Exp Brain Res (1988) 73: 127–137

Experimental
Brain Research

Oculo-manual tracking of visual targets: control learning, coordination control and coordination model

G.M. Gauthier, J.-L. Vercher, F. Mussa Ivaldi, and E. Marchetti

Université de Provence, Département de Psychophysiologie, Laboratoire de Contrôles Sensorimoteurs, Avenue Normandie-Niemen, F-13397 Marseille Cédex 13, France

Summary. The processes which develop to coordinate eye and hand movements in response to motion of a visual target were studied in young children and adults. We have shown that functional maturation of the coordination control between eye and hand takes place as a result of training. We observed, in the trained child and in the adult, that when the hand is used either as a target or to track a visual target, the dynamic characteristics of the smooth pursuit system are markedly improved: the eye to target delay is decreased from 150 ms in eye alone tracking to 30 ms, and smooth pursuit maximum velocity is increased by 100%. Coordination signals between arm and eye motor systems may be responsible for smooth pursuit eye movements which occur during self-tracking of hand or finger in darkness. These signals may also account for the higher velocity smooth pursuit eye movements and the shortened tracking delay when the hand is used as a target, as well as for the synkinetic eye-arm motions observed at the early stage of oculo-manual tracking training in children. We propose a model to describe the interaction which develops between two systems involved in the execution of a common sensorimotor task. The model applies to the visuo-oculo-manual tracking system, but it may be generalized to other coordinated systems. According to our definition, coordination control results from the reciprocal transfer of sensory and motor information between two or more systems involved in the execution of single, goal-directed or conjugate actions. This control, originating in one or more highly specialized structures of the central nervous system, combines with the control processes normally operating in each system. Our model relies on two essential notions which describe the dynamic and static aspects of coordination control: timing and mutual coupling.

Key words: Human oculo-manual tracking – Smooth pursuit – Coordination control – Oculo-manual coordination – Control learning

Introduction

Oculo-manual coordination in visually guided hand tracking of objects has functional significance. Numerous features of this coordination may be observed in common, as well as more specialized actions of everyday life: locating and stabilizing vision on a low contrast object occurs immediately if the hand is near the object, even if the hand is not visible to be used as a pointer. A young reader improves his performance considerably if he uses his index finger to proceed along the line. In this situation, the finger is used as a target to indicate both the position of a word and the direction of the next word. Behavioral studies suggest that the finger and arm kinaesthetic signals also provide useful information to the eye motor systems as evidenced by the improved eye movements which occur when a child uses finger tracking, even when the finger is hidden from view (Gauthier et al. 1981).

Oculo-manual and manuo-ocular interactions have been specifically investigated in several studies. Vibration applied to biceps or triceps of the immobile forearm may induce the sensation of an illusory motion of a small target attached to the tip of the hand if the experiment is conducted in an otherwise dark room. This phenomenon has been termed the oculo-brachial illusion by Lackner and Levine (1978). The oculo-brachial illusion is regarded as strong evidence supporting the influence of arm position information on the output of the oculomotor system. The work of Steinbach and Held (1968) and Steinbach (1969) showed that a subject (S) could better follow a visual target that was a projected

---

Offprint requests to: G.M. Gauthier (address see above) image of the S's hand movement than the hand movement of the experimenter. According to these authors, as well as Mather and Lackner (1980) working with a slightly different paradigm, the "active" tracking performance is better than the "passive" performance because the oculomotor system anticipates (predicts) the future motion of the target using a signal from the limb motor command (outflow). In a somewhat similar approach, Gauthier and Hofferer (1976) showed that smooth pursuit eye movements may result from the tracking of self-moved targets in total darkness. This result is in contrast to the purely saccadic eye movement which results when a normal S attempts to track a slow imaginary target in total darkness. Comparison of the eye movement patterns produced in total darkness in response to tracking an actively or passively moved arm, or an actively moved arm deprived of its afferents through ischemic block showed that the arm (or finger) inflow information was necessary and sufficient to release smooth pursuit. The efferent copy might play a role in the phase relationship and timing (prediction) between eye and finger events, and in the concomitant activation of the saccadic system (Gauthier and Hofferer 1976).

The above observations strongly support the idea that coordination control does exist between the subsystems subserving eye and hand tracking. A major part of this coordination control is based on visual information, but as suggested by the observations cited in the previous paragraph, a non negligible portion of this control relies on extra retinal sources of information such as arm movement inflow (afferent) and outflow (efferent copy) information.

The aim of the present paper is to describe some basic features of the interactions influencing visuo-oculo-manual tracking which arise from signals derived primarily from the arm controlled system. Two companion papers deal respectively with the role of arm proprioceptive information and the role of the cerebellum on oculo-manual tracking in Baboon. In the present study, the role of the arm motor signals in mediating oculomotor control was determined from a comparative analysis of eye tracking performance in tasks involving the eyes alone, or the eyes and the hand (used either to carry the visual target or as a pointer to track a visual target). Particular emphasis was placed on a comparison of smooth pursuit maximum velocity, gain, and delay in various tracking conditions. An attempt was made to formalize this interaction beyond a basic approach such as developed by Howard (1982) in which the coordination resulted simply by simultaneous activation of the two subsystems involved. Indeed, it is apparent that when the hand is used as a visual target not only does prediction occur but other static and dynamic characteristics of the oculomotor system and arm motor system are modified.

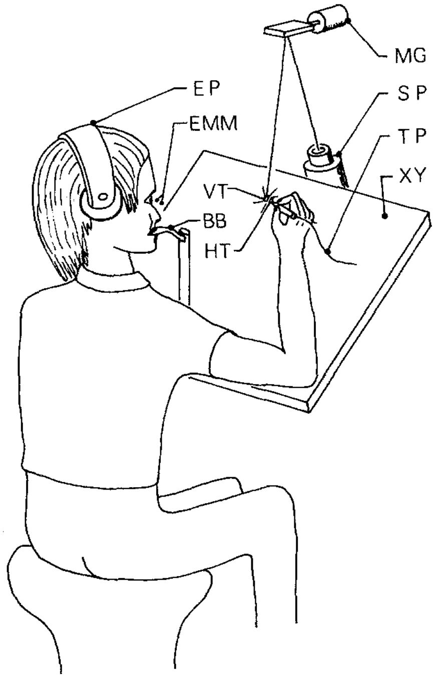

Fig. 1. Experimental apparatus. The S was seated in front of a X-Y recording table on which a moving visual target (VT) was presented. The horizontal target displacement was produced by a galvanometer-driven mirror (MG). The visual target was a spot of light 4 mm in diameter, produced by a projector (SP). The S held a pen-like tracker (TP) used to track the visual target. A small red LED, mounted on the side of the tracker tip, facing the S's eyes, constituted a visual reference for the position of the hand (HT). The S's head was immobilized by a bite-bar (BB). Horizontal eye movements were monitored by an infrared device (EMM). An earphone (EP) was incorporated to produce white noise or indicate the requested hand motion pace

