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Manuo-ocular coordination in target tracking.
II. Comparing the model with human behavior

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Abstract. Several studies have shown that humans track a moving visual target with their eyes better if the movement of this target is directly controlled by the observer's hand. The improvement in performance has been attributed to coordination control between the arm motor system and the smooth pursuit (SP) system. In such a task, the SP system shows characteristics that differ from those observed during eye-alone tracking: latency (between the target-arm and the eye motion onsets) is shorter, maximum SP velocity is higher and the maximum target motion frequency at which the SP can function effectively is also higher. The aim of this article is to qualitatively evaluate the behavior of a dynamical model simulating the oculomotor system and the arm motor system when both are involved in tracking visual targets. The evaluation is essentially based on a comparison of the behavior of the model with the behavior of human subjects tracking visual targets under different conditions. The model has been introduced and quantitatively evaluated in a companion paper. The model is based on an exchange of internal information between the two sensorimotor systems, mediated by sensory signals (vision, arm muscle proprioception) and motor signals (arm motor command copy). The exchange is achieved by a specialized structure of the central nervous system, previously identified as a part of the cerebellum. Computer simulation of the model yielded results that fit the behavior of human subjects observed during previously reported experiments, both qualitatively and quantitatively. The parallelism between physiology and human behavior on the one hand, and structure and simulation of the model on the other hand, is discussed.

1 Introduction

We presented in a companion paper (Lazzari et al. 1997) a dynamical model of arm-eye coordination based on the observation of human subjects visually tracking a target attached to their moving arm (self-moved target tracking, SMT). In previous studies, it has been shown that the ocular smooth pursuit (SP) system shows enhanced characteristics and performance when the subjects track a self-moved target as opposed to eye-alone tracking (EAT). In particular, the SP velocity saturation is higher (Gauthier et al. 1988), the target frequency bandwidth is wider (Vercher et al. 1993), and the SP latency is shorter (Gauthier et al. 1988; Vercher and Gauthier 1992; Vercher et al. 1995, 1996). The performance changes observed at the SP level when the visual target is hand-driven by the observer are supposed to be mediated by a specific system, called the *coordination control center*. Basically the model, which has been implemented using a System Theory approach, is based on the following statements:

1. Coordination control is based on an exchange of non-visual signals (proprioception, efference copy) between the arm motor system and the oculomotor system. Thus, the model of coordination control is not based on a common command addressed simultaneously to the arm motor system and to the oculomotor system.
2. Coordination control is mediated by a structure of the central nervous system (CNS), that receives information from both sensorimotor systems.
3. Efference copy from the moved arm plays a crucial role in timing aspects (synchrony between arm and eye motion onsets) while arm muscle proprioception is needed for spatial aspects (accuracy).

Indeed, there is clear evidence that the SP system and the arm do not share the same central command: for instance, gain and phase values of the arm and eyes show non-correlated features, suggesting specific commands for each system (Bock 1987). The independence between the arm movement and saccades during reaching is less evident: Gielen et al. (1984) showed that saccades and arm reaching toward a visual target are separately triggered, while Bekkering et al. (1994) showed an interference between saccade and arm latencies. Delreux et al. (1991) suggested that the final position of the saccade and the arm is specified by a common command, while Vercher et al. (1994) showed that the time of arrival is common. During simultaneous head-eye-arm pointing, gaze and arm movements start at different

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times but end at the same time. This synchronization appears to be due to a change in head motion parameters during simultaneous pointing as compared with gaze-alone pointing. As often seen in science, a single model is not sufficient to account for all the observed data. Indeed Frens and Erkelens (1991) showed that saccades are actually triggered by two different mechanisms: one visual, specific to the saccadic system, and the other cognitive, shared with the arm. The specificity of self-moved target tracking over simultaneous tracking or pointing is that in this condition there is no actual external signal triggering both eye and arm movement, and thus no input that could be shared or used to elaborate a common command. Also, as opposed to saccades, SP triggering and metrics are not under voluntary control.

The nonvisual nature of the coordination signals has been demonstrated in previous studies: in particular, by changing the relationship between the arm motion and the arm-attached target motion, we showed that nonvisual signals generated by the arm motion during eye tracking of a self-moved target are responsible for the synchronization between the arm and the eye motion onsets (Vercher and Gauthier 1992; Vercher et al. 1995). The respective roles of arm efference copy and proprioception have been demonstrated by testing passive arm movement on control subjects and active arm movement on people without proprioception (Vercher et al. 1996).

As to the neuroanatomical localization of the coordination control centre, Vercher and Gauthier (1988) proposed the dentate nucleus of the cerebellum as a potential candidate because lesions of this structure in trained monkeys disrupt the enhanced coordination between the eyes and the arm. More recently, Brown et al. (1993) supported this hypothesis with data from cerebellar patients. These authors showed that in a self-moved target tracking task, eye tracking latency was significantly longer in cerebellar patients than in control subjects whereas initiation of eye-alone tracking was not affected.

