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Self-Moved Target Eye Tracking in Control and Deafferented Subjects: Roles of Arm Motor Command and Proprioception in Arm-Eye Coordination

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SUMMARY AND CONCLUSIONS

1. When a visual target is moved by the subject's hand (self-moved target tracking), smooth pursuit (SP) characteristics differ from eye-alone tracking: SP latency is shorter and maximal eye velocity is higher in self-moved target tracking than in eye-alone tracking. The aim of this study was to determine which signals (motor command and/or proprioception) generated during arm motion are responsible for the decreased time interval between arm and eye motion onsets in self-moved target tracking.

2. Six control subjects tracked a visual target whose motion was generated by active or passive movements of the observer's arm in order to determine the role played by arm proprioception in the arm-eye coordination. In a second experiment, the participation of two subjects suffering complete loss of proprioception allowed us to assess the contribution of arm motor command signals.

3. In control subjects, passive movement of the arm led to eye latencies significantly longer (130 ms) than when the arm was actively self-moved (−5 ms: negative values meaning that the eyes actually started to move before the target) but slightly shorter than in eye-alone tracking (150 ms). These observations indicate that active movement of the arm is necessary to trigger short-latency SP of self-moved targets.

4. Despite the lack of proprioceptive information about arm motion, the two deafferented subjects produced early SP (−8 ms on average) when they actively moved their arms. In this respect they did not differ from control subjects. Active control of the arm is thus sufficient to trigger short-latency SP. However, in contrast with control subjects, in deafferented subjects SP gain declined with increasing target motion frequency more rapidly in self-moved target tracking than in eye-alone tracking.

5. The deafferented subjects also tracked a self-moved target while the relationship between arm and target motions was altered either by introducing a delay between arm motion and target motion or by reversing target motion relative to arm motion. As with control subjects, delayed target motion did not affect SP latency. Furthermore, the deafferented subjects adapted to the reversed arm-target relationship faster than control subjects.

6. The results suggest that arm motor command is necessary for the eye-to-arm motion onset synchronization, because eye tracking of the passively moved arm was performed by control subjects with a latency comparable with that of eye-alone tracking of an external target. On the other hand, as evidenced by the data from the deafferented subjects, afferent information does not appear to be necessary for reducing the time between arm motion and SP onsets. However, afferent information appears to contribute to the parametric adjustment between arm motor command and visual information about arm motion.

INTRODUCTION

When a subject tracks a target attached to the actively moved hand, smooth pursuit (SP) performance improves compared with eye-alone tracking: accuracy increases (Steinbach 1969), the number of saccades decreases (Angel and Garland 1972), the maximum SP velocity increases from 40 up to 100°/s (Gauthier et al. 1988), and the latency decreases from 90–120 ms in response to an external target to about zero when the target is driven by the subject's hand (Gauthier and Hofferer 1976). Moreover, the SP frequency limit is higher in self-moved target tracking than in eye-alone tracking in terms of gain and phase (Vercher et al. 1993). Lackner and Mather (1981) showed that an afterimage of the moving hand is sufficient to improve eye-hand tracking performance, but the performance is higher when the whole hand is visible (Mather and Lackner 1981). Gauthier et al. (1988) called this process "coordination control" and characterized it in terms of timing and mutual coupling.

The mechanisms responsible for SP timing and parametric control during eye-arm tracking may involve *1*) the command addressed to the arm muscles (outflow), *2*) an outflow copy, and *3*) afferent signals originating in the arm muscles (inflow). Several studies investigating the role of efferent/afferent information in eye-arm coordination have drawn different conclusions. Steinbach (1969) showed a poorer SP performance when subjects tracked a target attached to the passively moved arm than when subjects tracked a self-moved target, and proposed that SP improvement was due to arm motor efference. In contrast, Gauthier and Hofferer (1976) showed that inflow from a moving finger was necessary to trigger SP in subjects tracking the finger in total darkness: inflow suppression by an ischemic block applied to the arm prevented finger tracking (without visual target) even if the finger was actively moved by the observer.

The role of inflow in controlling SP movements has also been studied by Lackner (1975), who described pursuitlike slow eye movements in the vertical, downward direction, following the illusory movement of the forearm created by muscle tendon vibration (vibration activates muscle spindles, and the generated afferent signal is interpreted by the brain as a movement of the arm). However, SP eye movements were not induced in the horizontal direction in the study by Gauthier et al. (1988), except in one well-trained subject. Instead, 9 of 10 subjects tracked the illusory motion of the finger with a series of saccades. In monkeys, unilateral section of the dorsal roots innervating the arm produced specific effects on eye-arm coordination during self-moved target tracking (lower SP gain, higher number of saccades, lower SP maximum velocity) without affecting eye-alone tracking performance (Gauthier and Mussa-Ivaldi 1988). The ability to produce, in total darkness, slow eye movements in response to the ipsilateral moving arm disappeared, but SP latency in response to the contralateral moving arm was still short after surgery. This suggests that both outflow and inflow improve SP eye tracking of an arm-driven target.

The aim of the present work was to study the role of arm motor command and inflow signals in the nonvisual control of eye movements in self-moved target tracking. To determine which signal was responsible for the eye-arm short SP latency, we had control subjects perform eye tracking of a target whose motion was derived from either active or passive movement of the forearm. To study the contribution of the arm motor command in the absence of sensory information from the arm, the active arm movement condition was also tested in two subjects suffering complete loss of proprioception. We measured SP latency in eye-alone and self-moved target tracking, gain and phase as a function of target motion frequency (as Vercher et al. 1993 did with control subjects), eye motion response to a delay added between arm and target motions in self-moved target tracking (Vercher and Gauthier 1992), and eye motion response to reversal of the arm-to-target motion relationship (Vercher et al. 1995). Our results from passive arm motion in control subjects showed that the arm command is necessary to initiate short-latency SP of a self-moved target. Results from active arm motion in deafferented subjects showed that arm command is sufficient to generate SP. Proprioception on the other hand may contribute to the improvement in the spatiotemporal coupling between the arm and the eyes, after SP onset, because SP performance improved in self-moved target tracking in controls but not in deafferented subjects.

METHODS

Subjects

Six control and two deafferented subjects participated in the study. They were instructed and trained with the apparatus in a preliminary session, and they gave their consent to participate in the study. The protocols received agreement from the Local Ethic Committee. A clinician was present during the experiments. The control subjects (24–42 yr, 4 males, 2 females) were students or staff members from the University. They were right-handed, without known neurological problems, and used their preferred arms during the tests. The two deafferented subjects exhibit similar symptoms. G. L., a 46-yr-old woman, suffered two episodes of acute peripheral neuronopathy in 1975 and 1979. After the second episode G. L. remained with a permanent and selective loss of the large sensory (A-beta) myelinated fibers as revealed by a sural nerve biopsy (Forget and Lamarre 1995). Repeated electrophysiological investigations showed no evidence of motor fiber impairment. The reader may consult Forget (1986) for a description of G. L.'s case. I. W., a 43-yr-old man, suffered an acute sensory neuronopathy at the age of 19 yr (infectious mononucleosis). For a complete description of I. W.'s deficit, see Cole (1995) and Cole and Sedgwick (1992). Although both deafferented subjects are almost unable to produce accurate goal-directed motor behavior in complete darkness, they can produce, with visual control, almost all the movements required for a normal life: they can move by themselves (I. W. walks, G. L. uses a wheelchair), feed themselves, and write. The main difference between them is that I. W. has neck proprioception, whereas G. L. does not. G. L. is right-handed, I. W. is left-handed. When tested, the subjects used their preferred arms.

