assume that the predictive operator is not fully activated (Becker and Fuchs 1985; Ohashi and Mizukoshi 1992).

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Fig. 2 A Eye tracking of a self-moved target with random inversion of target motion relative to arm motion. *Solid line* represents eye motion, *dashed lines* represent arm motion and target motion (same as arm motion, but reversed). In most cases, the eyes started to move with a low latency (or even a lead) in the direction of the arm, but with a relatively low gain. After 100–150 ms, smooth pursuit direction changed, then 100 ms later a catch-up saccade allowed the visual target to be refoveated. From this moment on, the eyes tracked the visual target, with appropriate gain and low phase. **B** Correlation between initial arm velocity and eye velocity, as measured during trials with random inversion of the arm-to-target motion relationship (all subjects and all sessions). The slope of the regression line is 0.41, $r=0.69$
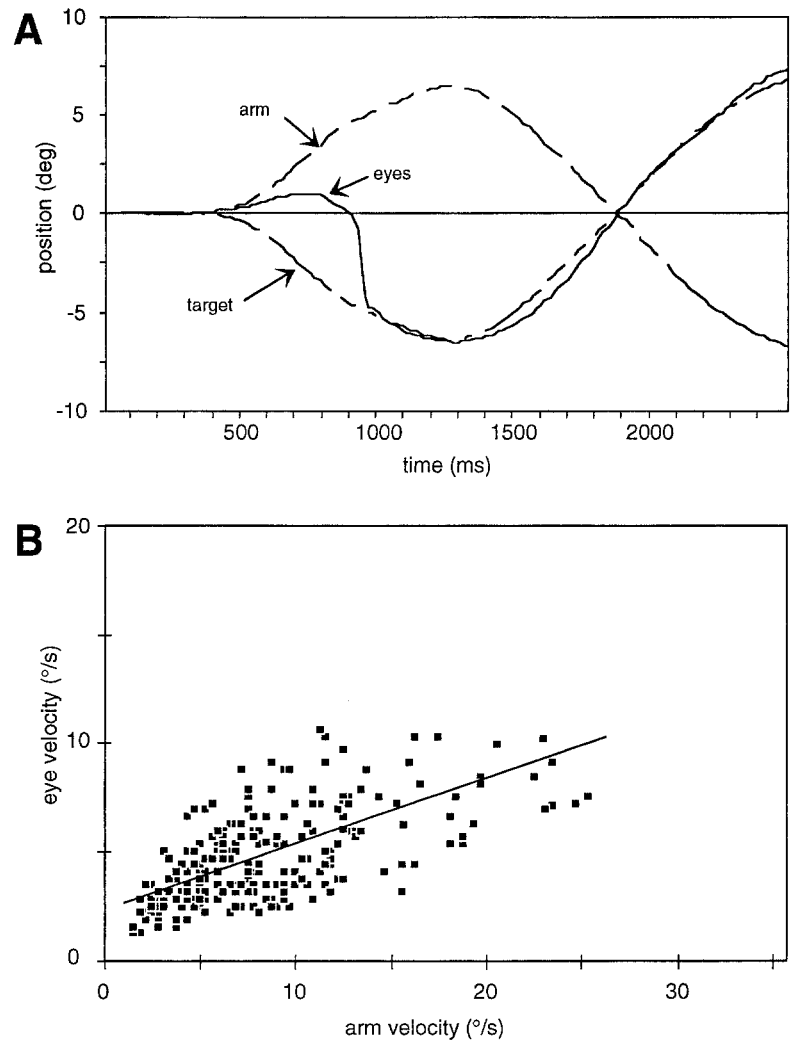
The latencies between target and eye motion were measured, as well as the initial gain of pursuit. Owing to the latency, just after SP onset the eye velocity may not be related to target velocity at the same time. The gain was defined as the mean eye velocity measured between 50 and 100 ms after SP onset divided by the mean target velocity measured between 50 and 100 ms after target motion onset. Latencies were assessed from velocity signals displayed on the screen by manually moving a graphic cursor to locate both target and eye movement onset. The repeatability of the measure has been tested (by the same experimenter or by different experimenters) and the variability of the estimate of onset was one or two data samples (2–4 ms). The direction of the initial eye movement relative to target motion was taken into account to define the sign of the gain. When both movements occurred in the same direction, a positive sign was assigned to the gain. A negative gain was assigned to tracking trials where eye and target moved in opposite directions. Numerical data are presented as mean value±SD. ANOVA and Student's t-test were applied to data. The difference between means was considered significant when P values were smaller than 0.05 (i.e. $P<0.05$).