Methods

Oculo-manual tracking

The experimental setup is shown in Fig. 1. The visual target was projected on a resistive substrate X-Y recording table (Prablanc and Jeannerod 1973) placed at a 30 degree angle in front of the S. The target projection area was located 37.5 cm from the S's eyes so that a 20 cm target displacement on the table resulted in a 30 deg angular rotation of the eyes. The tracking pen was held like a pencil and gently pressed onto the recording surface of the table. A small red LED, attached to the tip side of the tracking pen served both as a reference for the position of the hand and a tracking target. The S's head was immobilized with a head rest and a bite bar. Horizontal eye movements were monitored by means of a photo-electric device (Gauthier and Volle 1975). Calibration of the monitor was obtained by asking the S to fixate different targets stepping over the expected response range. The visual target was a circular spot of light 4 mm in diameter produced by an incandescent projector. This target was projected on the tracking table after reflection by a mirror galvanometer (General Scanning).

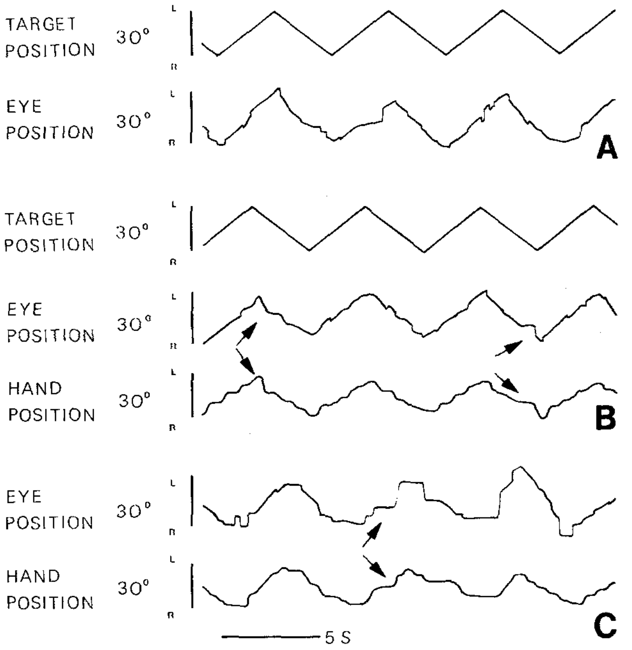

Fig. 2A–C. Ocular and oculo-manual tracking in children. Performance of a child in response to eye-alone tracking (**A**), eye and hand tracking of a visual target (**B**), and tracking of his hand (**C**) before training. The pairs of arrows indicate tracking sequences during which motion of the eyes was highly correlated to that of the hand

Oculo-manual control learning in young children

A group of 5 children between the age of 5 and 7 years was used in this experiment. The child was seated in front of the tracking table. Eye movements of the right eye were monitored. The task was described as follows: "try to pursue the visual target with the pen. Keep the pen target as close as possible to the target moving on the table". What the child should look at was deliberately not specified. A slow target velocity (5 deg/s) was first presented followed by increasing velocities. Each child underwent 4 to 5 sessions of oculo-manual target tracking on consecutive days during which target, eye, and hand position signals were continuously monitored. Data were selected from the practice period to illustrate learning in oculo-manual tracking.

Oculo-manual tracking in adults

The Ss, 5 adults from the Department of Psychophysiology staff and teaching crew with no known neurological deficits, were tested in 4 tracking tasks designated as:

Eye-alone tracking. The task consisted of tracking with the eyes alone the sine or triangular wave motion of a light spot moving across the screen over a 30 deg range at increasing frequencies. Each S was presented a series of target motions in the 10 to 120 deg per second range. Blocks of 20 cycles were recorded for each selected velocity. Maximum smooth pursuit velocity was calculated for each half cycle. Only the last 15 cycles of each block were used to determine the curves. The first five cycles were considered to be necessary to reach steady state performance level. A computer program allowed off-line rejection of the saccades through simultaneous presentation of eye position and velocity signals. The experimenter determined by eye, from the velocity trace, the beginning and the end of all saccades exceeding 0.5 deg. The computer identified the duration of the saccades and replaced them by linearly extrapolated segments.

Eye and hand tracking. The task consisted of tracking the visual target with the eyes and with the hand. The S attempted to maintain the red LED attached to the pen on the visual target.

Eye and masked hand tracking. The task was identical to the one previously described except that the hand and the tracking pen were masked from view by a dark screen ("kinaesthetic tracking"). The S was required to match the perceived position of his hand with the visual target on the table.

Eye tracking of the hand. The task consisted in moving the hand back and forth sinusoidally across the recording table, at approximately constant velocity, or sinusoidally, over a 16 deg range. The S was required to fixate the red LED attached to the pen. Every 10 cycles the experimenter asked the S to increase hand velocity until the resulting eye movement became exclusively saccadic. Sound clicks paced the frequency at which the S was requested to operate.

Data recording and analysis

Target, hand, and eye position signals, together with the corresponding velocities and the state of the lever target (on-off) were recorded on the paper recorder as well as digitized (100 samples/s) and stored on a computer disk. The off-line analysis of the data consisted of computing frequency histograms for position and velocity signals and histograms of the tracking errors between eye, hand, and target. The delay between the three position signals was measured directly from the high velocity paper recording and also calculated by means of crosscorrelation functions. The relationship between eye and target velocities was determined in three tracking conditions (eye alone, eye and hand, and eye tracking of the hand) by selecting on the computer screen, sets of points within saccade-freed segments of tracking.

Results

Ocular and oculo-manual tracking training in children

At the early stage of training the oculo-motor response to a purely visual target (eye-alone tracking) moving at constant velocity was not very precise (Fig. 2A). Smooth pursuit maximum velocity was low (20 deg/s) and most of the children did not respond with measurable eye and hand movements to target frequencies beyond 0.8 Hz.