Experimental setup

The subject was seated in front of a screen located 1.71 m from the eyes. The head was immobilized by a dental print bite bar. The forearm rested on a gutter, the hand pointing to the screen (Fig. 1*A*). Horizontal eye movements were recorded with an infrared corneal reflection device (IRIS, Skalar) and arm was recorded motion with a potentiometer positioned at elbow level. An ''external'' and a ''hand-driven'' target were projected on the screen after reflection on galvanometer-driven mirrors. The motion of the external target was generated by a computer. The motion signal of the hand-driven target was issued from the potentiometer measuring forearm motion. Both target paths were horizontal, separated vertically by 1 cm at eye level. The subject's arm was masked from sight. Target, eye, and arm position signals were digitized at 500 Hz and displayed on a screen, and 3-s sections were stored for off-line analyses. In a condition aimed to determine the frequency response of the deafferented subjects, periods of 21 s were recorded at 200 Hz.

In control subjects, SP latency was tested during tracking of a target driven by the arm, either actively or passively moved by a brushless servomotor (Baldor). The motor was mounted vertically at elbow level. The output axis of the motor was attached to the rotation axis of the forearm rest. The position of the arm was obtained from a synchroresolver mounted on the motor axis. The rotation motion trajectory of the arm was controlled by the computer, and was designed to simulate (in terms of position, velocity, and acceleration) a typical active arm motion. The trajectory was defined by 12 points and each point was linked to the next with the use of an algorithm generating movement segments with a velocity profile following a second-order law. The resulting motion was a sinewave-like position profile that started and ended at zero position, velocity, and acceleration (Fig. 1*B*).

In the active arm motion condition, the arm-to-target relationship could be modified either by adding a delay between the arm motion and the self-moved target motion or by reversing the arm and target motions relative to each other. Because data with control subjects have been previously reported, these protocols were tested with the deafferented subjects only.

Tracking tasks

EYE-ALONE TRACKING OF A VISUAL TARGET. The target was presented at the center of the screen and started to move horizontally in a sinusoidal manner. The starting direction was randomly chosen. The subjects were instructed to track the visual target with the eyes as accurately as possible.

OCULAR TRACKING OF A SELF-MOVED TARGET. The subject moved the arm sinusoidally at a learned frequency and amplitude and tracked the hand-moved target with the eyes, after a ''go'' signal. Arm movement amplitude and frequency were the same as target movement in the previous condition.

OCULAR TRACKING OF THE PASSIVELY MOVED ARM. This condition was tested only with the control subjects. The subjects tracked the visual target with the eyes. Subjects were informed that the arm resting on the gutter would be passively moved and that the visual target motion was derived from the arm motion as in the second condition.

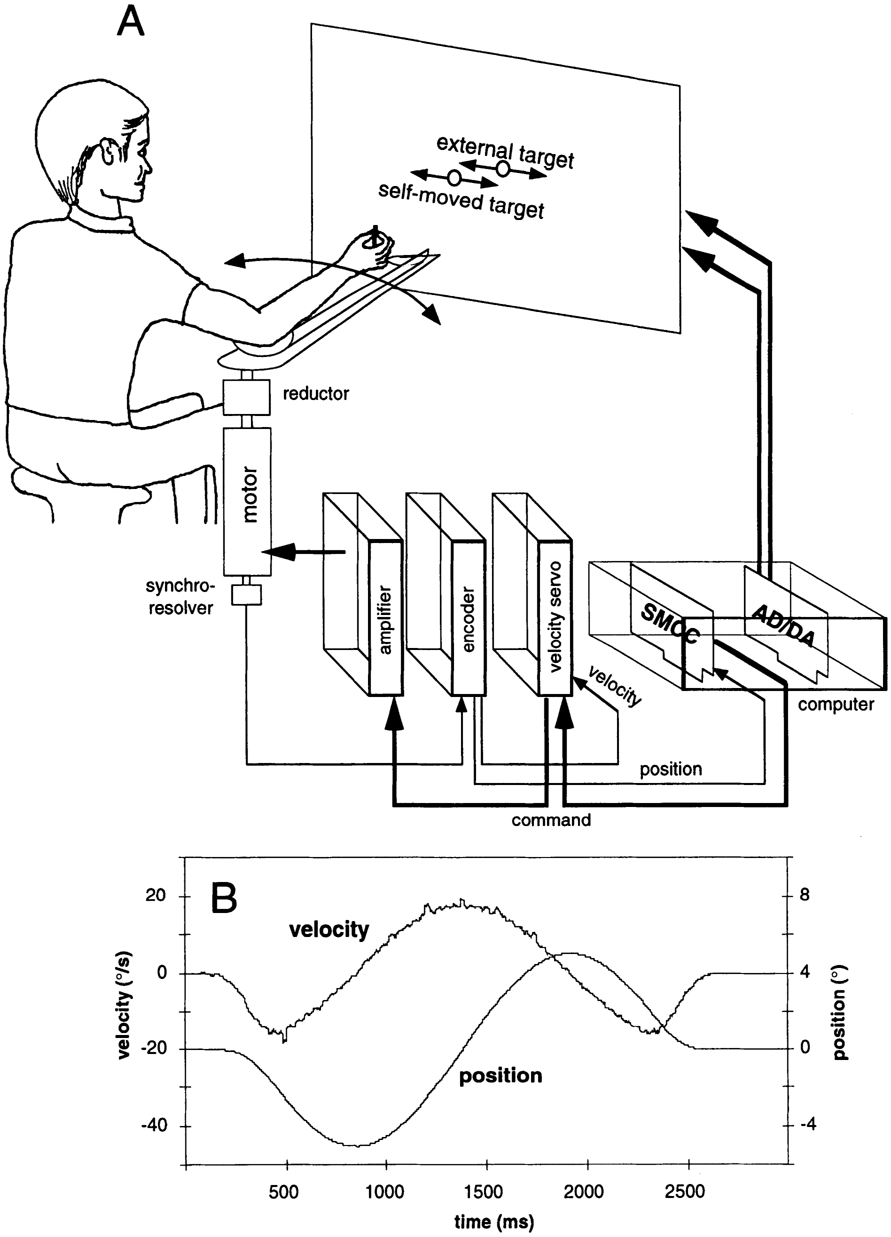

FIG. 1. *A*: experimental setup. The brushless servomotor used to produce passive arm movements was controlled by a PC card (SMCC) via a velocity servo-controller and an amplifier. The reference trajectory was downloaded by the computer and stored into the memory of the SMCC before a session. Each trial was initiated by a "START" command issued by the computer to the SMCC card and the motor's motion started immediately. *B*: position (*bottom trace*) and velocity profile (*top trace*) of the passive motion imposed by the motor on the arm.

The target motion amplitude was 10–15° peak to peak and the frequency was 0.3 Hz. In the frequency-response experiment performed with the deafferented subjects, the tested frequencies ranged from 0.1 to 2.5 Hz. The deafferented subjects were instructed *1*) to track with the eyes the visual target moving at a frequency ranging between 0.1 and 2.5 Hz over 15°, or *2*) to move the arm at a given frequency within the same range and to track the self-moved target with the eyes.