Results

General considerations

All subjects were submitted to a training session 1 day before the actual experiment. Within 15 min, the subjects

reached the requested level of performance, i.e. moving the arm sinusoidally at a frequency of about 0.3–0.4 Hz and an amplitude of 10° peak-to-peak, with corresponding SP of the target, without eye blinks or intrusive saccades for at least 15 s. No significant difference was found between subjects (SP latency, gain) except in experiment 3, so data from all the subjects were pooled together for the analysis. Factors related to the duration of the experiment (such as fatigue, discomfort from the eye movement monitor helmet), were taken into consideration to abort a recording session whenever the experimenter detected (or the subject reported) such occurrence.

Experiment 1: eye tracking of a external/self-moved target

The first experiment allowed a comparison of the tracking performance in terms of eye-to-target latency in eye-alone and in self-moved target tracking. The collected data were used as reference values for ensuing experiments.

The mean latencies were significantly different in the two tracking conditions: 152±24 ms in eye-alone track-

Fig. 3A,B Latency histograms (**A**) and eye motion direction inversion time histograms (**B**) in self-moved target tracking condition with random (*white blocks*, experiment 2) and systematic (*black blocks*, experiment 3) inversion of target motion relative to arm motion. Conventions are the same as in Fig. 1
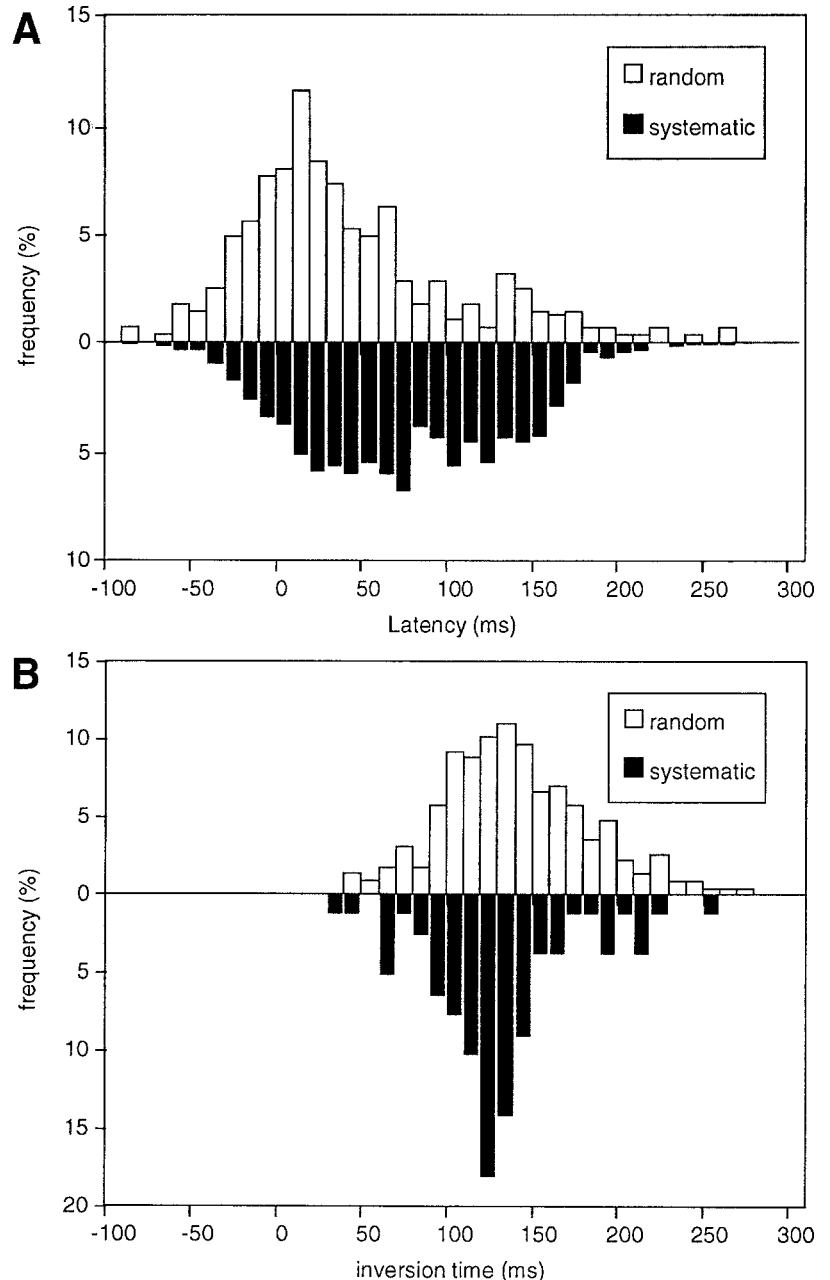
ing and 8±36 ms in self-moved target tracking (*P*<0.01). Sometimes, in the eye-alone tracking condition, SP was triggered with a low latency (as short as 80 ms). In these cases, the initial eye velocity, and thus the gain, were low (velocity <2°/s; gain 0.1–0.2).