Submitted for the first time to visual target tracking with the eyes and the hand under laboratory conditions, the young children responded with two main strategies attempted either in close succession or separately for short, random intervals (Fig. 2B). These strategies consisted of either tracking the visual target fairly closely with the eyes and only loosely with the hand, or closely tracking the hand target with the eyes while eyes and hand were only

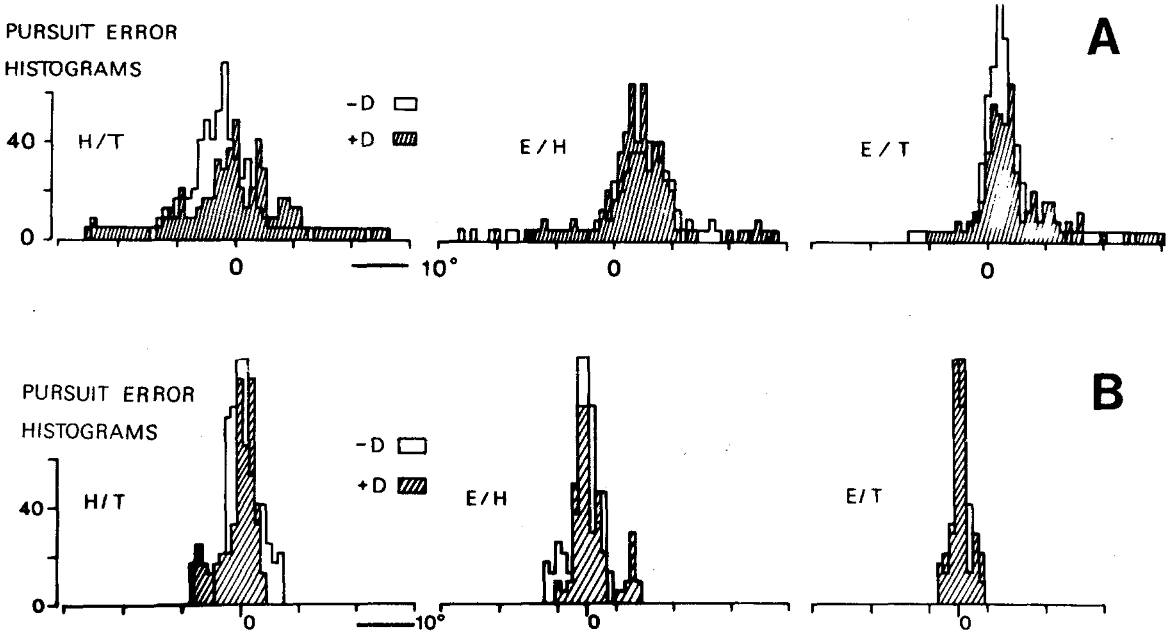

Fig. 3A, B. Tracking error in eye and hand tracking. Eye to target (E/T), eye to hand (E/H), and hand to target (H/T) position error histograms at the early stage of training in a 6 year old boy (**A**) and after 5 tracking sessions (**B**). The dashed (+D) and blank (–D) areas correspond to movements to the right and to the left, respectively. The data are derived from about 50 target cycles. The overall performance markedly increased through training

grossly in pace with the visual target. Whenever the eyes closely followed the target the hand position and velocity errors were rather large, and the hand had a tendency to proceed by small steps. In these instances, the eye tracking error was systematically larger than that observed between the eye and hand when the eyes were following the hand. The pairs of arrows shown on Fig. 2B indicate sequences during which the eyes were tightly following the hand target. In the eye tracking of the hand situation, although hand movement was not very uniform the eyes very closely followed its motion (Fig. 2C).

As training proceeded, oculo-manual coordination increased as well as smooth pursuit maximum velocity and frequency. In the course of 4 to 5 one-hour recording sessions, visual ocular and oculo-manual tracking performance gradually improved. The tracking error, as characterized by position error histograms, was seen to improve markedly between the first (Fig. 3A) and the final training session (Fig. 3B). The data shown here apply to a 6 year old boy whose tendency to follow the visual target with the eyes rather than the hand was particularly strong. The tendency did not change as a result of training as shown by narrow eye to target histograms, both before and after training.

The records shown in Fig. 4 illustrate the behavior of the same 6 year old boy near the end of the last recording session, for the three tracking situations. Visual examination of the records suggests that the performance of this child is comparable to that of an adult (Figs. 5 to 8). In eye-alone tracking, the overall precision and the eye movement smoothness have considerably improved (3A). Still, very little prediction occurred since, for extreme target positions, the eyes very often continued in the same direction for 100 to 200 ms while the target had reversed its course. Figure 4A shows three such examples. This typical pattern was called "asynchrony of eyes and target at reversal" by Mather and Lackner (1981).

A striking feature was that, after training, the eyes and the hand seemed to have acquired independent motor controls. Indeed, in the early training session the eyes tended to track in alternance the hand or the target in a very tight manner. After training, as in Fig. 4B, both the eyes and the hand tracked the visual target with high precision. No tight coupling was observed, for long periods of time, between the eyes and the hand or between the eyes and the target.

Another striking feature relates to prediction which affected both the timing and the pattern of the eye movements. When the hand was used to track the visual target as in Fig. 4B, eye movements were almost systematically rounded at both right and left extreme positions. The circle shows an exception. Increasing target frequency revealed that the chil-

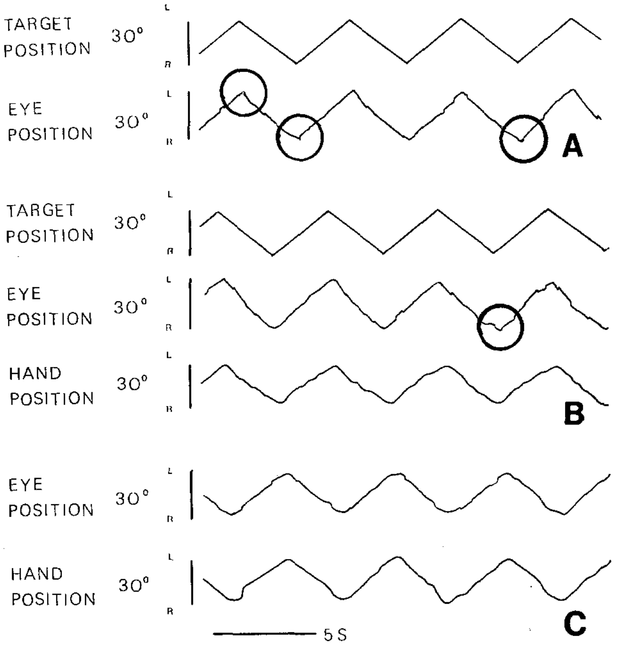

Fig. 4A–C. Ocular and oculo-manual tracking in trained children. Tracking precision and prediction increased between eye-alone (**A**), eye and hand tracking (**B**), and eye tracking of the hand (**C**). Circles show sequences where the eyes went on moving for 100 to 200 ms while the target had reversed direction, then produced a saccade to catch up with the target

dren could respond to high velocity targets with smooth pursuit velocities up to 60 deg per second.