The model developed, implemented and simulated on the basis of empirical research, was conceived as a prototype in order to test the veracity of the hypotheses addressing the way information about movement is used to coordinate different motor systems. We tried to maintain a high degree of parallelism between the model and what is known about the physiology of motor control. We also tried to make sure that one single model would behave in the appropriate way in the different tracking conditions. Indeed, all the simulations shown here have been produced without altering the model, whatever the condition.

We provide here results of the simulation in different tracking conditions, comparing the output of the model and observed behavior of human subjects as reported in previous papers, in particular in experiments in which the arm-to-target relationship was altered (Vercher and Gauthier 1992; Vercher et al. 1995). Together with the trajectories produced by simulation, we will provide details about how the model works and how the simulations were obtained. Since the aim of this paper is to compare the model's behavior with human behavior and thus to validate the model, we will focus on the model's structure, providing mathematical details only when necessary for understanding the simulations. More extensive details on the model structure and mathematical description of its components have been provided in a companion paper (Lazzari et al. 1977).

2 Experimental methods

2.1 Data acquisition

The experimental set-up for data acquisition in human subjects, the protocols and signal processing techniques have been described in detail elsewhere (Vercher et al. 1993, 1995, 1996). New data were collected in order to repeat the same conditions as for the simulations (target motion frequency, sampling rate, etc.). The subjects were seated in front of a screen located 171 cm away from their head which in turn was immobilized by a dental print bite-bar. Their forearm was attached to a horizontal gutter, the hand pointing in the direction of the screen. The movement of the arm was restricted to one degree of freedom (the elbow angle). The subject's arm was completely hidden from sight by a curtain. Horizontal eye movements were recorded with an infrared corneal reflection device (Iris, Skalar) and arm motion recorded by means of a potentiometer at elbow level. The signals were amplified, filtered (low-pass 200 Hz) and digitized at 500 or 200 samples/s, depending on the type of analysis (time or frequency domains). One or two visual targets (namely the external target and the self-moved target, displayed alone or together depending on the condition) were projected on the screen after reflection on galvanometer-driven mirrors. The motion of the external target was controlled by computer and followed a sinusoidal horizontal path in the frontal plane at eye level ($\pm 15^\circ$ at 0.3 Hz), except at the beginning and end of the path, where sections of cosine substituted the initial and final position changes in order to replicate the velocity profile of a typical arm movement. At target motion onset and offset, position and velocity were equal to zero. This was done to make the target follow trajectories with similar kinematics in both eye-alone and self-moved target tracking and to allow the comparison between the performances of the SP system in these two conditions. The motion of the self-moved target was driven by the signal from the potentiometer monitoring arm motion.

2.2 Tracking conditions

Data from human subjects were collected using protocols described in previous studies (Vercher and Gauthier 1992; Vercher et al. 1993, 1995, 1996). Basically, three tracking conditions were used: in the first condition (eye-alone tracking, EAT), the subject followed the external target only with the eyes; in the second condition (simultaneous eye and hand tracking, EHT), the subject followed the external target with both the eyes and the arm; in the last condition (self-moved target tracking, SMT) the subject moved the arm sinusoidally at learned amplitude and frequency ($\pm 15^\circ$ at 0.3 Hz) and tracked the self-moved target with his or her eyes. To distinguish between visual and nonvisual information coding the arm movement in the SMT condition, alterations of the hand-target spatio-temporal relationship were also introduced by delaying the target motion relative to the hand motion (Vercher and Gauthier 1992) or by spatially reversing the hand-target relation (Vercher et al. 1995).

2.3 Model implementation

The model has been simulated and tested using Matlab with Simulink (The Mathworks, Inc.) In brief, the model (see Fig. 1 of Lazzari et al., 1977), was concerned with the emulation of sensory and motor control structures at the CNS level and was not intended to represent accurately the biomechanical properties of the arm and eyes. All the viscoelastic characteristics of eye and arm motor systems are globally modelled through transfer functions, in the form $A(s)/B(s)$, with one or two poles.

The model features three main parts: the eye motor control section (containing a SP branch and a saccadic branch) based on the models proposed by Young (1971) and Robinson et al. (1986), the arm motor control section and the coordination control section. Coordination control is achieved by an exchange of information between the arm and the eye sensorimotor systems, mediated by signals such as vision, proprioception and motor command copy.

The input element of the model is represented by a *target motion generator (TMG)* block, which generates the input signals. In the first two conditions, EAT and EHT, this block plays the role of the external target generator, providing sinusoidal signals at given frequencies and amplitudes, while in the last condition, that of SMT, it represents the subject's intention to perform a determined movement and generates a cos-bell position wave. A *setup* block was introduced in the model to allow the selection of one of the three conditions. In the EAT condition, the *oculomotor system* receives an external signal produced by the TMG while the arm system input is constantly zero; in the EHT condition both eye and arm systems receive the external signal as input; finally, in the SMT condition, input for the arm system is represented by the 'intention' signal while the input for the eye system is the arm position.

2.4 Data analysis

The parameters used during the simulation (sampling frequency, trial duration, amplitude and frequency of target motion) were identical to those used during data acquisition from subjects in order to allow more precise quantitative comparisons. The same analysis procedure applied to the human data was also applied to the signals generated during the simulation. Offline signal analysis started with digital low-pass filtering (cut-off frequency 30 Hz) and differentiation. The time interval between target motion onset and eye motion onset was automatically detected using a method derived from Carl and Gellman (1987). This value could subsequently be refined by manually moving a cursor on the computer screen (Vercher et al. 1996).