The oculomotor behaviour observed in this experiment was similar to that observed in previous studies. Figure 1 shows typical records in eye-alone tracking (Fig. 1A) and self-moved target tracking (Fig. 1B) conditions. The histograms in Fig. 1C compare the distribution of eye/target latencies in the two tested conditions. In 30% of the trials in the self-moved target tracking condition (as in Fig. 1B), the eyes started to move *before* the arm (negative latencies in Fig. 1C). It must be noted that there is only a small overlap between the two histo-

grams, showing that the distributions are clearly different. Negative latencies were never observed in the eye-alone tracking condition. In contrast to eye-alone tracking, catch-up saccades never occurred at the beginning of self-moved target tracking.

Experiment 2: random inversion of arm-to-target motion relationship

In experiment 2, the subjects were exposed to a condition in which the direction of the target motion with respect to the arm motion was reversed for randomly chosen trials. Responses in non-reversed trials were similar to the one presented on Fig. 1B. In all the randomly re-

Fig. 4A–D Eye tracking of self-moved target with systematic inversion of arm-to-target relationship. **A** Response type 1: as in trials with random inversion, smooth pursuit (SP) started at the same time and within the same direction as the arm. **B** Response type 2: SP started in the same direction as the target (hence in the direction opposite to the arm) but with a longer latency, similar to the latency observed in eye-alone tracking. **C** Response type 3: SP started in the direction of the target, but with short latency, similar to the latency observed in self-moved target tracking without inversion. **D** First non-reversed trial after exposure to inversion: SP started in the opposite direction to that of both the arm and the target, with low latency. Conventions are the same as in Fig. 2A
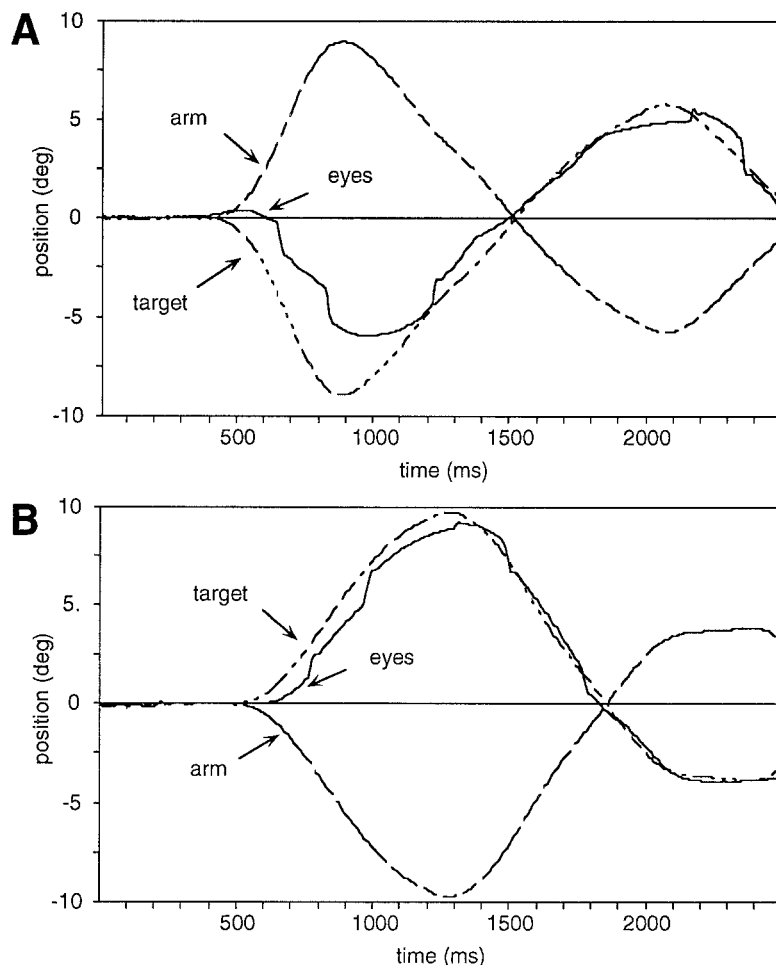
versed trials (Fig. 2A), the SP started with short latency in the direction of the arm motion, never in the direction of the target motion. The mean latency with reversed arm-to-target relationship was 13±38 ms and the mean latency measured in non-reversed trials was 10±37 ms. The latencies in reversed and non-reversed trials were not significantly different ($P>0.5$) from each other nor from latencies recorded in self-moved target tracking in the previous experiment ($P>0.5$). The initial SP gain (Fig. 2B) was 0.41±0.36. The eye velocity as measured during the early response was roughly correlated to arm velocity ($r=0.69$).