Eye tracking of the hand showed little position errors (Fig. 4C). In most children, on several occasions, smooth pursuit velocity reached values up to 100 deg per second when they were required to increase the velocity of hand movement.

Ocular and oculo-manual tracking in adult humans

As observed in children, but to a lesser extent in adult Ss, high and stable oculomotor control was not immediately reached during the initial phase of an experiment. In fact, in most Ss several trials were necessary to achieve reliable performance.

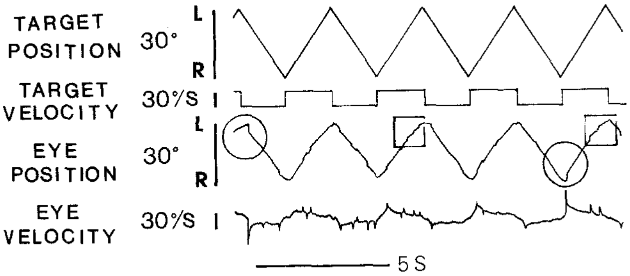

Fig. 5. Eye-alone tracking in adults. Circles show lack of prediction characterized by segments of smooth pursuit in the inappropriate direction followed by saccades to catch up with the target. Squares show sequences with lower-than-unity smooth pursuit gain with position error corrective saccades. Note that in all velocity time recordings shown, saccade velocity is slightly truncated by the time constant of the analog differentiator

Figures 5 and 6 show the same features as those mentioned above with regards to tracking in trained children, that is: 1) higher prediction of the tracking wave, as demonstrated by rounded trajectories instead of a segment of smooth pursuit beyond the target followed by a returning saccade, 2) greater smooth pursuit precision, 3) greater regularity and smoothness and 4) higher velocity when the hand was used in combination with the eyes to track the visual target. These latter characteristics were particularly clear in the velocity traces which show more correcting saccades and less of a square wave pattern in eye-alone tracking (Fig. 5) when compared to eye and hand tracking (Fig. 6). Figure 5 also shows long sequences of lower-than-unity gain tracking with correcting saccades (squares) and no prediction of target direction reversals (circles).

As mentioned earlier, the eye and hand tracking condition was characterized by alternate segments of eye tracking of the hand and eye tracking of the visual target. Whenever the eyes followed the hand, the eye movement was less saccadic while maintaining fairly high precision in position tracking.

Figure 7 shows that in eye and masked hand tracking the smooth pursuit system increased its performance with respect to eye-alone tracking as evidenced by higher prediction and smooth pursuit

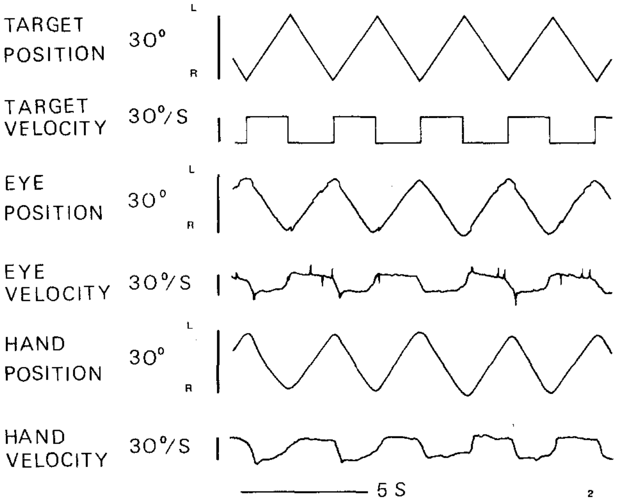

Fig. 6. Eye and hand tracking of a visual target. Eye and hand tracking showed similar precision. Target direction changes were highly predicted and smooth pursuit gain was close to unity as shown by the few small amplitude corrective saccades (eye velocity trace)

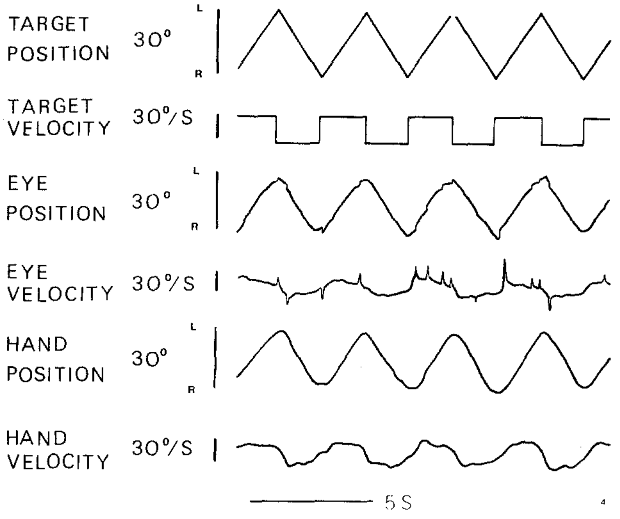

Fig. 7. Eye and hand tracking of a visual target with the hand masked from view. Eye movement prediction and smoothness was greater than in the eye-alone tracking condition

maximum velocity and fewer correcting saccades per unit of time (smoothness). Assuming an interaction between the hand and eye sensorimotor systems, the eye motor system was more likely to benefit from the hand system since the tracking precision of the hand is very high. An alternate condition would occur if the hand tracking precision was poor since this strong interaction would obviously degrade the visually controlled ocular tracking.