Data analysis

Off-line signal analysis started with digital low-pass filtering (cutoff frequency of 30 Hz) and differentiation. The time interval between target and eye motion onsets (which we will call "latency" for simplification: positive latencies meaning that the eyes are lagging the target, negative latencies meaning the eyes are leading the target) was measured with the use of the following procedure. For each velocity signal, the motion onset was determined by means of a combined velocity-acceleration criterion (2°/s over the variance of noise absolute mean value). In the few cases in which the program failed to properly detect eye motion onset, the latency was interactively determined by the experimenter by manually moving a cursor on the computer screen. The initial SP gain was also calculated. The gain was defined as the ratio of the mean eye velocity during the first 80 ms of tracking to the mean velocity of the target during the first 80 ms of target motion (Vercher et al. 1995). To determine the gain and phase as a function of target motion frequency, a fast Fourier transform algorithm was applied after removing saccades, filtering and differentiating the resulting cumulated eye position signal. Here, the gain was defined as the ratio between the modules of the peaks of the spectrum (corresponding to target motion frequency) obtained from the eye and the target motion signals. The amount of time shift (phase) between the two position signals was determined by applying a cross-correlation algorithm to target and eye position signals (see Vercher et al. 1993 for more details). In the RESULTS section, values are means ± SD from all subjects. An analysis of variance (ANOVA) was applied to the data. The Student's *t*-test was applied to determine significant differences. A significant difference was taken as $P < 0.05$, and a highly significant difference as $P < 0.01$.

RESULTS

Eye tracking of active or passive arm movement in control subjects

In control subjects we measured the SP latency in response to a visual target whose motion was either generated externally or derived from the motion of the subject's arm. In this latter condition, the subject's arm motion was either self produced or passively induced by a servomotor. During a training session performed the day before the experiment, all the subjects reached a fairly stable level of performance within 15–20 min, moving the arm sinusoidally and producing SP without eye blinks or intrusive saccades for ≥20 s. For each subject, 100 trials were recorded in each condition. No effect of trial order on SP latency was observed under any of the conditions.

EYE TRACKING OF EXTERNAL TARGET AND SELF-MOVED TARGET. Figure 2 shows examples of tracking performance in eye-alone tracking (Fig. 2*A*) and self-moved target tracking (Fig. 2*B*). Figure 2*C* shows latency histograms in eye-alone tracking and self-moved target tracking. The ANOVA revealed a significant effect of the condition on SP latency ($P < 0.001$), but no significant difference between subjects ($P > 0.5$). The mean latencies in eye-alone and self-moved tracking conditions were 150 ± 29 (SD) ms and −5 ± 35 (SD) ms, respectively. This shortening of SP latency was systematically observed in all subjects, even the very first time the subject was exposed to the self-moved target tracking task. In the eye-alone condition, eye tracking started with a saccade in 31% of the trials. In these cases, the mean latency was 219 ± 26 (SD) ms. In self-moved target tracking all the trials started directly with SP, never with a saccade. The nonoccurrence of a saccade during the first 200 ms of tracking is likely a consequence of the smaller retinal slip in the initial portion of tracking, due to the short latency between the arm (target) and the eyes.

PASSIVELY MOVED ARM TRACKING. In the passive arm movement condition, the latency of eye motion onset relative to target motion onset was on average 125 ± 30 (SD) ms when starting with SP (92% of the trials). The mean latency was significantly higher than in active self-moved target tracking ($P < 0.001$) and significantly shorter than in eye-alone condition ($P < 0.05$). About 8% of the responses started with a saccade in the direction of target motion (as opposed to 31% in eye-alone tracking and none in active self-moved target tracking). Two subjects of the six started most of the trials with a saccade. The mean latency of the trials starting with a saccade was 177 ± 36 (SD) ms. The histogram in Fig. 3, *top,* shows that the distribution of the eye-arm latencies from the responses starting with SP exhibits two peaks. The mode of the highest peak is at 115 ms, the other is at 165 ms. Because the distribution differs from the ones in the other tracking conditions and because the ANOVA detected a significant difference between subjects under this condition only ($P < 0.01$), individual data are also shown. It appears that some subjects have only one peak (either for shorter latencies, i.e., subject O. M., or for longer latencies, i.e., subject J. B.), but most of the subjects have a distribution with two peaks.

Self-moved target tracking in deafferented subjects

The training session did not last much longer with the deafferented subjects than with the controls. At the early stage of the training session G. L. experienced difficulty in moving the arm without direct vision of it. G. L. concentrated on the visual target whose motion was controlled by the arm. During the early trials, G. L. also produced very rapid arm movements that were too fast for the SP system. However, G. L. rapidly learned to produce slower movements. I. W. had previous experience with tracking tasks, although under different conditions (Miall et al. 1993), and experienced no difficulty even at the beginning of the session in moving the arm with a small light spot on the screen for visual feedback.

SP LATENCY IN EYE-ALONE AND SELF-MOVED TARGET TRACKING. The ability of the deafferented subjects to initiate short-latency SP when tracking a visual target moved by their own arms was also tested. As with most of the controls, G. L. and I. W. were unable to voluntarily produce SP in the absence of visual target (in total darkness) while imagining a pendulum. When tracking a visual target, the deafferented subjects produced SP with characteristics similar to those of control subjects. Figure 4 shows typical recordings from the eye-alone tracking condition (Fig. 4*A*) and the self-moved target tracking condition (Fig. 4*B*). Both G. L.'s and I. W.'s data were similar (average and SDs) to controls'. SP latency decreased markedly and reached about zero when the deafferented subjects self-moved the visual target: the mean latencies were 162 ± 34 (SD) ms (G. L., 76% of the responses started with SP) and 159 ± 28 (SD) ms (I. W., 81% of the responses started with SP) in the eye-alone tracking condition and −9 ± 68 (SD) ms (G. L.) and −8 ± 51 (SD) ms (I. W.) in the self-moved target tracking condition. As with control subjects, all responses in the self-moved tracking condition started with SP. Figure 5 shows latency distribution histograms corresponding to the two tracking conditions in both deafferented subjects. The deafferented subjects were not tested in the passively moved arm tracking condition because previous studies have shown that G. L. was unable to sense and localize the passively moved arm without vision (Forget 1986). We checked I. W.'s perception of passive arm movement by passively moving the subject's right arm with the motor-driven manipulandum. I. W. was asked to replicate the unseen movement with the left arm. I. W. was unable to sense the right arm position and motion and consequently maintained the left arm stationary.

GAIN AND PHASE OF SP IN EYE-ALONE AND SELF-MOVED TARGET TRACKING. SP accuracy was assessed in the deafferented subjects by determining the gain and phase frequency response. Data with control subjects have been previously reported (Vercher et al. 1993). In summary, in controls, the upper frequency limit was higher in self-moved target (0.9 Hz) than in eye-alone target tracking (0.6 Hz), both in terms of gain and phase. More specifically, some controls showed a clear increase of the frequency limit in terms of gain, others in terms of phase.