Following this first 100 ms of tracking (during which the eyes moved in the direction of the arm rather than in the direction of the target), the eye motion velocity decreased. Subsequently, its sign changed, on average, 139±53 ms after SP onset (a change of velocity sign corresponds to a change in direction of movement). We shall call the time elapsed between eye movement onset and the change of direction of the SP "inversion time". Thus, pursuit changed direction and continued in the direction of the visual target motion (opposite to the direction of arm motion). Soon after pursuit direction changed, a saccade was triggered towards the target, and then SP was in pace with visual information. Eye direction and velocity were then correlated to target motion and direction rather than to arm motion. The inversion

time of SP reported above was not significantly different from the eye-to-target latency observed in eye-alone tracking ($P>0.5$). The white block histograms in Fig. 3 show the distribution of both latency (Fig. 3A) and inversion time (Fig. 3B) under this condition.

Experiment 3: systematic inversion of arm-to-target relationship

The aim of experiment 3 was to test whether the reversed arm-to-target motion relationship could be learned, as observed in reversing prism experiments. In contrast to experiment 2, in which only two types of responses were observed, one specific for reversed and one for non-reversed arm-to-target relationship conditions, in this experiment three different behaviours became apparent as the session progressed. The three response types were qualified as follows:

Response type 1. SP started in the direction of the movement of the arm as in the previous experiment, with low (sometimes negative) latencies: 13±40 ms (Fig. 4A).

Response type 2. SP started with high latencies (140±42 ms, as in the eye-alone tracking condition of ex-

Fig. 4C,D
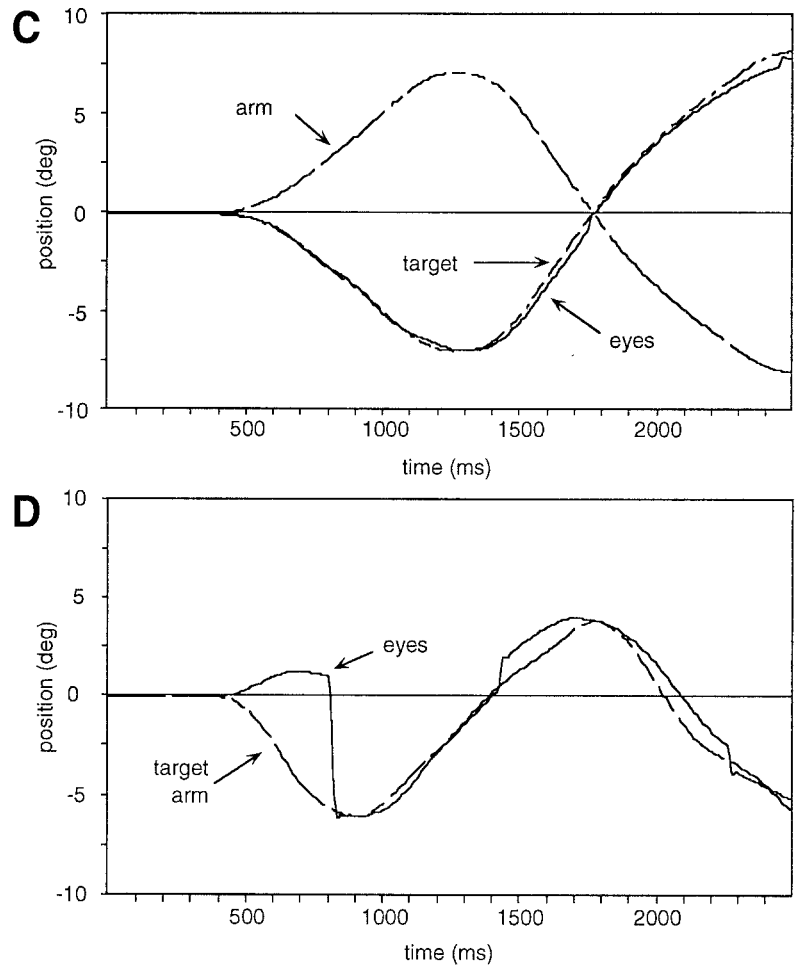
periment 1), in the direction of the visual target motion, thus opposite to arm motion (Fig. 4B).

Response type 3. SP started with quite high gain in the same direction as the visual target, as in type 2, but with low latencies (32±47 ms), comparable with latencies measured in trials corresponding to type 1 responses (Fig. 4C).