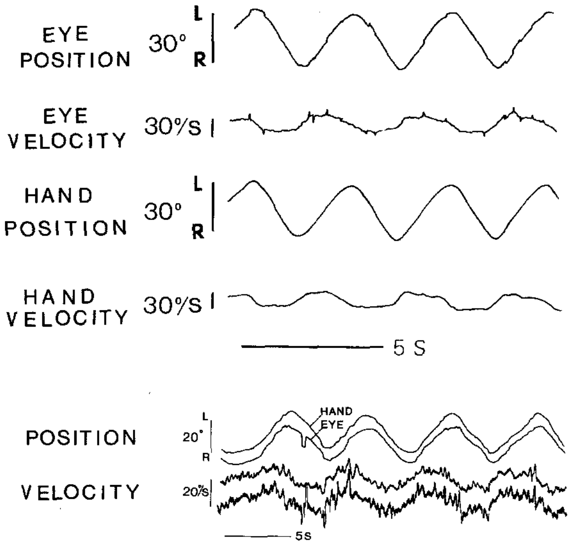

Fig. 8. Eye tracking of the hand. High sensitivity, large band-pass recordings show that smooth pursuit gain was close to unity and small saccades occurred in both directions around target position. Perfect "prediction" of the hand motion by the hand motor system makes eye and hand signals appear highly correlated (upper records). High correlation between eye and hand movements is even more evident in high gain recordings showing similarity of macro and micro velocity changes (lower records).

Figure 8A shows a sequence in eye tracking of the hand condition with the same recording parameters as in Figs. 5 to 7. The eye movement was smooth and tracking precision expressed as position and velocity errors was high as indicated by the few small amplitude correcting saccades and similarity of the velocity signals. The high sensitivity recordings of Fig. 8B illustrate the marked similarity between eye and hand velocity signals. This similarity is observed for both macro and micro velocity variations.

Oculo-manual coordination in the trained human

Eye movement delay and prediction. One of the most striking observations derived from our eye-hand tracking study relates to the delay of the eye in response to target motion when the self-moved hand constitutes the target, or when both eye and hand track a visual target. A previous study conducted on man (Gauthier and Hofferer 1976) has shown that the eye movement delay in response to tracking the motion of the finger or the hand was close to zero. On some occasions the eyes were seen to move prior to the active motion of the hand or finger. Since then, other data have supported this observation (Gielen et al. 1984). The present paper provides further data gathered in human oculo-manual tracking.

The method used to train children and evaluate some aspects of oculo-manual tracking had to be improved to determine eye to target delay in eye-alone and hand tracking. A visual target was presented on a large oscilloscope screen using a step-ramp stimulus protocol. The eye movement delay was measured in response to the motion of a spot of light presented on the oscilloscope screen or set in motion by the active displacement of the S's arm. The S's arm rested on a horizontal plate rotating around a vertical axis activated the spot position with a delay of less than 2 ms. The combined data from five S's show that the average latency in eye-alone tracking was 150 ± 30 ms (Fig. 9). Although the onset of target motion was unpredictable, a non-negligible number of responses occurred with a very short delay of about 80 ms. These response delays may well be smooth pursuit counterparts of the "express-saccades" released in particular situations by the saccadic system (Fischer and Ramsperger 1984).

With the above protocol, the human eye movement response to tracking the target actively displaced by the arm had an average delay of 30 ms ± 10 ms (Fig. 9). These data did not differ from data gathered in equivalent situations with the apparatus described in the methods section (Fig. 1) except that with the tracking board used for training we could

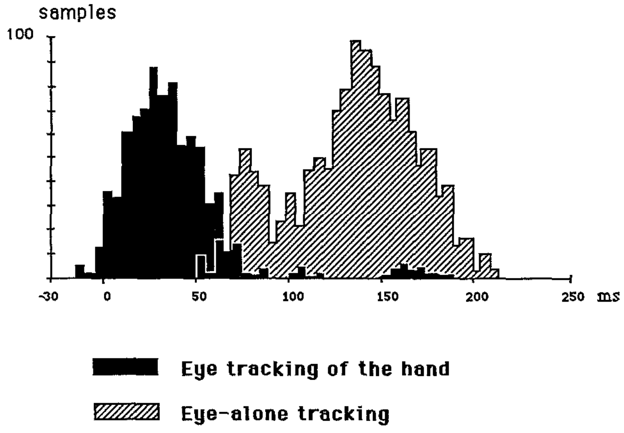

Fig. 9. Eye movement delay. Smooth pursuit delay histograms in eye-alone and eye tracking of the hand derived from 5 adult humans. The number of samples per 5 ms bins are plotted in ordinates

not use a step ramp stimulus to induce a pure smooth pursuit response. Still, we could select a large number of responses with no early saccade, providing an estimate of smooth pursuit delay.

Whether the smooth pursuit system of primates other than man has predictive control is still a debated matter. As already mentioned with regard to training, prediction was seen to develop in children as a result of training. Of relevance to oculo-manual coordination is the observation that whenever the hand was used in tracking a predictive target trajectory, predictive control developed more rapidly than the prediction in eye-alone tracking. It was characterized by shortening of the eye-to-target phase lag and changes in eye movement pattern, as in Fig. 4.

Smooth pursuit maximum velocity

Sets of curves describing the relationships between target and eye velocity were determined for the condition where the target was presented on the screen and the eye-alone (head still) was involved in the tracking and for the conditions where the eye and the hand were involved.

Figure 10 shows the cumulated results from 5 Ss. It shows that the eye-alone condition yielded a maximum smooth pursuit velocity of about 40 deg per second, eye and hand tracking about 90 deg per second, while ocular tracking of the hand condition showed average values over 100 deg per second. As shown by the standard deviations, a large number of samples exceeded 120 deg per second. These data definitely suggest that the hand has a unique status as a visual target since it allows the smooth pursuit system to reach output velocities far beyond those measured when tracking the target with the eyes alone.