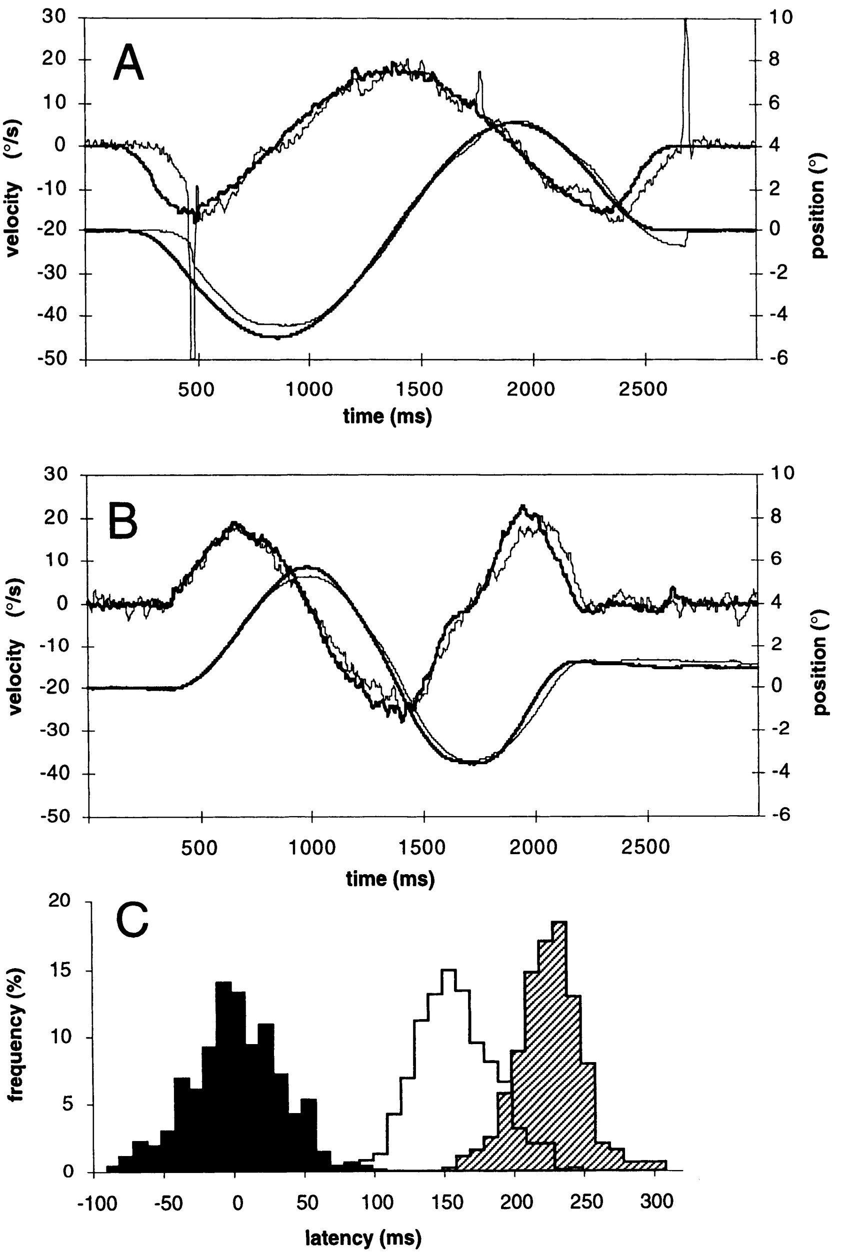

FIG. 2. Performance of a control subject in the 2 tracking tasks. *A*: eye-alone condition. *B*: self-moved target tracking condition. In each graph, the thin lines represent eye position (*bottom trace*) and velocity (*top trace*), and the thick lines represent target position and velocity. *C*: control subjects' latency histograms. White bars: eye-alone tracking starting with smooth pursuit (SP). Dashed bars: eye-alone tracking starting with a saccade. Black bars: Self-moved target tracking. Ordinates plot relative frequencies (% of total trials, for all subjects and all sessions) and abscissas carry the eye-to-target (eye-alone tracking condition) or eye-to-arm (self-moved target tracking condition) latency (10-ms bins).

Both deafferented subjects reported that moving the arm was easier at high frequencies (0.8–2.2 Hz) than at low frequencies (0.1–0.7 Hz). Figure 6 shows the SP system gain (G. L.: Fig. 6*A;* I. W.: Fig. 6*C*) and phase (G. L.: Fig. 6*B;* I. W.: Fig. 6*D*) as a function of visual target motion frequency in the two tracking conditions. Whereas the ANOVA did not reveal significant difference in SP performance between the two conditions in terms of phase, there were substantial differences in terms of gain. In particular, in contrast to control subjects (see Fig. 6, *E* and *F,* adapted from Vercher et al. 1993), the gain from the two deafferented subjects was lower in the self-moved target tracking than in eye-alone tracking. There was no significant difference in terms of gain between the conditions at frequencies <0.3 Hz for G. L. The difference was significant for the target moving at a frequency between 0.4 and 0.9 Hz ($P < 0.01$) for G. L., and <1.30 Hz ($P < 0.01$) for I. W. Above 1.0 Hz (G. L.) and 1.40 Hz (I. W.), no difference was found between the mean gains in both conditions, and this was true for target frequencies up to 2.2 Hz, which was the highest frequency at which both deafferented subjects could produce measurable SP.

EFFECT OF ADDED ARM-TO-TARGET DELAY. G. L. and I. W. were submitted to the protocol described in Vercher and Gauthier (1992) in which a delay was artificially introduced by the computer between arm motion and arm-driven target motion (0–400 ms in steps of 50 ms). The deafferented subjects were not informed that a delay would be added, but they were asked to report any abnormality in the arm-to-target relationship that might be due to ''software bugs.'' When tracking the self-moved target, G. L. did not report any alteration of the arm-to-target relationship, even when the introduced arm-to-target artificial delay reached 400 ms. Conversely, when asked to track a visual target simultane-

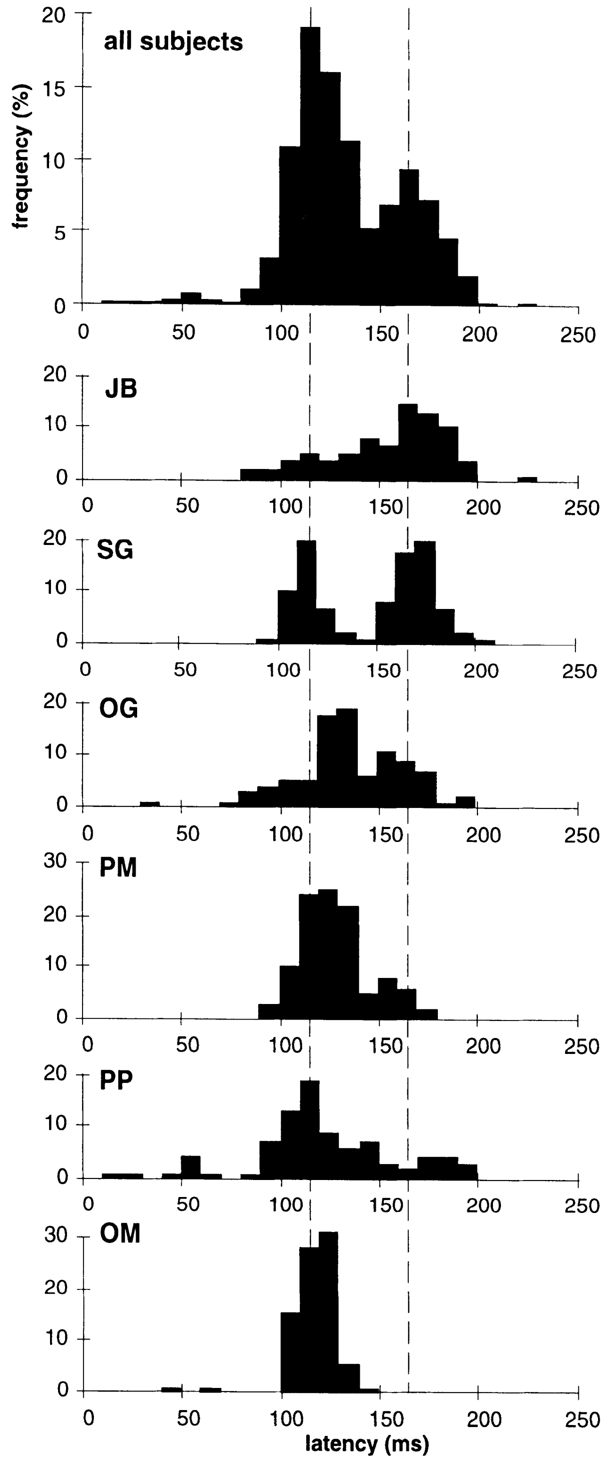

FIG. 3. Latency histograms in the passively moved arm tracking task for all control subjects and all sessions (*top*) and for each of the 6 control subjects. Some subjects showed only 1 peak of latency (J. B. showed a peak at 162 ms and O. M. at 124 ms), whereas the others showed 2 peaks (1 around 160 ms, the other around 120 ms) with relative heights that varied from 1 subject to another. Vertical dashed lines: peak modes in the all-subject histogram.