After 60 trials with reversed arm-to-target relationship, the inversion was suppressed without informing the subjects. The first, non-reversed trial after exposure induced an unexpected behaviour (Fig. 4D). Here, the SP started with low latency (average 25 ms) in the direction opposite to both the arm and the target motions. The next nine trials (without inversion) produced responses close to normal, that is, similar to those recorded in the first experiment, with self-moved target tracking condition without inversion. Some subjects reported that at the end of the experiment they were no more aware that the arm-to-target relationship was reversed, and they were unable to confirm whether the first trials on which the normal relationship was re-established were reversed or not.
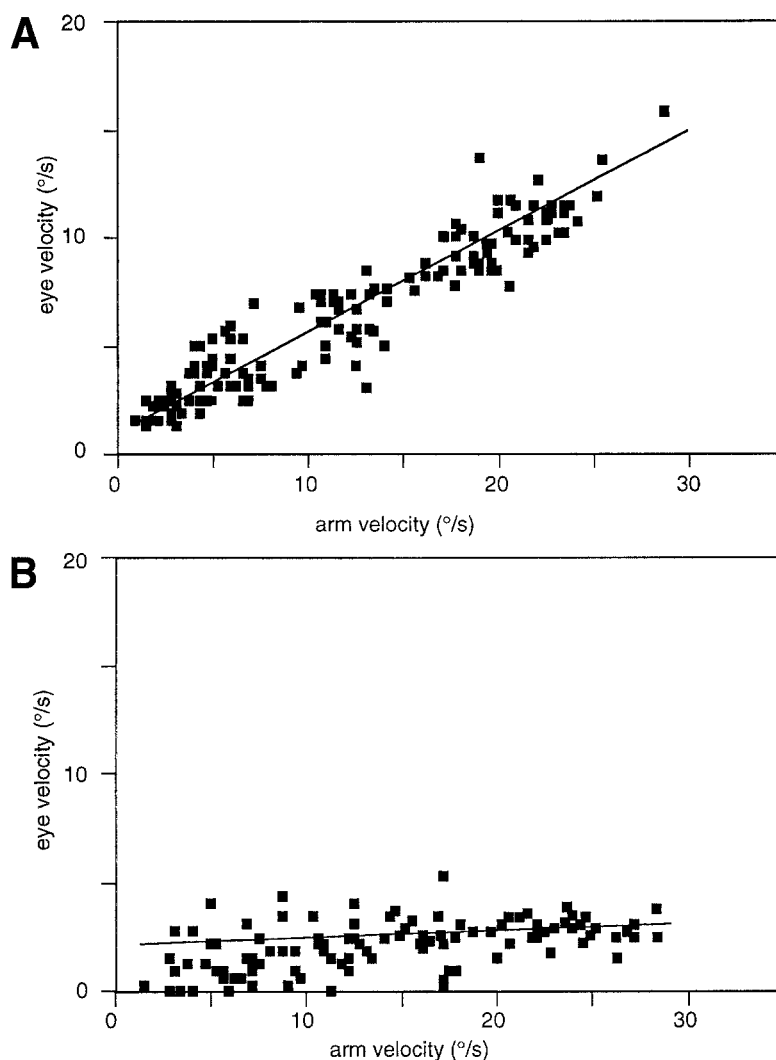
SP latencies

Figure 3 compares the distribution of latencies and SP inversion time, for trials with random inversion and trials

with systematic inversion. In the black histogram in Fig. 3A (systematically reversed arm-to-target relationship), although two peaks are slightly emerging, the distribution appears rather as a continuum between low and high latencies. It follows that the different types of responses were not distinguishable on the basis of latency, but rather on the direction of the initial SP movement (same direction as the arm or same direction as the target). Type 1 responses appeared almost exclusively at the beginning of the exposure (during the first 10 reversed trials) and represented 26.5% of the total number of responses, type 2 responses appeared more frequently during the second third of the exposure and lasted until the end of exposure (55% of the responses), while type 3 responses appeared with a lower frequency (18.5%, but some subjects did not show it at all: three of the tested subjects produced almost one-half of these responses), and were exclusively found during the last third of exposure.

Initial gain

SP movements found in types 1 and type 3 responses (e.g. with short latencies) were characterised by low initial gain. Type 1 response trials (as in Fig. 4A) resulted

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in initial eye velocity correlated to arm velocity (*r*=0.70; Fig. 5A) and ranging between 2 and 18°/s. Conversely, in type 3 response trials the mean initial velocity (during the first 100 ms) was low (mean 3.1±1.8°/s) and not correlated (*r*=0.01) to arm initial velocity (Fig. 5B).