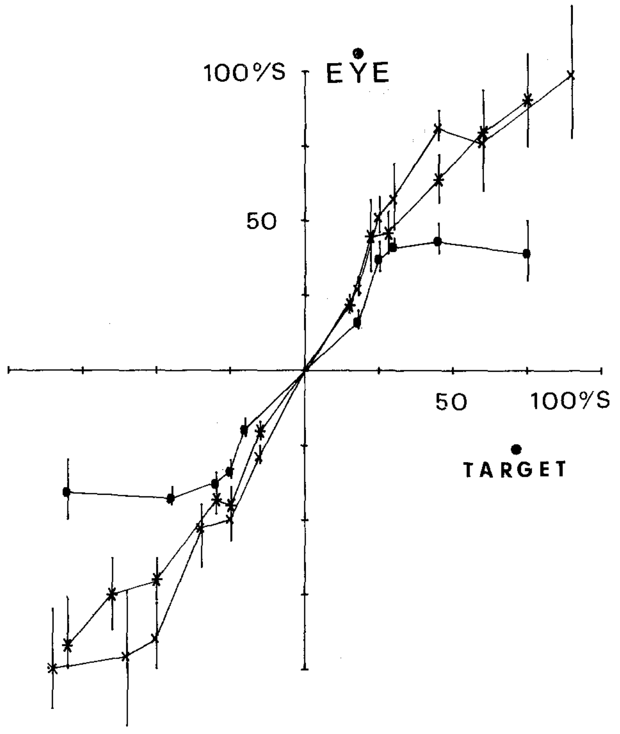

Fig. 10. Smooth pursuit maximum velocity. Velocity of the eyes as a function of target velocity in eye-alone (dots), eye and hand (stars) and eye tracking of the hand (crosses) conditions. The data are derived from recordings in 5 Ss

Eye movement and illusory limb motion induced by vibration

No definite interpretation of the oculo-brachial illusion (cf. introduction) has yet been proposed. The main question which must be investigated with regards to the problem of oculo-manual coordination is whether biceps or triceps vibration, known to almost exclusively activate Ia afferents, can induce eye movements. Figure 11 illustrates eye movement recordings from various experimental situations involving triceps vibration. Eye movements in response to tracking a target held between thumb and index finger, are shown for calibration purpose and as comparison for ensuing experimental conditions (Fig. 11.1). The results show that vibration applied to the triceps (or biceps) tendon does not produce eye movements if the Ss are requested to fixate a real target (Fig. 11.2), or imaginary target (Fig. 11.3) in total darkness. This is also true when, in the latter situation, the S experiences a strong

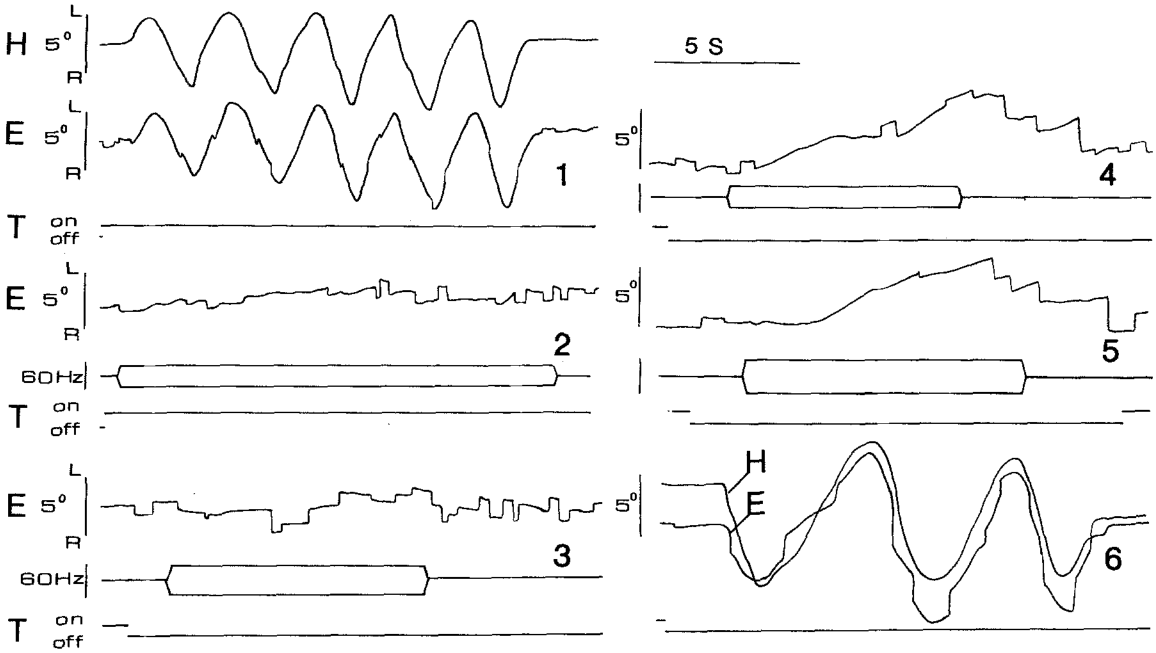

Fig. 11. Ocular response to imaginary target tracking. High sensitivity infrared corneal reflection eye movement (E), target state (T) and hand position (H) in human tracking a self moved target attached to his right index finger (1). While attempting to maintain steady fixation on a real (2) or imaginary target (3) attached to his index finger tip a 60 Hz vibration was applied to the triceps tendon. The eye movement in response to attempted tracking of the illusory forelimb motion in the same subject submitted to the same vibration (5) is shown for comparison. The eye movement response to tracking an imaginary target (6) attached to the actively rotated limb is shown as calibration and reference for smooth pursuit tracking of real and imaginary target, respectively. Among 10 Ss tested, only one showed eye movements upon tendon vibration while fixating an imaginary target (4). Note the smooth nature and the direction of the movement compatible with the illusion. The data shown were gathered with the subject seated in total darkness, with the right forelimb resting on a board rotating about a vertical axis. A potentiometric device monitored the board rotation. Board movement could be blocked to induce illusory movement upon biceps or triceps vibration

illusory limb movement. The only usual vibration-induced effect may be an increase of fixation eye movement (larger microsaccades). However, there might be exceptions. Figure 11.4 shows one example of eye movements induced by triceps vibration while the S was attempting to maintain steady fixation on an imaginary target attached to his hand. Only one S out of 10 tested produced such eye movements in response to vibration. The eye movements produced when the S was requested to follow the illusory motion of his arm (Fig. 11.5) or track an imaginary target attached to his actively moved hand, in absence of vibration (Fig. 11.6) are shown for comparison (the experimental conditions and apparatus are described in the figure and figure legend).

Discussion

The data presented here regarding smooth pursuit delay and maximum velocity together with the observations derived from training of children in ocular and manual tracking demonstrate some singularities of the smooth pursuit system when the hand is used either as a target or as a pointer to a visual target.