ously with the eyes and the arm (which provided a temporal reference for the arm-driven target motion), G. L. reported an alteration in the working of the setup as soon as the delay reached 200 ms (instead of 100 ms for control subjects, Vercher and Gauthier 1992). G. L. reported feeling ''physically'' a mechanical change in the gutter, as if it were resisting the subject's motion. I. W. behaved slightly differently and detected the delay introduced in the visual feedback of his arm motion in self-moved target tracking when it reached 300 ms. I. W. reported that the target was moving farther than the arm. With a 350-ms delay, I. W. reported that the target was not moving in synchrony with the arm. After some trials, I. W. could detect this alteration at the reversal of the right and left end positions of the target motion path, but only when the delay was ≥250 ms.

Figure 7*A* shows a typical response in the self-moved target tracking task, with a 250-ms delay introduced between arm and target motions. The target motion is represented together with the arm motion, which is the same but shifted in time by the amount of delay artificially added. In this task, the mean eye-to-arm latency was -12.0 ± 30.8 (SD) ms (the eyes started before the arm motion onset and thus long before actual target motion onset). There was no significant difference between trials with different added delays. In the trials with added delay, during the first 200–300 ms, the SP motion was correlated with the arm motion path. Between 500 ms and 1 s of eye tracking, a succession of corrective saccades finally moved the gaze to the visual target (Fig. 7*A*). The average latency was quite similar to the one observed with control subjects (Fig. 7*B*, ●, derived from Fig. 9 in Vercher and Gauthier 1992). The main difference between deafferented and control subjects' performance was that deafferented subjects could not produce low-amplitude and low-velocity trajectories: the maximum amplitude of arm movement reached 40° when 15° were requested; the accelerations were much higher than in the previous experiments, where no delay was added. Similar behavior was sometimes observed with control subjects the first time they were exposed to large (>300 ms) delays introduced between arm and target motion (see Vercher and Gauthier 1992).

REVERSED ARM/TARGET COUPLING. In this experiment, the relationship between arm and target motions was reversed, i.e., when the subjects moved the arm from left to right, the target moved from right to left. This protocol strongly dissociated visual and nonvisual information in self-moved target tracking. In deafferented subjects, the protocol allowed discrimination between visual information and arm motor command in the control of SP. The arm-to-target relationship was either randomly reversed (overall, 1 reversed for 3 nonreversed trials; the subjects were not informed about the inversion before the trial) or systematically reversed (the subjects were informed about the permanent inversion before the beginning of the session): the systematic target inversion condition was tested after the random inversion condition. A similar experiment has been carried out with control subjects and published elsewhere (Vercher et al. 1995).

In this experiment, as opposed to the artificial delay condition, the deafferented subjects detected and reported immediately that the relationship between arm and target motions was changed. After the first trial, G. L. was confused and reported believing that she had moved the arm in the ''wrong'' direction (not the one decided on). In consequence, G. L. continued moving the arm in the same direction, without moving the arm back and forth. G. L. was then

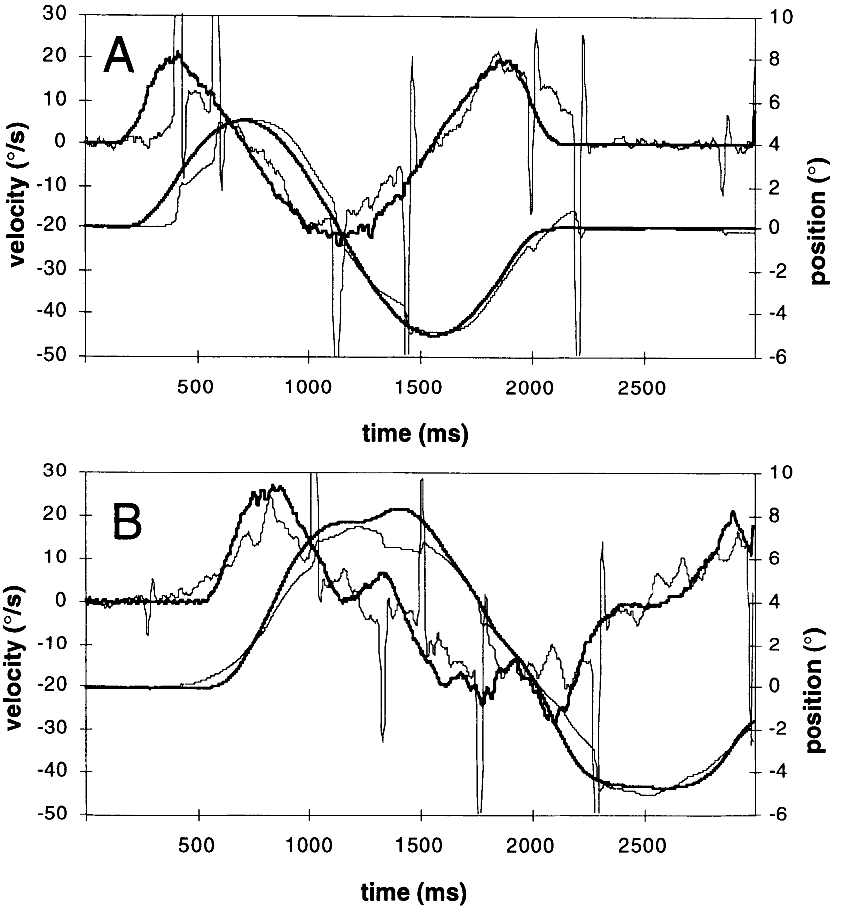

FIG. 4. Tracking performance from deafferented subject G. L. *A*: eye-alone tracking. *B*: self-moved target tracking. Conventions are the same as in Fig. 2. Typical features, compared with controls, are an increase in the number of saccades in both conditions and a decrease in accuracy in the self-moved target tracking condition.

instructed to continue to move the arm sinusoidally and to track the arm-driven target with the eyes whatever happened.

Figure 8*A* shows a trial under the random inversion condition. Mean eye-to-target latencies were not significantly affected [9 ± 64 ms, mean ± SD (G. L.) and 2 ± 46 ms, mean ± SD (I. W.) for reversed trials, and −2 ± 7 ms, mean ± SD (G. L.) and 18 ± 43 ms, mean ± SD (I. W.) for nonreversed trials]. The latencies were longer at the end of the session than at the beginning. During reversed trials, SP always started in the direction of arm motion. The SP initial gain was consistently lower in the reversed (0.37 ± 0.41, mean ± SD) than in the nonreversed trials. Such a low gain in reversed trials was also observed in control subjects: 0.41 ± 0.36 (SD) (Vercher et al. 1995). After 100–150 ms, SP direction changed, then 100 ms later a catchup saccade allowed the eyes to reach the visual target.