*Latency and gain changes along a training session*

As reported above, response type 1 occurred more frequently at the beginning of the exposure, while the two other types appeared later. Still, no clear transition was observed between the three response types. Figure 6 shows the SP latency and initial gain time-course over a complete test session, for a single subject. The negative gains in Fig. 6A mean that SP started in the direction opposite to target motion (i.e. same direction as the arm). The negative latencies in Fig. 6B mean that SP started before arm motion onset. During control trials, mean latency and gain were 4 ms and 0.91, respectively, as in experiment 1. For the first trial with inversion the latency was, on the average, 8 ms, while mean gain was –0.70. Subsequently, mean latency progressively increased to

reach 74 ms. Gain absolute value decreased to 0.41 for the remaining reversed trials. SP started almost always in the direction of target motion (response types 2 and 3) until the end of the 60 reversed trials. The first trial after exposure (non-reversed) showed low gain (–0.58), and low latency (21±41 ms), with SP starting in the direction opposite to both arm and target motions (as reported above). During the last nine, non-reversed trials of the series, latency and initial gain progressively returned to pre-exposure values (mean latency 24 ms; gain 0.87). It is worth noting that the variability of both latency and gain values was much higher during the exposure than in pre-exposure trials, and higher than in the experiment 2.

Discussion

We further studied eye-arm coordination control in an experiment where the motion of the target was randomly uncoupled from the motion of the arm, by reversing the direction of target movement with respect to arm motion. This paradigm allowed us to separate the signals used in the initiation and control of eye SP motion direction as

Fig. 6A,B Time course of initial gain (**A**) and eye-to-target latency (**B**) during exposure to systematically reversed arm-to-target motion relationship, for a single subject. Negative gains mean initial SP in direction opposite to actual target motion. Negative latencies mean a lead of the eyes over target motion. The *dashed line on the left* (just after trial *10*) indicates the beginning of the reversed condition and the *vertical dashed line on the right* (just before trial *70*) its end
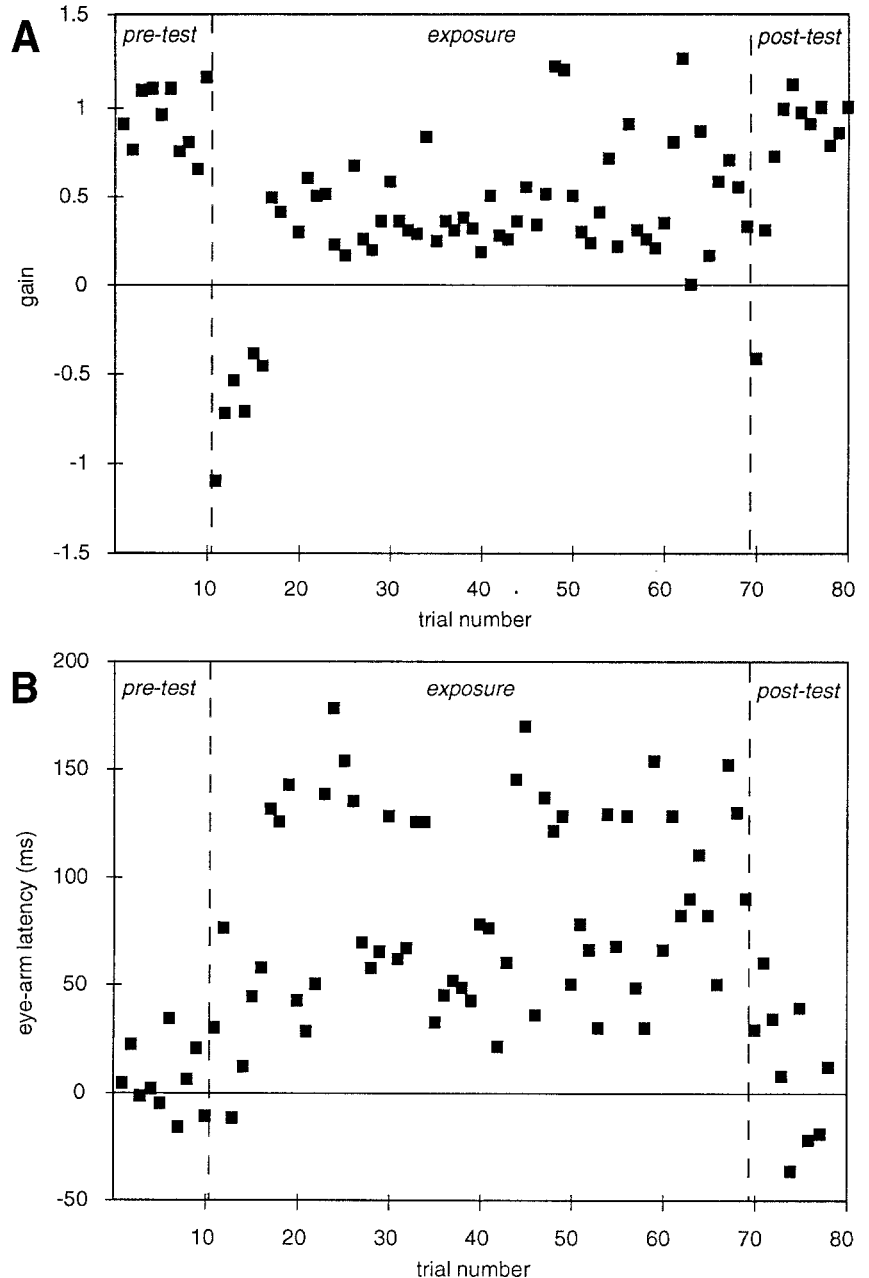
visual information coding target motion direction and non-visual information related to arm motion.