3 Comparison of model simulation output with human behavior

In the three tracking conditions described above, the model outputs have been compared with the behavior of humans instructed to perform similar tasks. Since the model works in a deterministic way, there is no variability in eye and arm trajectories and in target-to-eye latencies, provided target trajectory and model parameters are constant. In contrast, although one may identify a constant pattern in trajectories produced by humans, these trajectories display some variability (mostly in terms of timing of the saccades). In previous studies (Vercher and Gauthier 1992; Vercher et al. 1996) we described a typical response which globally described the behavior observed for all subjects and all trials for a given condition, including ones where the visuo-manual relationship was altered. To illustrate the comparison between the model simulations and the data from humans, we arbitrarily selected a set of trials in which arm and eye trajectories were estimated to be representative of the typical behavior of the human subjects as described in the previous studies (latencies, gain, time course, presence of saccades, etc., equal to the average over all the trials from all the subjects in the same condition).

3.1 EAT: the ocular pursuit model

In the EAT condition, the subjects were instructed to fixate a target and then follow it, as accurately as possible, as the target started to move. A typical response from a human performing in the EAT condition is shown in Fig. 1A. After a latency of 130 ± 29 ms, the subject's eyes start to move in the direction of the target motion. Then the subject makes a saccade to catch up with the target and compensate for the position error due to the lag of the eyes with respect to the target. The subject's eyes then follow the target with a slow movement, fewer saccades and no lag. This coordination pattern of slow (SP) and rapid (saccades) eye movements is typical of the behavior exhibited by a human subject tracking a visual target moving in a predictable way (Bahill and MacDonald 1983a). This behavior (e.g. the zero-lag tracking of a sinusoidally moving target) implies that subjects predict the target position and/or velocity, in order to overcome the 130-ms delay of the SP system (Stark et al. 1962; Bahill and McDonald 1983a,b; Yasui and Young 1984; Barnes and Ruddock 1989). This ability improves with training: subjects can learn to track with their eyes a predictable waveform, provided that target motion frequency, velocity and acceleration do not exceed given limits. The prediction is also evidenced when the target stops moving suddenly and unexpectedly: the eye motion stops with a latency of 180 ms (Bahill and McDonald 1983a).

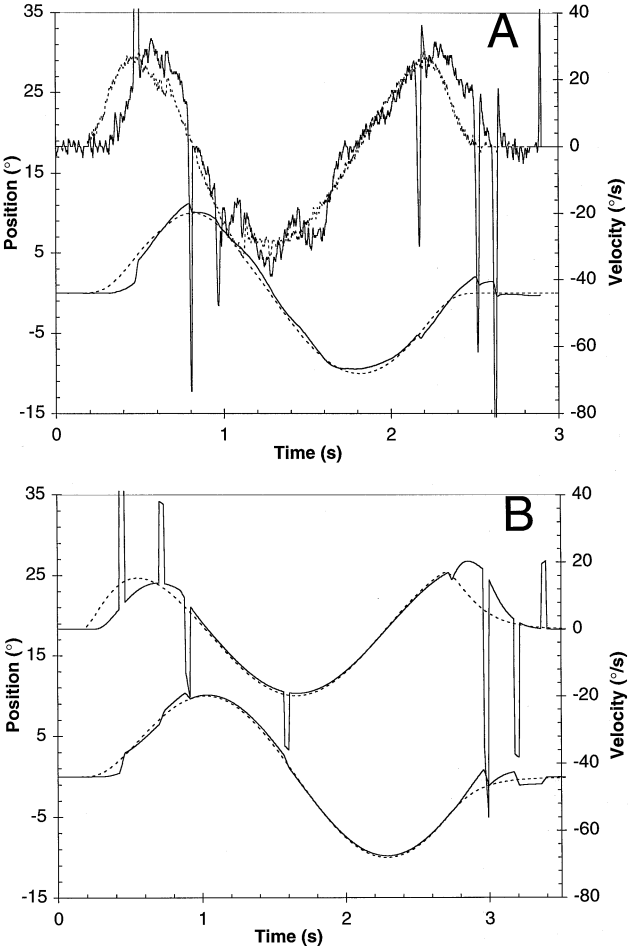

Fig. 1. A Performance of a human subject during eye-alone tracking (EAT condition) of a sinusoidally moving visual target (±10°, 0.5 Hz). Position and velocity of target and eyes are plotted as a function of time. **B** Output of the eye-tracking model following a sinusoidal target, with the same characteristics as above. In each graph, the *thin lines* represent eye position (*bottom trace*) and velocity (*top trace*), while the *dotted lines* represent target position and velocity