Observations carried out during training of the oculo-manual tracking system disclosed, in young children, a very tight coupling between eye and hand motions. Early practice in ocular and manual tracking of a target showed near unity correlation between eye and hand movement velocities over a remarkably large range. However, the error between either the eye or the hand and the visual target was large as measured in terms of position and velocity components. As training proceeded, the average tracking error decreased for both the eye and the hand while, surprisingly, the correlation between eye and hand motion decreased. The correlation decreased to such a point that fine analysis of eye and hand motions showed no constant relation between eye and hand instantaneous velocity, direction of motion, and amplitude of position error. This independence implies that the input provided by the visual system reaches two separate processing units each of which provides the appropriate signals to the eyes and to the hand. Signals may be exchanged between the two processing units yielding spatial and temporal coordination of the two motor outputs.

Another view may be proposed in which the visual input provides a rough control of arm and hand motions. The arm motion would, in turn, activate the oculomotor system through some hardwired reflex. As this activation occurs with a shorter delay it would override the visual input. In these views, functional maturation through training would tend to decrease the apparently tight coupling between the two subsystems, a coupling which may be attributed to either feedforward (dual activation), or feedback (manual-ocular reflex) arrangement. After training, the two subsystems develop independent controls from the two visual signals, specificially, the error between eye and target and between hand and target. One may speculate that the lack of proper maturation of the visuo-oculo manual tracking system might be responsible in certain cases of athetosis for the synkinetic motion of eye, head, and hand seen when an attempt is made to track a visual target.

Our data on children and adult human Ss suggest that optimal control is not reached unless frequent practice occurs under tightly controlled conditions. Training requires only a few minutes in adults, longer in children. Improvement of visuo-oculo-manual control was seen to follow various stages. During the early training sessions the eyes followed alternatively either the target or the hand. This behavior may be related to that described by Piaget (1936) and White and Held (1967) in which a young baby attempting to reach for a fixed object used eye movements alternating between hand and target until contact was established.

Training led to an apparently paradoxical effect: after training, the central nervous system had learned to share its control "equally" between the eye and hand motor systems. In a visuo-manual pointing task, Prablanc et al. (1979) have shown that the separation between the two motor outputs arising from a visual input occurs in the early stages of sensory processing. Learning processes (maturation) may be necessary to completely separate the two command signals. The acquisition of fine and independent control over eye and hand motor systems may be regarded as a disruption of the tight coupling between the manual and oculo-motor systems, or as the development of the ability to mediate the interaction between the two systems.

Our data show that the performance of the smooth pursuit system in tracking a slowly moving target can be improved by appropriate training. This confirms earlier results gathered in both normal and cerebral palsied children (Gauthier et al. 1981). Although the smooth pursuit system is continuously sollicited, even in young children of the age range studied, the initial performance measured under controlled laboratory conditions was not optimal. A few hours of training were necessary to raise the performance level.

It has also been shown that smooth pursuit velocities higher than those commonly reported in the literature (Westheimer 1954a) can be achieved if certain conditions are satisfied (Schalen et al. 1982, 80 deg per second; Buizza and Schmid 1986, 75 deg per second; Meyer et al. 1985, 80 deg per second; Barmack 1970, 100 deg per second). Our results show that any given S, trained or untrained, can spontaneously more than double smooth pursuit maximum velocity if the hand is used to track the target. No specific target waveform or amplitude is necessary to produce this phenomenon.

The particularities of the oculomotor system resulting from the concomitant involvement of the hand motor system in the tracking task may be summarized as follows:

1- The oculo-motor system releases a smooth pursuit command in response to the tracking, in the dark, of an imaginary target if the hand is used as a pointer. In total darkness, most Ss track an imaginary target not associated with arm or finger movement with exclusively saccadic eye movements. The release of smooth pursuit has been suggested to be due to a signal derived from the arm afferent information (Gauthier and Hofferer 1976).

2- The smooth pursuit maximum velocity reached when the arm was used to point at a visual target is much higher (80 to 100 deg per second) than that attained in response to a pure visual target (40 deg per second Westheimer, 1954b). Even higher velocities were reached when the arm was used as a visual target (over 120 deg per second).

3- When the arm is used as a visual target, the delay between eye and arm movements is much shorter than the delay in eye-alone tracking. In fact, the delay is almost zero (Gauthier and Hofferer 1976) as compared to 125 ms for the smooth pursuit system (Westheimer 1954b; Robinson 1965) and 200 ms for the saccadic system (Westheimer 1954a; Stark et al. 1962).

4- Young children first exposed to visuo-oculo-manual tracking have a strong tendency to produce eye movements more closely correlated with the arm movement than with that of the target, even if the arm is masked from view. The controlling signal activating the smooth pursuit system may be derived from the kinaesthetic afferent signal from the arm (Gauthier and Hofferer 1976).

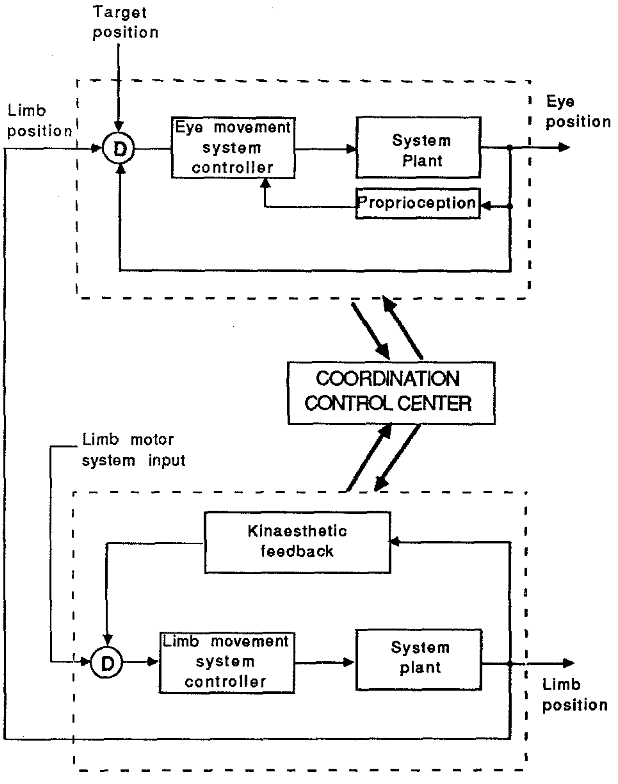

Fig. 12. Descriptive model of oculo-manual coordination control. Coordination control results from reciprocal exchange of information between two systems (eye motor system and arm motor system) involved in the execution of a common task. This control superimposes its action on the control proper to each system. The sites of action of the signals generated by the coordination controller are hypothetical. The schema illustrates the tracking condition in which the hand is used as visual target. The model assumes that coordination control is mediated by a specialized structure (coordination controller) receiving information from both systems. These information may be a combination of afferent and efferent signals issued from the sensorimotor systems involved in the task. The model is represented in the eye tracking of the hand situation where the limb constitutes the visual input activating the eye movement system