Smooth pursuit latency

In eye-alone tracking, we measured a mean latency of 152 ms. This value is markedly higher than values previously reported and considered as the intrinsic SP latency. Rashbass (1961) and Collewijn and Tamminga (1984) reported a 120 to 130-ms latency. Carl and Gellman (1987) recorded a latency as short as 90 ms. Since SP latency depends markedly on the nature of the target motion, we shall interpret our findings by considering the peculiarities of our target motion. In fact, the target mo-

tion we used was designed to approach the motion of a typical movement of the forearm, as measured in the self-moved target tracking condition. This allowed us to compare eye-alone to eye-arm tracking with a similar target motion. The initial part of the target displacement was characterised by a slow motion, known to increase the motion detection threshold of the SP system, hence the longer latency as compared to the step-ramp stimulus (Rashbass 1961).

In the self-moved target tracking condition, the decrease in eye-to-target latency was similar to that reported in previous studies and clearly showed that SP latency becomes very short when the observer drives the target himself (Steinbach 1969; Gauthier and Hofferer 1976; Gauthier et al. 1988; Vercher and Gauthier 1992). This

short tracking latency is presumably not due to prediction of visual origin as in eye-alone tracking (Bahill and McDonald 1983) which is highly dependent on target motion dynamics (i.e. waveform, frequency), nor due to anticipatory eye movements (Kowler et al. 1984; Kowler 1989). Indeed, in our experiment, when the visual input to the SP system was opposite to the arm movement, short-latency SP was always triggered in the direction of the arm rather than in the direction of the visual signal. In this condition, the gain was low as compared to external target tracking, but the initial SP velocity was much higher (3–18°/s) than in anticipatory eye movements recorded in 1989 by Kowler (from 15 min arc/s to 1°/s). Thus, SP can be triggered by non-visual information issued from the arm motor system, before visual information related to target motion reaches the SP system, confirming the Gauthier and Hofferer (1976) experiment with imaginary target tracking. Furthermore, we have previously shown (Vercher and Gauthier 1992) that if the visual feedback of the arm is delayed, SP begins long *before* actual target motion, thus suggesting that eye-arm coordination was not due to SP prediction.

Non-visual triggering of smooth pursuit

The effect of arm motion on eye tracking movements was evidenced in experiment 2, where arm motion influenced both SP initiation time and motion direction. It was clear from trials with random inversion of the arm-to-target motion relationship that SP was initiated in a direction opposite to target motion, thus increasing retinal slip, in contrast to the primary function of the SP system. This type of response illustrates a conflict between rapid, non-visual triggering of SP and slow visual processes. Obviously, the non-visual signals issued from the arm motor system do not control SP with the same accuracy as those obtained from visual inputs. In particular, SP generated on the basis of non-visual information has an inappropriate gain much like that observed when tracking an imaginary target (Jordan 1970; Gauthier and Hofferer 1976). In the present study (experiment 2), when the target motion was reversed with respect to arm motion (as in Fig. 2A), the initial gain was lower than when the visual target moved in the direction of the arm motion (Fig. 1B).

Detailed analysis of the time course of the eye motion in the reversed target motion protocol suggests the following interpretation. Because the eye motion occurred systematically in the direction of the arm motion, though with low gain but relatively short latency, non-visual information was definitely responsible for that part of the ocular response. About 100–130 ms after the beginning of the arm motion (target motion as well), the eye velocity decreased rapidly then the eyes changed their course to move in the direction of the visual target, first with SP, then with a saccade to correct for the large accumulated error. Since the beginning of the eye velocity decrease coincided with the closing of the visual feedback loop

(the first 100 ms of SP precedes the first moment of visual feedback: Lisberger et al. 1981; Tychsen and Lisberger 1986), this portion of the tracking must be basically under visual control. A similar interpretation has previously been proposed by Domann et al. (1989). They reported that SP always started in the direction of the visual target, irrespective of the arm-to-target motion relationship. In fact, Domann et al. (1989) did not mix direct and reversed arm-to-target condition in a same session (as opposed to our experiment 2). The data from experiment 3, where arm motion and visual target motion were systematically reversed, revealed two ranges of latencies, suggesting that two processes were involved in the initiation of SP (retinal and non-retinal processes). In contrast, in experiment 2, where arm and target motion directions were randomly reversed, SP was presumably almost always triggered by non-visual information and occurred with short latencies in the direction of arm motion.