As for the simulation results, in the EAT condition the *setup* block acted as follows: the input of the arm motor system was constantly set to zero in order to prevent arm movements and the output of the TMG was sent to the retina. The setup sets the tracking condition to be used for the simulation: the *visual reconstructor* sent the reconstruction of the *external target* position in space to the SP branch, and sent the retinal error relative to the external target, to the saccadic branch, so that the oculomotor system tracked this target only. Figure 1B shows the output signals obtained from the simulation in the EAT condition. When the target starts moving, the eye exhibits the usual 130-ms delay of the SP system and the subsequent SP-saccade coordination pattern produced to catch the target. The first time the target reverses its direction, the SP system is still responding with a lag due to internal delays; the position error is compensated by a series of saccades. After about 830 ms from the onset of eye movement, the contribution of the *predictor* allows the eyes to be perfectly on the target and to follow it with no phase lag. When target motion stops, the eyes continue their motion in the same direction for 200 ms and cease moving after a couple of saccades. Several studies have focused on modelling and simulating prediction in the SP system (Bahill and McDonald 1983b; Barnes 1994; Koken et al. 1996). All these models produce realistic behavior but are too sophisticated to be integrated 'as is' within our model without greatly increasing the simulation time. In order to emulate the predictive behavior, a very simple predictive component was introduced, because the way prediction actually works was not central to our aim. We followed the idea of Greene and Ward (1979), who stated that future target motion is predicted through a polynomial extrapolation of previous values (see Lazzari et al. 1997). The predictor is placed in parallel with the *SP controller*, whose role is to set the SP gain for unpredictable target motions and to prevent sharp changes in eye velocity.

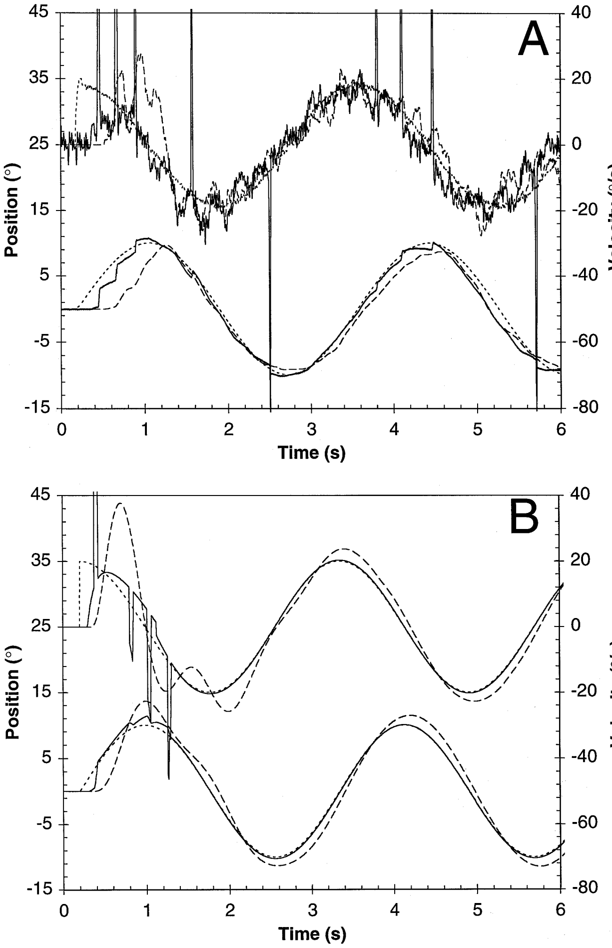

Fig. 2. A Performance of a human subject during simultaneous eye and arm tracking (EHT condition) of a sinusoidally moving visual target (±10°, 0.3 Hz). **B** Model outputs of both the eye and the arm motor systems tracking a sinusoidal target. The *conventions* are the same as in Fig. 1. The *dashed lines* represent arm position and velocity

3.2 EHT: the arm tracking model

In the EHT condition, the subjects were instructed to track the external target with both the eyes and the arm. This condition assessed the performance of the arm motor system. In Fig. 2A the trajectories produced by a human subject are shown. In this condition, the performance of the SP system is similar to its performance in EAT (same latency and saccade pattern). The latency of the arm is longer than the latency of the SP system. The lag of the eye is compensated by a saccade, while the lag of the arm is compensated by a corrective movement whose velocity exceeds the velocity of the target. After at least half a cycle of tracking, the subject can follow the target without lag with the eyes and the arm. The presence of sudden changes in the arm velocity profile implies the existence of a corrective mechanism based on visual information of the arm tracking error (Navas and Stark 1968; Miall et al. 1993a). The arm motor system attempts to reduce the tracking error with discrete movements of the arm, comparable to some extent to saccadic eye movements.

During the simulation of the EHT condition, the *setup* block worked as follows: the output of the TMG was sent to the retina, which also received the output of the arm motor system (depicting the arm-driven visual target position). The *visual reconstructor* was instructed to rebuild the position of both the target and the arm relative to space. The reconstruction of the external target position was sent to the SP system. The retinal position error about the external target was sent to the saccadic system. Both the external and the self-moved target positions were sent to the *visual corrector* of the arm motor system. These signals allow computation of the error between arm and target positions and the generation of a correcting signal transmitted to the arm plant. The presence of such a visual corrector is evidenced by the fact that the arm tracking movement becomes smoother when vision of the arm is occluded (Miall et al. 1993a).