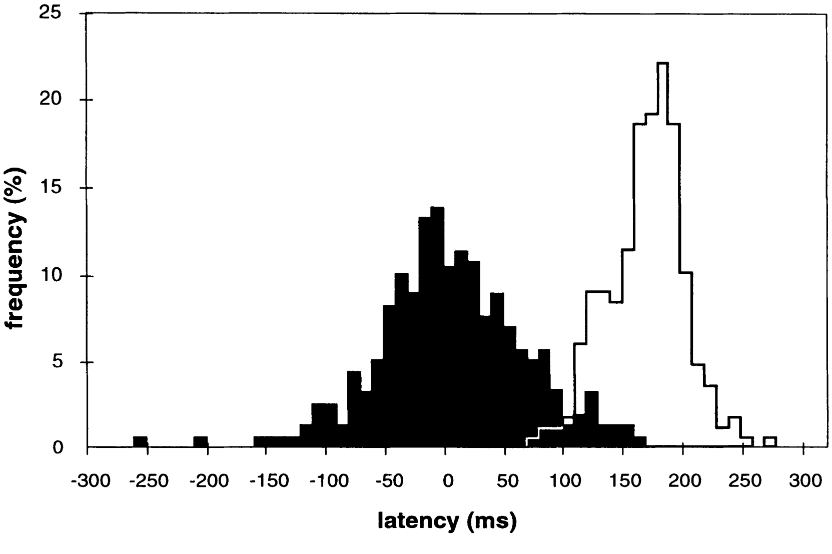

FIG. 5. Latency histograms from the 2 deafferented subjects. White bars: eye-alone tracking task. Black bars: self-moved target tracking task. Conventions are the same as in Fig. 2*C*. Note that the distributions of latencies are close to those obtained with the control subjects.

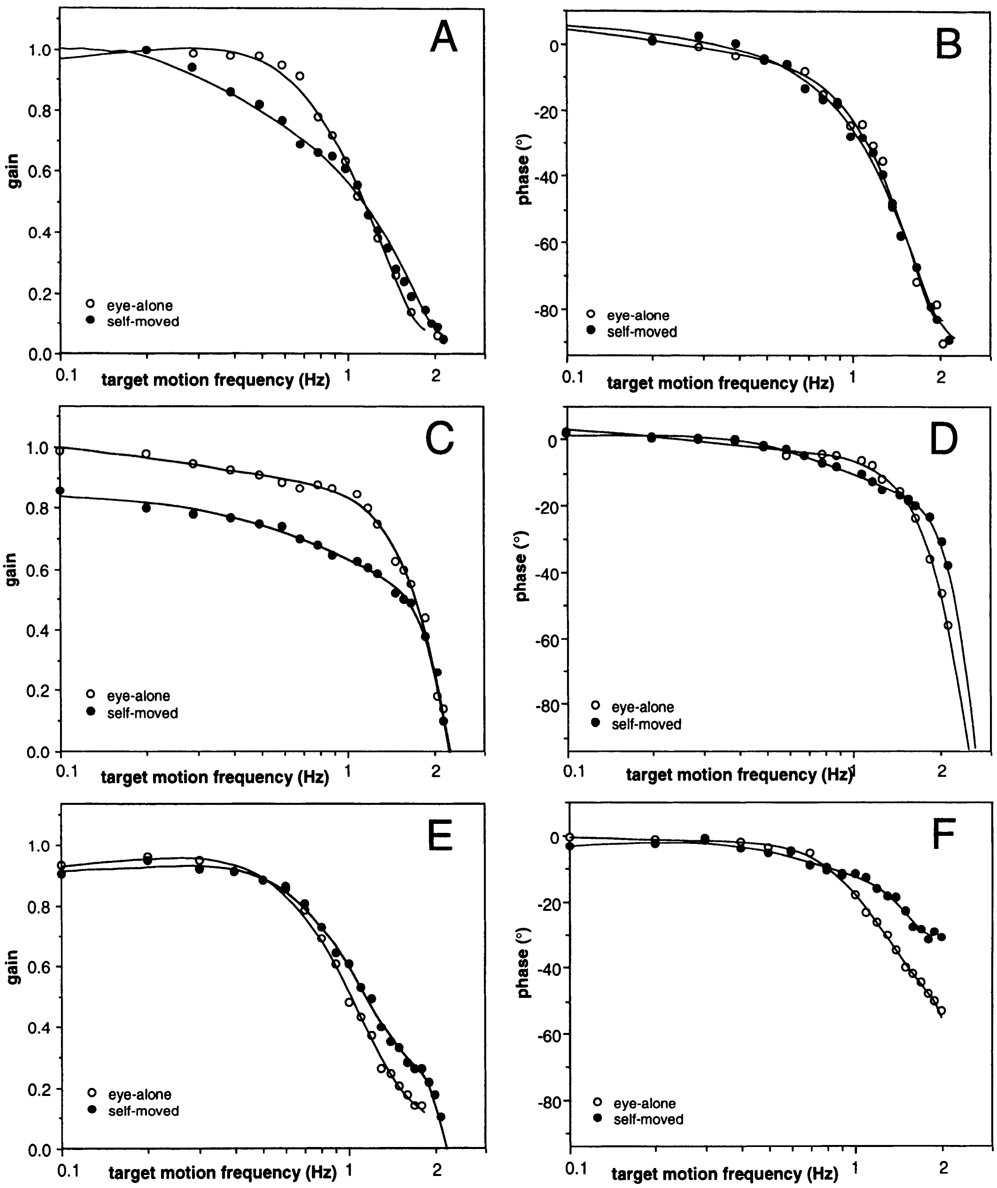

FIG. 6. Mean velocity gain vs. frequency response of the SP system during eye-alone tracking (○) and self-moved target tracking (●), for the deafferented subjects (*A*: G. L.; *C*: I. W.). Mean phase vs. frequency response (*B*: G. L.; *D*: I. W.). Mean gain (*E*) and phase (*F*) for 5 control subjects, in the same conditions.

From this moment on, the eyes tracked the visual target, with appropriate gain and low phase shift.

In a separate session, the arm-to-target relationship was systematically reversed. During the first trials SP started in the direction of arm motion, thus opposite to target motion direction (as in Fig. 8*B*, applying to the condition where the relationship was randomly reversed), with mean latencies of −3 ± 82 (SD) ms (G. L.) and 13 ± 38 (SD) ms (I. W.). After five trials, SP started directly in the direction of target motion (thus opposite to arm motion, Fig. 8*C*) with mean latencies [43 ± 81 ms, mean ± SD (G. L.) and 28 ± 58 ms, mean ± SD (I. W.)] significantly longer than mean latencies when the arm-to-target relationship was randomly reversed ($P < 0.05$). The latencies were particularly short during the second half of the session (sometimes negative, SP starting in the direction opposite to arm motion, as early as 118 ms before arm movement onset). Compared with G. L. and I. W., control subjects needed >20 trials to show a similar behavior. Control subjects never showed negative latencies in this case (Vercher et al. 1995).