The eye motion pattern suggests a simple and comprehensive model where both the control signal from the arm movement system and the control signal from retinal system will combine to drive the SP system controller. Because the non-visual signal has a shorter latency, the eyes will first be driven in the direction of the arm, then later visual and non-visual inputs conflict with each other. Finally the retinal input alone seems to drive the SP system, while the input from the arm system is either inhibited or overridden by the visual input.

Adaptation to exposure to reversed arm-to-target motion relationship

Is there a parallel between adaptation to reversing prisms and arm-to-target motion relationship inversion? Domann et al. (1989) suspected that reversal of SP relative to the intentional signal about arm motion was due to an adaptive process similar to the one observed during vestibulo-ocular reflex adaptation to reversing prisms. The aim of our 3rd experiment was to test whether a human subject could adapt to such an alteration in the arm-to-target relationship. In experiments where the visual image of the arm position is altered by means of optical devices such as prisms, arm movement re-calibration occurs rapidly, providing the subject is allowed simultaneous vision of the target and his arm (a so-called visual closed-loop condition). If prisms reversing right and left directions are used (Harris 1965), visuo-manual reorganisation also develops, but slower than with regular prisms. Several days of prism wearing are needed to reach normal behaviour.

The visuo-manual alteration used in experiment 3 is similar to that produced by "dove" prisms (reversing right and left) and the results, if taken according to their main trend, show visuo-manual rearrangement similar to that observed with such prisms. Indeed, after a few trials, the eye motion occurred in the direction of the visual target rather than in the direction of the arm motion. When the arm-to-target relationship returned to normal without

notice after 60 trials, the subjects first initiated SP in the direction opposite to both target and arm motions (Fig. 4D). This response illustrated a typical after-effect usually observed in hand pointing tasks, when, after a period of exposure to prisms, the subject is suddenly returned to the non-altered visual condition.

Still, quite a few observations related to the time course of the responses make experiment 3 different from prismatic experiments: in particular, adaptation seems to develop slower. The type 1 response (with short latency and motion direction opposite to visual target motion) did not continuously evolve towards type 2 response (with long latency and appropriate direction and gain). It rather appears that type 2 responses resulted from a deliberate attempt by the subject to either inhibit or consciously ignore the control signal issued from the arm movement system or "wait" in place for the retinal signal to become available. Eye-arm coordination control being quite robust and effective, cognitive control over it might not be effective in every trial, explaining why type 2 responses intermingled with type 1 responses during the first 20 or 30 trials. As this process went on, changes occurred in the brain to reorganise eye-arm coordination in a less cognitive way. A hypothesis worth testing is based on the fact that, in visual manual tracking of a self-moved target, the input to the oculomotor system is produced by an internal representation of target motion, built on the basis of information generated by the arm motion. The inverted relationship between the arm motion and the target motion could then be included in the generation of this internal model. Angel showed in 1976 that a central representation of the intended movement allows one to modify a movement during or just before its execution, leading to extremely short latency corrections to external perturbations, incompatible with a visual loop. Harris (1965) also proposed that adaptation of arm motion to displaced or reversed vision resulted from a change in the internally registered position of the different body segments. A similar interpretation has also been proposed for the adaptation of the vestibulo-ocular reflex (VOR) in response to prisms inverting left and right (Gonshor and Melvill Jones 1976).

Conclusion

This study confirmed that non-visual information generated by the arm motion are responsible for eye-to-arm synchronisation in eye tracking of self-moved target. In the case of conflict between visual information and arm motion, SP is triggered with short latency in the direction of the arm motion.

The data also showed that in spite of the predominant role played in oculo-manual coordination by visual information, signals issued from the arm motor system can trigger SP more precociously than vision. This synchronisation between arm motion and eye motion compensates for the "slowness" of visual information and allows a spatio-temporal consistency during manipulation under visual control. When conflicts occur between visual motion and kinaesthetic information from the arm motion, the central control system first attempts to inhibit or compensate the activation of SP in the direction of arm movement. Control is then slowly modified to restore accurate visual tracking. This adaptive change will involve a reorganisation of the central representation of the target motion.

The present study does not allow us to determine which signal from the arm sensory-motor system is responsible for eye-arm movement coordination control in visual manual tracking. Preliminary results from an experiment involving eye tracking of a target attached to a passively moved arm suggest that the eye-arm movement timing is controlled by the arm efferent copy rather than by the proprioception. If confirmed, these data will support the hypothesis according to which the arm efferent copy is somehow used to trigger the eye movement as the arm starts moving, while the afferent information contributes to the SP control once initiated (Gauthier et al. 1988).

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