In the model, two feedback loops act on the arm motion system. One is concerned with arm position, the other with arm velocity. Experiments with deafferented monkeys (Knapp et al. 1963) and humans (Cooke et al. 1985; Bard et al. 1995; Vercher et al. 1996) have shown that though arm movements are possible without afferences, their characteristics are largely degraded, especially in the absence of visual control. The delays within each control loop are set according to current literature: 100 ms for the central controller, 15 ms for both position and velocity proprioceptive loops (Lamarre et al. 1983; Cordo et al. 1994).

The simulation (Fig. 2B) shows features similar to the behavior of humans. We will focus here on the performance of the arm system, since the behavior of the oculomotor system has been described in the previous section. The latency of the SP system is 130 ms, while the latency of the arm motor system is 150 ms. At the onset of hand tracking, the *visual corrector* (of the arm motor system) is responsible for the high-velocity corrective movement that compensates for the delay. After two large corrective movements, clearly evidenced by the velocity traces on Fig. 2B, the arm follows the visual target appropriately but still with a small lag (no prediction has been implemented in the model though humans certainly show predictive abilities: Stark 1968; Miall et al. 1993b). The visual corrections also exist in the traces from the human subject (Fig. 2A), more or less at the same time from the beginning of the trial (the first half cycle of tracking, e.g., the first 2 s of recording). The corrections appear to be sharper in the human data and more rounded in the model, possibly due to small differences in arm dynamics, that are only approximated in the model.

3.3 SMT tracking: the coordination control model

The SMT condition consisted in tracking with the eyes a target actively moved by the observer's arm. Prior to the session, the subjects were trained to produce sinusoidal arm movements at a frequency of ∼ 0.3 Hz and with a peak-to-peak amplitude of ∼ 30° with minimal variations. Figure 3A shows the performance of a human subject during an SMT tracking task. The most striking features are the reduction in the delay of the SP system at the onset of target (arm) motion from 130 ms on average (in the EAT condition) to a merely -5 ± 35 ms (in the SMT condition), and the immediate and accurate ability to follow the target with close-to-zero lag, as evidenced by the absence of any saccades in most of the trials. A relevant contribution to this performance is presumably under predictive control by the SP system, as evidenced by the continuation of SP when the arm stops moving.

In the simulation of the SMT condition, the *setup* block functioned as follows: the output of the TMG was sent to the arm system in order to simulate the intention to move the arm. The *visual reconstructor* was instructed by the setup block to send the visual reconstruction of the arm position in space to the SP system and the retinal error between the eyes and the arm positions to the saccadic system. No visual corrections were produced in this condition since arm and target position signals were coincident.

The timing characteristic of the coordination control (low SP latency) supports the existence of an exchange of information between the arm and eye motor systems (i.e., an informational path issued from the arm system and addressed to the eye motor system). This allows the eyes to anticipate the arm motion, and to begin to move before the target displacement is visually perceived. The simulation of this behavior has been achieved on the model through the introduction of the *coordination control system* (CCS): an element placed between the two subsystems and dedicated to the control of the information flow from the arm system to the eye system. As proposed by Vercher et al. (1996), the information used by the SP system to overcome the initial delay is provided by the arm motor efferent copy. This signal, acquired from the arm motor branch just before the arm plant, is processed in the CCS and then sent to the eye motor branch, just before the *pulse-step generator*. This allows the long processing delay introduced by the visual branch to be bypassed, eliminating the initial delay of 130 ms, as illustrated by Lazzari et al. (1997).

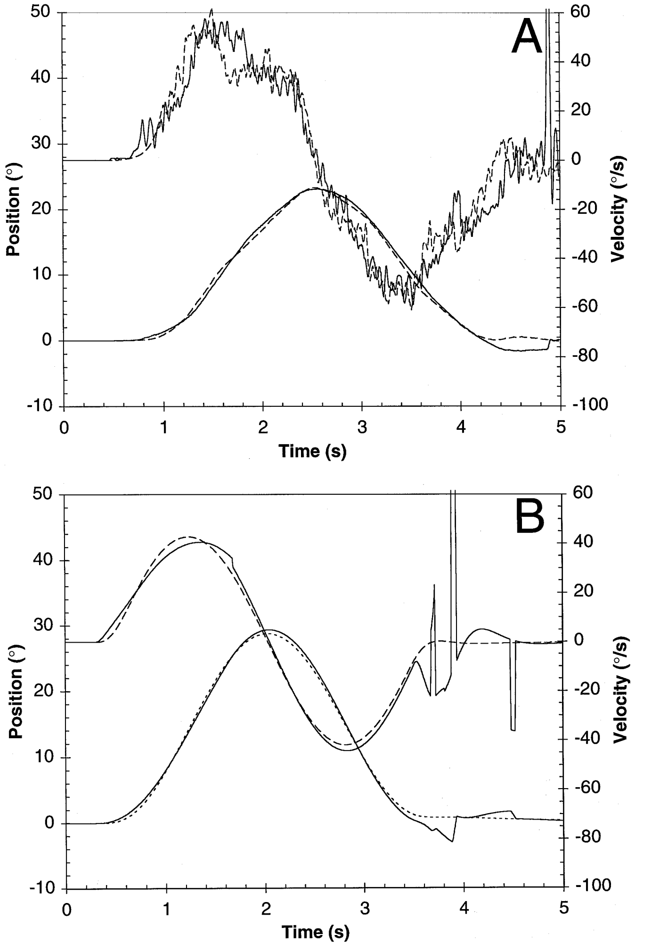

Fig. 3. A Performance of a human subject during self-moved target tracking (SMT condition: target motion is controlled by the subject's arm motion). **B** Output of the model tracking an internally generated sinusoidal target (±15°, 0.3 Hz) with the arm and tracking the arm motion with the eye system. Conventions are the same as in Figs. 1 and 2