DISCUSSION

The aim of this study was to determine the signals involved in arm-eye coordination control. Gauthier et al. (1988) and Vercher and Gauthier (1988) suggested that efferent signals to the arm are used to synchronize the onset of arm and SP eye motion. In contrast, proprioceptive signals appear to play a role in the mutual coupling between the eye and hand motor systems once the movement has started, because SP system characteristics such as maximum velocity, gain, and accuracy are affected when proprioception is perturbed (Gauthier and Hofferer 1976; Gauthier et al. 1988). These observations have been confirmed and ex-

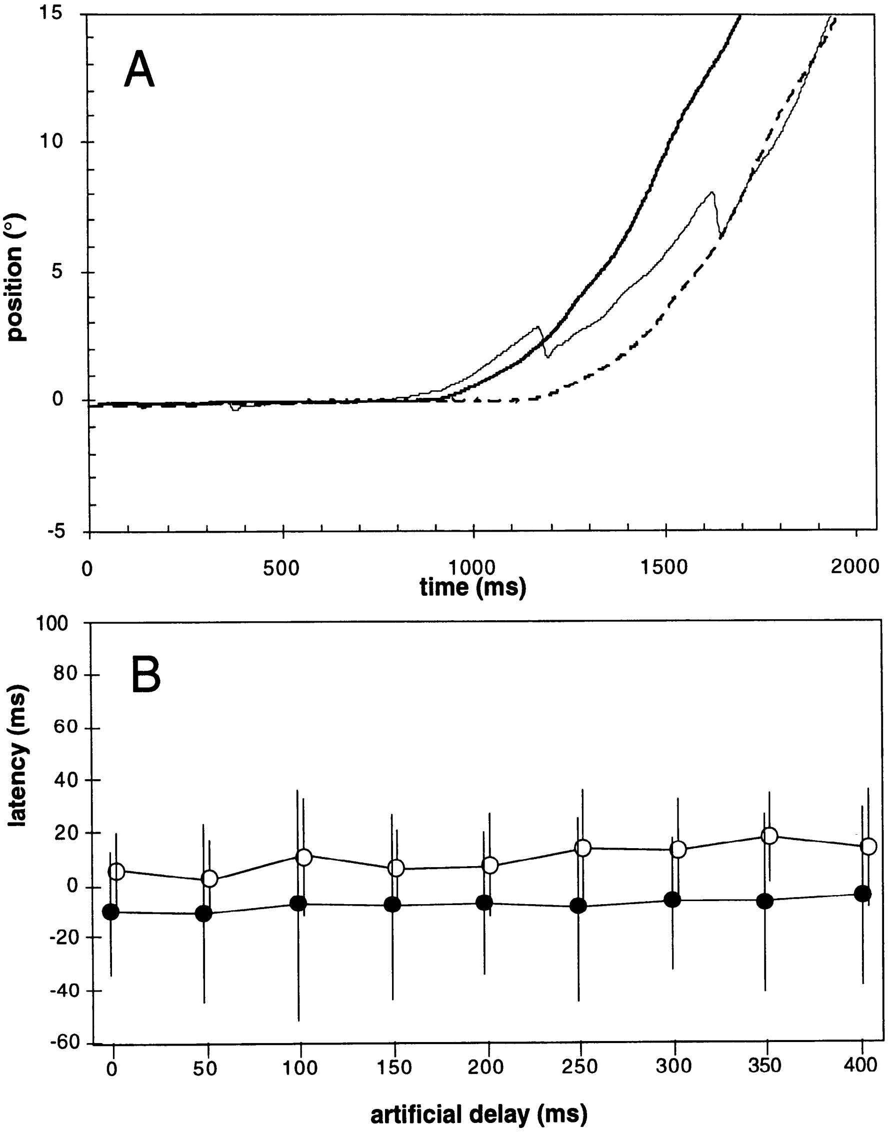

FIG. 7. Tracking with a delay added between the arm and the self-moved target motions. *A*: performance of deafferented subject G. L. Thin trace: eye motion. Thick, continuous trace: arm motion. Dashed trace: target motion (same as arm motion but delayed by 250 ms). *B*: mean values and SDs of time interval (in ms) between the eye movement and the arm movement as a function of the artificial delay (between the arm and the self-moved target) for the deafferented subjects (●) and for control subjects (○). Negative values correspond to a lead of the eyes. Positive values correspond to a lag.

tended in the present work with passive arm motion in control subjects and active arm motion in deafferented subjects.

Nonvisual triggering of SP

A major issue of this study was to determine which signal generated during arm movement is used to trigger early SP of the self-moved target. The experiments with control subjects tracking the actively or passively moved arm showed that the intention to move is necessary to synchronize arm and eye movements: afferent signals generated during passive arm movements do not trigger SP with a latency as short as in active self-moved target tracking. The experiments with the deafferented subjects showed that arm motor command was a sufficient signal to trigger SP with short latencies in the absence of proprioception: mean latencies in both tracking conditions were not distinguishable from control subjects' latencies, except that the deafferented subjects sometimes showed SP starting long before the arm motion onset. Such lead (reaching 260 ms in some cases) was never observed with control subjects. How might this anticipation occur?

This short tracking latency may be due to anticipatory eye movements observed when a subject directly controls target motion onset time by pressing a button (Kowler et al. 1984). Kowler (1989) attributed anticipation to cognitive expectation of target trajectory rather than to training. In our experiment, the gain was low compared with external target tracking, but the initial SP velocity was much higher (3–18°/s) than in anticipatory eye movements recorded by Kowler (from 15 minarc/s to 1°/s). However, it could be argued that observers were always aware that the target would move and anticipated its motion because they moved the target themselves. Anticipation due to expectation (long lead of the eyes with low, constant SP velocity) was clearly detected in 5% of the trials performed by I. W., none with G. L. An alternative explanation is based on the fact that the motor delay is longer in the arm motor system than in the oculomotor system. Steinbach (1969) and Gauthier and Hofferer (1976) used this argument to explain why they observed negative latencies in self-moved target tracking. Control subjects may use inflow to be informed of, and compensate for, the longer motor delay involved in moving