5- Observations conducted on cerebral palsied children with severe athetosis show marked synkinesia between eye, head, and arm movements (this was also observed in normal young babies). Close examination reveals (Haberfelner 1978, personal communication) that an arm movement directed towards a target very often triggers eye movements in spite of attempts to maintain steady fixation. We hypothesize that this synkinesia is the expression of the tight sensory-motor interaction between manual and ocular systems. A delayed maturation, caused by other aspects of the cerebral palsy syndrome does not allow the proper control structures to develop or permit the necessary mediation of the manual ocular reflex. It follows that a single input inevitably drives both manual and ocular systems.

6- The oculo-brachial illusion indicates that the assignment of a visual direction can be influenced by positional information about an orientation other than that derived from retinal and oculo-motor sources (Levine and Lackner 1979). It also indicates that one signal activating the smooth pursuit system may be derived from the arm kinaesthetic afferent information and may be related to muscle spindle primary afferents. Obviously, the data gathered from experiments using vibratory stimuli to induce either target motion or eye motion do not prove that Ia afferents provide the basis for coordination control in the visuo-manual tracking. Rather, Ia afferents may only be one of several signals acting either in conjunction or individually.

We propose a model to describe the interaction between two sensorimotor systems which may become involved in a common task. This model applies to the visuo-oculo-manual tracking system, but may be generalized to other interacting systems such as the manuo-manual, oculo-cephalic and manuo-oculo-cephalic systems. The model describes the changes of the functional properties of each of the coordinated subsystems resulting from the activation of a specialized neural center responsible for the elaboration of this control of coordination.

Our model of coordination control relies on a notion of coordination rather than a simple aspect of simultaneous actions such as the model developed by Howard (1982). Howard's model constrains the aspects of coordination to a synchronization of the muscular activities engaged in a visual manipulation task. Our concept relies on two essential notions: timing and mutual coupling. Timing describes the temporal aspects of the control (delays) and generalized the notion of synchronization. Mutual coupling describes all parametric (static and dynamic, including lags) changes, which occur in the two subsystems whenever they are called for a "coordinated action".

According to our view, the control of coordination results from reciprocal exchanges of information between two, or more sensorimotor systems involved in the execution of a common, or conjugated tasks. This control is elaborated from sensory and motor information derived from the subsystems involved in the coordinated action. The control of coordination acts as a complement to the normal control in each subsystem. We therefore assume that the control of coordination as defined above is the result of the activation of a specialized central nervous structure which is inactive when a subsystem is operating alone or independently of other subsystems. Figure 12 illustrates our description of the control of coordination. At birth, the wiring between the two processing units is functionally very tight. Maturation and motor learning allows a mediation of the interaction between the two systems.

The nature of the coordinating and mediating signals is still poorly defined (Gauthier and Hofferer 1976) and the definition of the "oculo-manual coordination center" as a neural entity can only be hypothetical. Subsequent studies examine the nature and sites action of the coordination signals issued from the manual system which controls the eye movements in oculo-manual tracking of visual targets. The two companion papers introduce data on the role of the arm afferent signal in coordination control (Gauthier and Mussa Ivaldi 1988) and the role of the cerebellum as a coordination controller (Vercher and Gauthier 1988).

Acknowledgements. This work was supported by INSERM and CNRS UA 372 grants. F. Mussa Ivaldi was supported by an European Training Program grant. The authors are grateful to Pr. J.L. Semmlow for reviewing the manuscript, to L. Bakalian for designing the electronics equipment, and to N. Bachi for typing and secretarial assistance.

References

Barmack NH (1970) Dynamic visual acuity as an index of eye movement control. Vision Res 10: 1377–1391

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

Fischer B, Ramsperger E (1984) Human express-saccades: extremely short reaction times of goal-directed eye movements. Exp Brain Res 57: 191–195

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

Gauthier GM, Hofferer JM, Mussa-Ivaldi F (1981) Etude des troubles oculomoteurs affectant certains enfants infirmes moteurs cérébraux: semiologie instrumentale et possibilités de rééducation. Ann Med Physique 24: 64–76

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

Gauthier GM, Volle M (1975) Two dimensional eye movement monitor for clinical and laboratory recordings. EEG Clin Neurophysiol 39: 285–291

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

Howard IP (1982) Adaptation to discordant stimulation. In: Human visual orientation. John Wiley and Sons, New York, pp 480–520

Lackner JR, Levine MS (1978) Visual direction depends on the operation of spatial constancy mechanisms: the oculobrachial illusion. Neurosci Lett 7: 207–212

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

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

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

Meyer GH, Lasker AG, Robinson DA (1985) The upper limit of human smooth pursuit velocity. Vision Res 25: 561–563

Piaget J (1936) La naissance de l'intelligence chez l'enfant. Del et Niestle, eds. pp 1–426

Prablanc C, Jeannerod M (1973) Continuous recording of hand position in the study of complex visuo-motor tasks. Neurophysiology 11: 123–125

Prablanc C, Echallier JF, Komilis E, Jeannerod M (1979) Optimal response of eye and hand motor systems in pointing at a visual target. Biol Cybern 35: 113–124

Robinson DA (1965) The mechanisms of human smooth pursuit eye movement. J Physiol (London) 180: 569–591

Schalen L, Henriksson NG, Pyykko I (1982) Quantification of tracking eye movements in patients with neurological disorders. Acta Otolaryngol 93: 387–395

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

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

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

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

Westheimer G (1954a) Mechanism of saccadic eye movements. AMA Arch Ophthalmol 52: 710–724

Westheimer G (1954b) Eye movement responses to a horizontally moving visual stimulus. Arch Ophthalmol 52: 932–941

White BL, Held R (1967) Plasticity of sensorimotor development in the human infant. In: Mellmuth J (ed) The experimental infant, Vol 1. Special Child Publications, Seattle

Received June 15, 1987 / Accepted June 27, 1988