3.4 Altered visuo-manual relationship in SMT tracking

The model also produced SP movements similar to those of human subjects when the relationship between arm motion and visual target motion was altered by a delay (Vercher and Gauthier 1992) or by reversal of target motion relative to arm motion (Vercher et al. 1995). The goal of these previously published experiments was to artificially dissociate visual from nonvisual information about arm motion, in order to determine the relative pattern of action of both signals (afferent and efferent) on triggering SP. Similar situations may appear in the real life when a human is tele-operating a re-

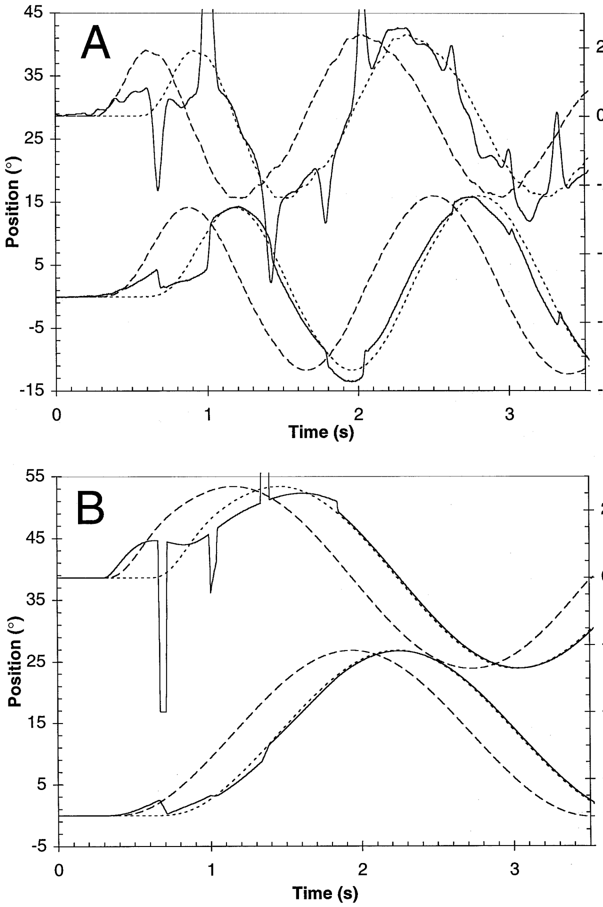

Fig. 4. A Performance of a human subject moving the arm sinusoidally (±15°, 0.3 Hz) and tracking the arm motion with the eye when an artificial delay is introduced between arm motion and arm-attached target motion (Vercher and Gauthier 1993). **B** Output of the model during the SMT condition with an arm-target delay of 300 ms. *Conventions* are the same as in Figs. 1 and 2

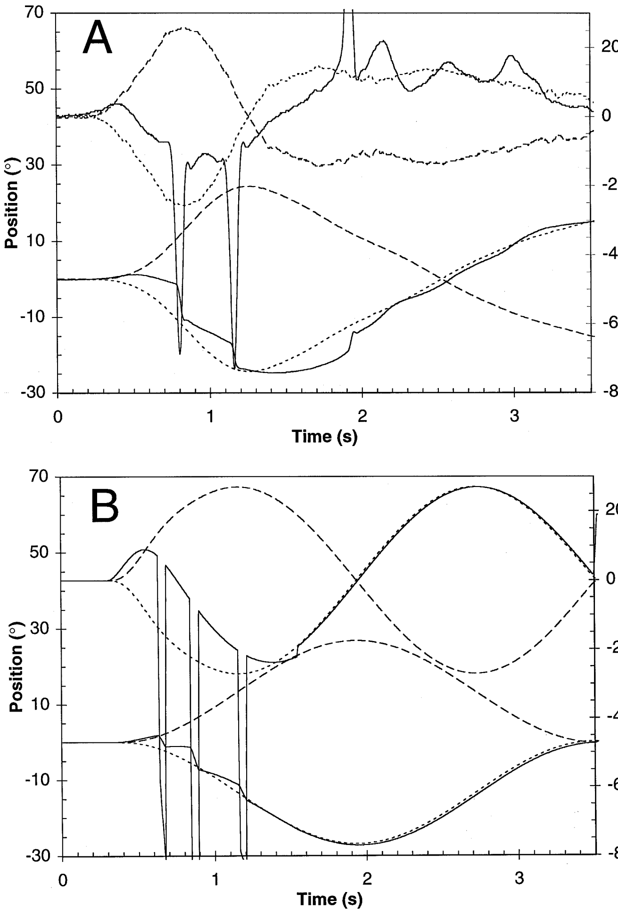

Fig. 5. A Performance of a human subject during the SMT condition when the relationship between the arm and the arm-attached target is reversed (Vercher et al. 1995). **B** Output of the model tracking an internally generated sinusoidal target (±15°, 0.3 Hz) with the arm and tracking the visually-reversed arm motion with the eye system. *Conventions* are the same as in Figs. 1 and 2