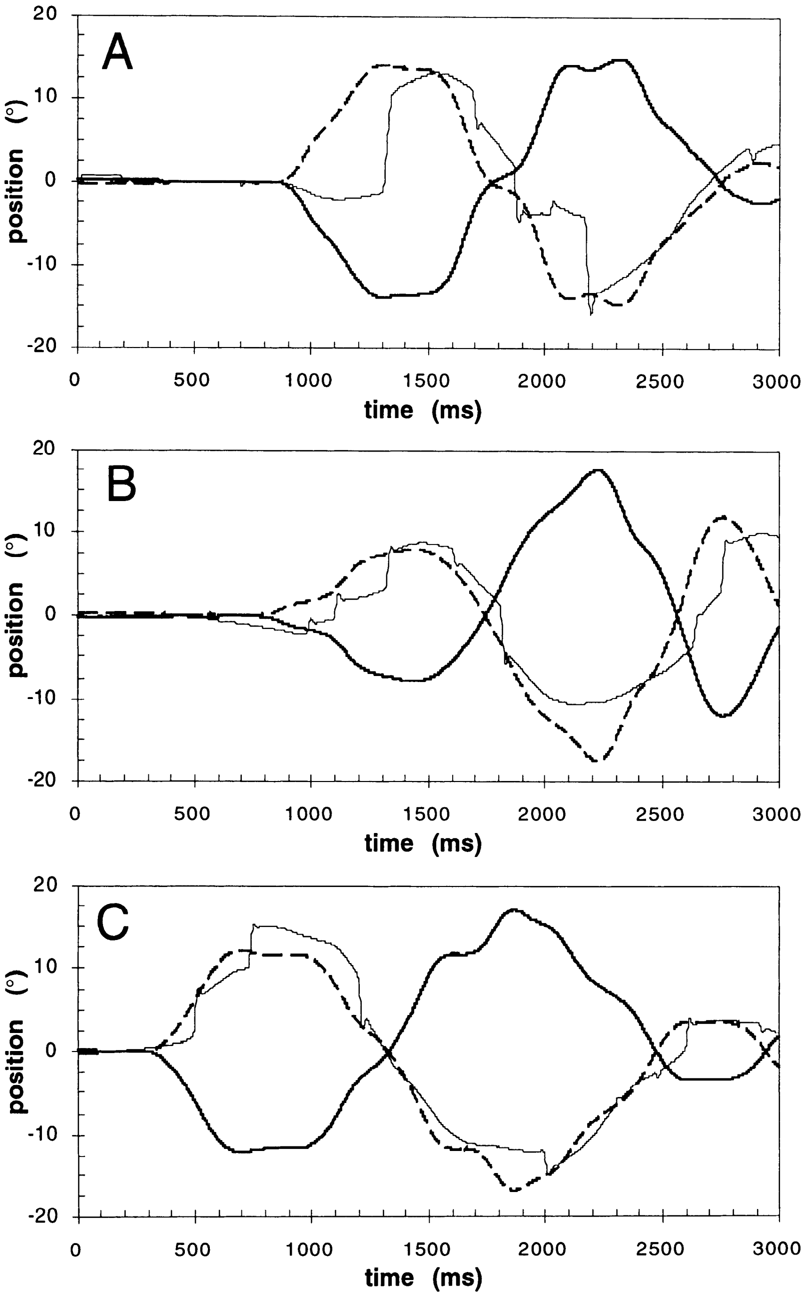

FIG. 8. Eye tracking of self-moved target from deafferented subject G. L. Thin lines: eye motion. Thick lines: arm motion. Dashed lines: target motion (same as arm motion, but reversed). *A*: with random inversion of target motion relative to arm motion. *B*: eye tracking of self-moved target at the beginning of the session with systematic inversion of arm-to-target relationship. Eyes start moving in the direction of the arm. *C*: eye tracking of self-moved target after 10 trials in the systematically reversed condition, showing that the eyes started moving in the direction of the target.

the arm. Without vision of the arm, deafferented subjects are not aware of this motor delay and cannot compensate for it. Thus even a command that does not produce a measurable arm movement may trigger an eye tracking movement. The deafferented subjects will then increase the command until the arm moves. In such trials SP onset will occur long before arm motion onset. From an experiment testing the role of arm proprioception in the control of limb movements (in which G. L. was involved), Ghez et al. (1990) suggested that proprioception allows control subjects to take into account the inertial properties of the limb. At the beginning of an arm movement, a lag due to inertia might be perceived by the deafferented subjects as a latency difference between the command onset and the mechanical effect of the command.

Mutual coupling between arm movement and SP

Previous observations from temporary deafferentation in humans (Gauthier and Hofferer 1976) or surgical deafferentation in monkeys (Gauthier and Mussa-Ivaldi 1988) were confirmed here with the chronically deafferented subjects: these subjects were unable to produce SP in response to active arm motion in total darkness (without a visual target). Furthermore, in contrast to control subjects (Vercher et al. 1993), in the deafferented observers, gain and phase of SP tracking were not improved by active control of target motion. The upper frequency limit of tracking remained unchanged in terms of phase under both eye-alone and self-moved tracking conditions. SP gain was even lower in self-moved target tracking for the low frequencies. This lower gain was partly compensated for by an increased number of saccades. A similar degradation of eye-arm target tracking performance was observed in cerebellar patients by van Donkelaar and Lee (1994). One may propose that the decrease of SP performance resulted from the increase in cognitive load needed to move the arm in the absence of proprioception. The deafferented subjects made more saccades when moving the target with the arm compared with the eye-alone condition. Likewise arm motor control was poorer in deafferented subjects than in control subjects. To test the idea of an increased cognitive control load, in a separate experiment, we asked I. W. to perform the eye-alone tracking task alone or together with a mental or a motor task. While visually tracking a target moving at 0.3 Hz over 10° (no arm tracking), I. W. showed an SP velocity gain of 0.94 (after saccade removal). When I. W. performed a mental task while tracking, the SP gain decreased to 0.87. When clapping the hands while tracking with the eyes, the gain decreased to 0.83. In this latter case, the arm motor task was not spatially or temporally related to target motion. Thus these observations suggest that the decrease of SP performance during self-moved target tracking was not specific to arm-eye coordination but rather due to the increased attentional cost of performing the motor task during eye tracking. In control subjects too, SP gain is known to be dependent on subject's attentional level, but to a lower extent (Wyatt and Pola 1987).

Perception of movement in deafferented subjects

Experiments with deafferented subjects reported in the literature allow study of the role of efferent signals in the control of movement and in the sense of self-motion. The intensive use of visual information by the deafferented subjects has been used to explain deafferented subjects' compensation for their deficit. In the present study, when an artificial delay was introduced between arm and target motion in eye-arm tracking of an external target, G. L. was never aware that a pure delay was added to the arm's motion: G. L. interpreted the delay as a load imposed on the arm. I. W. detected the delay, but this subjects had previous experience with a similar protocol (Miall 1996). To interpret this observation, one may consider what G. L. is likely to do in order to initiate an arm movement to track an external target. G. L. sends a command to the arm muscles, but because of the artificial delay, nothing occurs during the time equal to the delay. G. L. increases the arm command until the arm-moved target finally moves. This is indeed what G. L. does in everyday life to displace something heavier than expected. Thus G. L. may be able to scale the motor command by evaluating the time between arm motor command onset and the first movement visually detected.

A similar interpretation may account for the scaling weight experiments, which showed that under visual control of their lifting arm motion, both I. W. (Cole and Sedgwick 1992) and G. L. (Fleury et al. 1995) can estimate the relative weight of objects of similar visual shape and size, and classify them with an accuracy of 5–10%. This is a fairly impressive performance, even for control subjects (Kilbreath and Gandevia 1993). Fleury et al. (1995) showed that preventing vision of the lifting movement (liquid crystal glasses were used to occlude vision as soon as the object was raised over the table) suppressed G. L.'s ability to scale the weights. The authors suggested that the deafferented subjects might be using slight differences in trajectory dynamics to estimate the object's weight. However, G. L. still had some ability to evaluate the heaviest objects if vision was prevented when the contact between the object and the table was released. An alternative explanation could be that G. L. was also using the time between the activation of the muscles and the object lift as a cue to evaluate its weight (or inertia). This ability disappeared when G. L.'s head was immobilized, indicating that G. L. might have used vestibular information generated by small movements of the head when moving the arm (Fleury et al. 1995). This is in strong support of the hypothesis that G. L. was using vestibular information for scaling the object's weight.

Coordination control model

The present experiments allow further conclusions about the mechanisms of arm-eye coordination control. Our model (Gauthier et al. 1988) was based on the demonstration of the exchange of information between the systems involved in simultaneous eye and hand tracking and in self-moved target tracking, rather than being based on a common command addressed simultaneously to the arm motor system and the oculomotor system (Howard 1971). A centrally generated command signal may indeed contribute to activate simultaneous eye and head movements (Galiana and Guitton 1992), whereas experimental evidence suggests that this model does not apply to arm/eye coordination in tracking tasks. Indeed, latencies of fast eye and arm movements in response to target motion onset are not correlated (Gielen et al. 1984), and gain and phase responses of the arm and the eyes show noncorrelated features (Bock 1987) suggesting specific commands for each system.

Overall, the results of the present study demonstrate *1*) that active control of arm movement is necessary and sufficient (if tracking a visual target is allowed) to initiate short-latency SP in self-moved target tracking tasks, *2*) that passive arm movements are not as efficient as active movements in triggering short-latency SP, and *3*) that the lack of proprioception from the actively moved arm does not suppress short-latency SP. However, comparison of the eye tracking behavior between control and deafferented subjects clearly showed that proprioception enhances performance in terms of gain, phase, and accuracy, and may also play a role (although limited) in the synchronization between eye and arm motor systems.

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