mote system (robot or vehicle) and monitoring the motion of the device through a video display. A long delay between the operator action and the remote system response would correspond to the first situation. We would see the second situation if the camera were positioned in such a way that when the action of the operation is directed rightward, the response of the system is oriented leftward (from the operator's point of view). Both experiments showed a common feature: that is, in case of conflict between visual and nonvisual signals coding arm motion, the SP system is largely influenced by nonvisual signals during the early stage of tracking (e.g., the eyes track the real arm motion instead of the visual target) while during steady-state tracking (after 1/2 s at 0.3 Hz) the SP system seems to be driven exclusively by visual signals (the eyes track the visual target).

Figures 4 and 5 illustrate the type of behavior produced by both human subjects and the model when the arm-target relation is delayed or reversed, respectively. In the former experiment (for more complete data recorded during this experiment see Vercher and Gauthier 1992) the subjects were instructed to move the arm sinusoidally and keep the eyes on the arm-driven target. At random, the target was delayed (50–500 ms) relative to arm motion. A delay of 50 ms was never detected by the subjects.

Observations during this experiment showed that SP can be triggered by a nonvisual signal and that this signal is no longer active a few hundred milliseconds after movement onset. This helped in designing the processing function applied within the CCS to the arm motor command issued by the arm motor system (Lazzari et al. 1997). There was no significant inter-individual difference in the eye response pattern, whatever the artificial delay. SP always started in close synchrony with the onset of real arm motion rather than with the visual target motion, showing the crucial role of nonvisual information in triggering self-moved target SP. The arm-eye latency did not depend on the added delay (36 ± 63 ms without added delay, 41 ± 56 ms over the full range of added delay). When the delay was higher than 150 ms, a saccade was always triggered in the direction opposite to arm motion, e.g., towards the still motionless target. At 500 ms after tracking onset, SP was clearly driven by vision only (high gain, low phase relative to visual target motion). During the present work, we recorded data from human subjects by adding an artificial delay of 300 ms (Fig. 4A) since a large amount of data was already available (Vercher and Gauthier 1992).

Simulation of the model, where a delay of 300 ms was added between the *arm position* in space signal and the *retina*, is shown in Fig. 4B. The pattern of SP produced by the model is similar to the pattern produced in a typical trial by a human subject: SP starts at low gain just before arm movement, a saccade is triggered back toward the (still motionless) visual target 250 ms after arm movement onset, then SP is phased-locked with the visual target motion.

In the second experiment, in which an alteration of the visuo-manual relationship was used, the target path was reversed relative to the arm path without informing the subject. During the first 200 ms of ocular tracking, initial SP movement was produced in the direction of arm motion, and thus opposed to the visual stimulus (for more details and data, see Vercher et al. 1995). After that initial interval, the eye velocity slowed down, and a saccade was made in the direction of the visual target motion; for the rest of the trial time, the eyes were tracking the visual target (Fig. 5A). When the subjects were submitted to this situation for a high number of trials (about 80), this pattern of tracking was progressively changed until the oculomotor system could trigger SP directly in the direction of the visual target motion. In brief, when exposed to a systematically reversed arm-to-target visual relationship, the subjects presented a succession of three SP patterns: during the first four or five trials the pattern was the same as when the subjects were randomly exposed to the reversal. Then, during a variable number of trials, a long arm-to-eye latency appeared (140 ± 42 ms) and SP started directly in the direction of the visual target. Finally (and only in two thirds of the subjects) SP was initiated with a short latency (32 ± 47 ms) directly in the direction of visual target motion (Vercher et al. 1995).

The model behaved in a way very similar to a human subject submitted for the first time to this type of visuo-manual alteration (Fig. 5B). The model is not yet provided with adaptive and/or learning capabilities and so was not able to emulate the adaptive behavior change that human subjects exhibit after a series of trial where the visuo-manual relation is systematically reversed.

4 Discussion

What we have presented in this paper is a qualitative evaluation of the model. Our goal was to validate the model by showing that when it is ‘exposed’ to different tracking conditions, without changing the structure of the model or the parameters, the model behaves in a specific way (all the changes were concentrated in the ‘setup’ block, which is not really part of the model). We showed that, for each condition, the model behaves in the same way as humans. We based the comparison of the model simulation output and human data on experiments previously published by our research group. A more quantitative evaluation of the model has been provided in the companion paper (Lazzari et al. 1997) together with a detailed description of the model. The changes in SP gain and frequency bandwidth over tracking conditions, observed with the simulations, fitted closely the observed human behavior, as did the change in SP latency. This was not surprising, since this was the principal goal of the model. More interesting was the similarity of the model and the human pursuit pattern in terms of the coordination between saccades and SP as illustrated by Figs. 1 to 5.

As stated in Sect. 1, our goal was not only to synthesize the behavioral observations on arm-eye coordination and to present a model emulating human behavior, but also to take into account the neurophysiological knowledge about this issue, and to make the model as realistic as possible, both behaviorally and physiologically. Therefore, a correlate in the CNS can be found for most of the components of the model. We will now provide some cues about the possible nature of the structures of the CNS that may be represented by some of the blocks of the model. We will not comment on the SP and the saccadic systems, which have be extensively described in the literature, but will focus on the new aspects introduced in the present study, e.g., the action of the *visual corrector* and the *CCS* blocks on the two sensorimotor systems.

Concerning the arm motor system, the site of the visual correction system was attributed by Stein et al. (1987) to the cerebellum, which plays a key role in producing and controlling corrections of arm trajectory when tracking slowly moving visual targets. The involvement of the cerebellum in visual control of arm movement is evidenced not only by observations in cerebellar patients and lesion experiments in monkeys, but also from psychophysics: the intermittent pattern of arm motion observed in both humans and monkeys tracking a visual target disappears when vision of the arm is occluded. The authors attributed this intermittency to visual corrections increasing the accuracy of arm tracking when target motion is unpredictable. Temporary deactivation of the cerebellar cortex by cooling techniques markedly reduces the efficiency of corrections.

Concerning the SP system, the model implies that signals related to arm motion may change the SP controller dynamics. According to Lisberger et al. (1987), acceleration and velocity saturation of SP are due to the properties of the cells in the medial temporal (MT) and medial superior temporal (MST) areas. In the MT area the retinal error is coded 50 ms after target onset (Kawano et al. 1990) while the MST area codes the intended eye velocity (Newsome et al. 1988). The MST area, together with the posterior parietal cortex, may play a role in the internal representation of target motion in space (Eckmiller 1987). It remains to be determined whether the effect of the tracking condition on SP gain is due to an influence of arm proprioception on these visual areas (which to our knowledge has yet to be elucidated) or to the fact that these areas, supposedly responsible for velocity limitation, are by-passed when the target is moved directly by the observer’s hand.

Concerning the localization of the coordination control center, Vercher and Gauthier (1988) and Brown et al. (1993) showed in monkeys and human patients respectively, that lesions of the cerebellum disrupted the coordination between arm and eye in tracking tasks while maintaining the ability to produce eye and arm tracking movements in isolation. SP performance is even poorer when cerebellar patients are asked to track a target simultaneously with the eyes and the arm (van Donkelaar and Lee 1994). For these reasons, in our model, the site of information exchange between the arm and eye motor systems is attributed to the cerebellum.

We tried to make the model credible not only in terms of nervous structures, but also in terms of information transfer. The model implies that information related to arm movement (proprioception and efference copy), transiting through the dentate nucleus (DN), is available at the level of the oculomotor complex. We recently demonstrated that active control of arm movement is necessary and sufficient (if fixation of a visual target is allowed) to trigger short-latency SP in SMT tracking tasks, whereas the lack of proprioception from the moved arm in deafferented subjects does not suppress short-latency SP (Vercher et al. 1996). However, comparison of the eye tracking behavior between control and deafferented subjects clearly showed that proprioception allows enhanced SP performance (in terms of gain, phase and accuracy) and may also play a role (though limited) in the synchronization between eye and arm motor systems (indeed, the deafferented subjects sometimes produced early SP, leading the arm movement onset by hundreds of milliseconds. Such very early eye movement was never observed in non-deafferented subjects). A functional pathway linking the DN to the oculomotor complex has not been explicitly described, though Gonzalo-Ruiz et al. (1988) showed projections from the DN to the oculomotor nuclei in primates. Another path was identified in rodents by Ho and Leong (1977): fibres from the DN were found in the pontine nuclei (NRTP). The frontal eye field–NRTP–cerebellum path has been proposed by Suzuki et al. (1994) as an alternative to the MST–dorsolateral pontine nuclei–cerebellum path (Thier et al. 1994) to trigger and control SP. There is no direct evidence that these connections mediate information about arm movements, but Suzuki et al. (1994) proposed that converging information from frontal eye fields, cerebellum and primary motor cortex to the pontine nuclei may play a role in eye-hand coordination.

5 Conclusion

In conclusion, the model presented in the companion paper (Lazzari et al. 1997) allowed us to test several original hypotheses regarding arm-eye coordination control, especially the respective role of arm motor command and proprioception in the timing and mutual coupling of the coordination, respectively. The model may also allow testing of the involvement of CNS structures on eye-hand coordination. The most appealing feature of the model is that, as opposed to others, it is not necessary to change its structure or its parameters to make it produce human-like arm and eye trajectories under different conditions or when the visuo-manual relationship is altered, as shown by the qualitative evaluation presented here. Nevertheless, possible improvement of the model concerns auto-adaptation when exposed to prolonged visuo-manual alterations or to changes of the mechanical conditions of movement.

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